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# EXAMINING SOCIOLOGICAL DIFFERENCES AND THE INFLUENCE OF PREY DISTRIBUTION AND ENVIRONMENTAL VARIABILITY IN THE DISTRIBUTION OF A TOP MARINE PREDATOR, THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

A Dissertation Presented

by

STEFANIE K. GAZDA

Submitted to the Office of Graduate Studies,
University of Massachusetts Boston,
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2015

The Intercampus Marine Sciences Graduate Program

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EXAMINING SOCIOLOGICAL DIFFERENCES AND THE INFLUENCE OF PREY DISTRIBUTION AND ENVIRONMENTAL VARIABILITY IN THE DISTRIBUTION OF A TOP MARINE PREDATOR, THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

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Ellen Douglas, Campus Coordinator
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ABSTRACT

EXAMINING SOCIOLOGICAL DIFFERENCES AND THE INFLUENCE OF PREY DISTRIBUTION AND ENVIRONMENTAL VARIABILITY IN THE DISTRIBUTION OF A TOP MARINE PREDATOR, THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

December 2015

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M.S., University of Massachusetts Dartmouth
Ph.D., University of Massachusetts Boston

Directed by Associate Professor Solange Brault and Professor Richard Connor

The purpose of this dissertation was to examine the influence of environmental variability on the distribution of prey, and the influence of prey spatial structure and habitat variability may have on the distributions of bottlenose dolphins (*Tursiops truncatus*). Additionally I examined how sociological differences (behavior type and the changes in a foraging behavior specific to Cedar Key Florida) influences the relative roles of bottlenose dolphins within the population.

The Gowans et al. scheme assumes that small groups form small communities and that foraging groups are small and rare as there are few foraging benefits to promote grouping. Using network analysis, I found that foraging occurs in small groups or alone,

but there were preferential associations between individuals in Overall, Socialize, and Travel networks.

I examined driver-barrier foraging behavior over several field seasons to assess the prediction that there are few foraging benefits to promote grouping. The driver dolphin does have greater catch success than the barrier dolphins regardless of group size. There is also evidence that barrier dolphins may have a role in increasing foraging efficiency by decreasing the number of incomplete bouts. Both the driver and barrier dolphins do better in larger groups when incomplete bouts are factored in. Therefore there are some foraging benefits that can promote grouping.

In bottlenose dolphin foraging research, it is often assumed that habitat use is related to prey availability, though this is rarely directly tested. From my collaborative work using a database collected by the Florida Fish and Wildlife Commission's Fisheries-Independent Monitoring (FIM) program, I evaluated the abundance of potential prey and their relationship to habitat and other biological and physical variables. I used MULTISPATI, which uses principal components analysis to partition and display patterns of spatial variation. The results show that there are correlations between fish-site scores and environmental variables. Spatial analysis of fish produced clear results, however neither PCA nor MULTISPATI could explain dolphin distribution. This is likely because the spatial scales are not the same grain for the comparisons; dolphins are highly mobile large marine predators (the scale is fine grained), and their prey are significantly smaller and habitat-specific (the scale is coarser).

ACKNOWLEDGMENTS

All work was performed under MMPA Permit no. 779-1633-02 and approved by the University of Massachusetts Boston Institutional Animal Care and Use Committee (UMB IACUC no. 2009.115). This research was supported by the National Geographic Society, International Fund for Animal Welfare, the American Society of Mammalogists, The Explorer's Club, the Goranson Endowment, and a grant from the School for Marine Sciences.

Firstly, I would like to thank my esteemed committee members Timothy Killingback and Eugene Gallagher for the extensive support with my research. I would also like to thank my advisors Solange Brault and Richard Connor. Thank you for being willing to negotiate the perils of having a Ph.D. student in an intercampus program!

Thank you to the staff and faculty of the Biology Department, especially Alexa MacPherson, Maria Mahoney, Rick Kesseli, and Yvonne Vaillancourt. Thank you for all of the logistical and emotional support throughout this process! From applying for grants to encountering new hurdles as a Lecturer, I could not have done it without you.

Thank you to my geographically wide- ranging and eclectic field assistants: Sarah Hosford, Olivia Harries, Ian Paynter, Emily Griffiths, Christina Ciarfella, and Caitlin Soden. We weathered hurricanes and oil spills, learned how to fix boat engines and troubleshoot equipment, caught some spectacular dolphin behaviors, established transects and data protocols, collected hundreds of fish and dozens of biopsy samples, ate dollar hot dogs and giant peanut butter shakes, hit oyster bars and crab pots, and my work in Cedar Key is all the better for it.

Thank you to the staff (especially Caleb Purtelbaugh and Anthony Knapp) at the Florida Fish and Wildlife Conservation Commission at the Senator George G. Kirkpatrick Marine Lab for taking a chance on a group of marine mammal nerds and letting us collect fish on your boat. Thank you as well to the staff at the Southeast Fisheries Science Center (Keith Mullins, Patricia Rosel, and Kathy Foley) first for allowing me to be a Investigator on your permit but also for sending dart experts (Tony, Jesse, and number one dart monkey Kevin) to my field site to get samples, especially as the Deepwater Horizon oil spill was wreaking havoc in the Gulf of Mexico. It could have easily been dropped from the list but wasn't, and I am grateful. Thank you to Carl Walters for early advice and suggestions.

To the Cox family: Since my arrival as an inexperienced field researcher in 2001 through now (as a moderately more experienced researcher!), you have welcomed me into your family with open arms. It has always been a source of great comfort to know that there is "family" close by. Thank you.

To my friends: Thank you for your emotional and logistical support. Kate, thank you for the GIS help. Rob, thank you for your statistics brainstorming sessions! Martine, and Amanda, thank you for letting me vent to you for what must have been hours of your life! Heather and Anthony, thank you for being the best friends I could ever have. Your support has meant so much to me.

To my parents: Thank you for letting me borrow your truck for months on end, for letting me take up space in storage with my research equipment, and for offering

logistical support while I was in the field. Thank you for encouraging me to follow my dreams and offering so much emotional support. You made me who I am today.

To my husband, Jeff: I cannot express in words how much your support has meant to me. I could not have done this without you, and I cannot tell you how much I appreciate you encouraging to go for my dreams, even though it's meant months where we have been far apart, and also meant fiscal austerity. You are my life partner and part of my soul.

To my daughter Audrey: You can't read this yet, but know that I hope you are able to look at me not just as your mom, but as a dedicated research professional. I wish for you to follow your path in life, whatever that may be, and know that you have the love and support of your parents and family.

Argos, you are the wise old man; Greta, the wild backwoods Floridian; Parker, the judgmental (and occasionally hostile) presence during this saga. Thank you for being there, even with the extra fur you all bring!

Thank you to the people of Cedar Key, especially the Pattillos, the Treats, and Molly Jubitz. It has been an honor to study your population of dolphins, and I hope you know how much of privilege it has been. While living in a (really) small, isolated town took a little bit of adjustment, it was nice knowing that if we didn't make it back to the dock, someone would notice. Thank you to the dolphins of Cedar Key as well! It's been an adventure and one I can't wait to continue! Your behaviors and social interactions are so complex, there is so much more to learn from you.

Lastly, I would like to thank two more people. Kel Dalton, my eighth grade science teacher, introduced me to the field of marine biology, and helped me pick out my first microscope (which I still have today). Not everyone knows what they want to do in seventh grade, but you made me realize it early.

Finally, Frank Cox. You are no longer with us but you are never far from my thoughts. Without your persistence and belief that the feeding behavior you videotaped was important, I would never ever made it to Cedar Key. You were right; it was important.

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# CHAPTER 1

# INTRODUCTION

## BACKGROUND

Bottlenose dolphins (family Delphinidae, *Tursiops truncatus*) are known for their fission-fusion grouping pattern, in which group membership and size can change on a daily or even hourly basis. Individuals can have variable numbers and strengths of same-sex associations. Some dolphins are relatively solitary, while others are quite social. Bottlenose dolphins also are known as generalist predators and employ a wide variety of feeding strategies throughout the world. They pursue prey in and on the bottom substrate, throughout the water column, in the air (e.g., driver-barrier feeding in Cedar Key, Florida; Gazda et al. 2005) and on the beach (they beach themselves to grab prey in South Carolina and Shark Bay Australia; Sargeant et al. 2005, Duffy-Echevarria et al. 2007). Their prey can be schooling or solitary. Within populations individuals often exhibit foraging specializations: in Shark Bay, Australia, certain dolphins use sponges on their rostrum to push their rostrums into the substrate, (Smolker et al. 1997, Krutzen et al. 2005, Sargeant et al. 2007), or kerplunking in Shark Bay, Australia (Connor et al. 2000), Sarasota Bay (Nowacek 2002) and Cedar Key, Florida (Gazda, unpublished data).

Bolnick et al. (2003) emphasized that a number of different mechanisms may lead to within-population variation in foraging tactics. A simple cause is variation in the spatial distribution of food in the range of a population. Territorial animals will often

have different amounts of different kinds of food in their territory, leading to individual dietary differences (Bolnick et al. 2007). Such localized differences in food availability for animals restricted in their movements can explain all of the cases of individual foraging specialization in terrestrial mammals found in Bolnick et al. (2003; R. Connor pers. comm.). Dolphins have repeatedly been shown to not be territorial (Randić et al. 2012), therefore individual dietary differences are unlikely to be fully explained by being limited to certain areas. Top predators in both terrestrial and marine ecosystems tend to be highly mobile with large home ranges that encompass multiple habitats (McCauley et al. 2012). Knowledge of a specific spatial range may help to maximize the return in a prey search. Individual bottlenose dolphins in Tampa Bay, Florida have narrower geographical ranges than expected given their capabilities in ranging (Urian et al. 2009).

The dolphins in the Cedar Keys can be classified as an inshore community. The density estimate in the inshore habitat (area = 47 $km^2$) translates into about 1.4 resident dolphins per $km^2$, which is comparable to that of the closed estuarine system of Sarasota Bay, Florida (1.3 per $km^2$; Irvine et al. 1981, Quintana-Rizzo 1999), and the semi-open estuarine system of Aransas Pass in Texas (1.4 residents per $km^2$; Shane 1980, Quintana-Rizzo 1999).

Gowans et al. (2007) attempted to categorize delphinid social strategies based on ecological factors (Figure 1.1). Briefly, when resources are predictable (spatially and temporally), dolphins should reside in relatively small areas as they do not need to travel far to access these resources (resident populations). However, when resources are not predictable, delphinids may have to travel further, and therefore they are not resident in

one area (they are transient). The Gowans et al. (2007) scheme hypothesizes that predictable resources are found in complex inshore environments, and dolphins can hide from predators or avoid areas with high predator density because of these structures. Unpredictable resources are found in offshore environments where dolphins cannot hide from predators. Because prey is sparsely distributed, the scheme states that this may act to reduce foraging competition. Cooperative foraging and herding of prey schools may be advantageous in these situations. Therefore, dolphins in inshore populations should have smaller group sizes to avoid predators, whereas offshore dolphins should form larger groups to defend against unavoidable predators. Additionally, available food resources may limit group size, especially in inshore populations because they are limited in range. Therefore, in inshore populations, there are few benefits to forming large groups and more benefits to being solitary or in small groups. Because there are few foraging benefits to promote grouping, small groups will form small communities with few long-term associations (Gowans et al. 2007).

While there is some support for aspects of this scheme (see Gowans et al. 2007), I believe that there are some logical problems with it. The scheme hypothesizes that inshore communities should have smaller groups because they are able to hide from predators. Dolphins in Shark Bay, Australia are under intense predation pressure from tiger sharks (*Galeocerdo cuvier*). Based on this model, dolphins should form smaller groups to hide from them, but the opposite has been found (Heithaus and Dill 2002), in that dolphins form larger groups in the more dangerous (higher shark density) habitats.

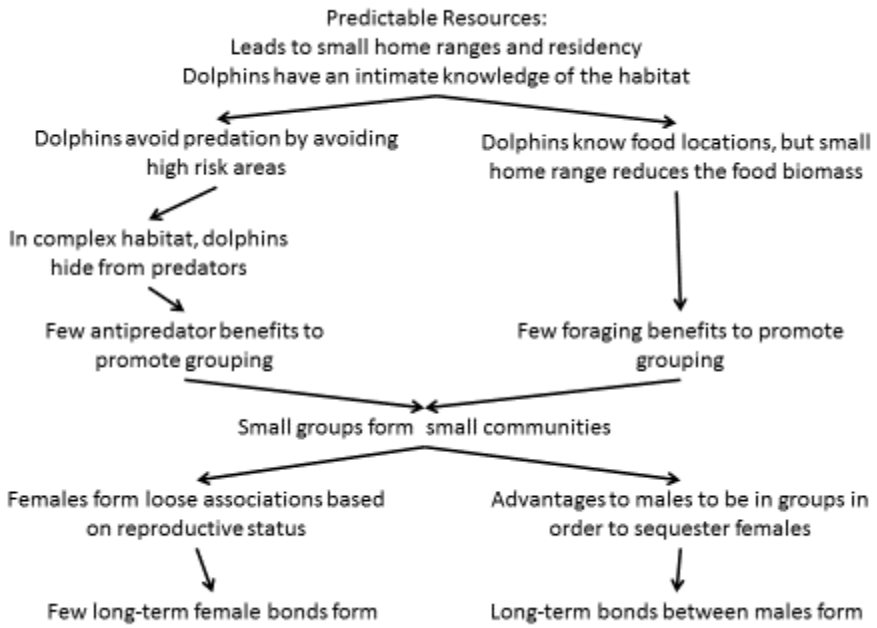


Figure 1.1: Predictions of the Gowans et al. (2007) scheme of dolphin grouping for inshore delphinid societies.

The scheme also hypothesizes that since resources are predictable and available biomass is lower, competition for food should be another driver for smaller groups as they engage in scramble-type competition: individuals or groups cannot exclude others from access to prey (Milinski and Parker 1991), and therefore they should distribute themselves so that resources are equally distributed amongst themselves (ideal free distribution; Fretwell and Lucas 1970). However, this hypothesis of how dolphin groups should be smaller is based on the entire premise that their food is evenly distributed throughout the area and that there are no large schools of fish. Even if large schools of fish are predictably distributed throughout the area, cooperation may still be required to catch or find this prey, which would be a driver for larger group sizes.

The purpose of this dissertation is to examine the influence of environmental variability on the distribution of prey and the influence of prey spatial structure and habitat variability on the distributions of predators. Additionally I will examine how the behavior type of groups influence the grouping patterns of bottlenose dolphins and how the changing group size of a foraging behavior specific to Cedar Key, Florida influences the fish capture success of the dolphins that participate. The Gowans et al. (2007) scheme is a framework to examine possible explanations for dolphin spatial and social structure.

*Chapter 2: Does behavior influence grouping patterns?*

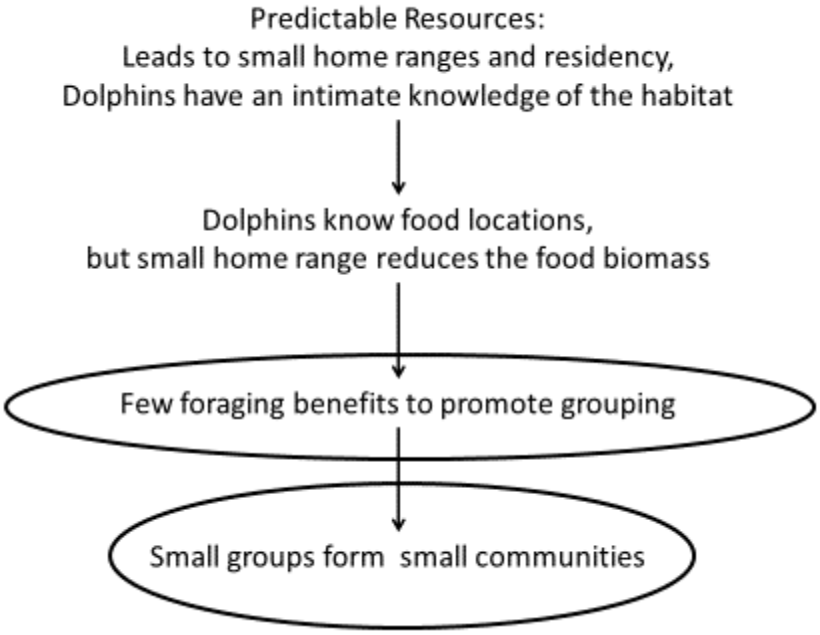


Figure 1.2: Prediction that small groups form small communities; there are predictable resources but limited biomass. The first part will be addressed in the second chapter.

There is extensive literature on the fission-fusion social patterns of large-brained mammals (reviewed in Aureli et al. 2008) where group size and composition change daily or even hourly. The Gowans et al. (2007) scheme assumes that small groups form

small communities; how are these small groups comprised? The scheme also assumes that there are few foraging benefits to promote grouping; is this the case? Are foraging groups small and rare?

The scheme discusses foraging specifically but I was interested in other behaviors recorded as well. Social animals are enmeshed in a network of relationships. These relationships are traditionally analyzed at the dyadic level (the relationships within duos), but these relationships can extend to a network. Network analysis has become an important approach in understanding systems of interacting objects, including those of biological organisms (Lusseau and Newman 2004, Lusseau 2006, Lusseau 2003); the systems are represented as networks in which the nodes correspond to the interacting objects and the edges correspond to the interactions among them.

Networks help to clarify the associative complexities of animal groups by providing insight into behavioral dynamics at the population level through analysis of overarching network properties. Network analysis is complementary to dyadic analyses in that it analyzes complexities of animal groups beyond the dyad (Wey et al. 2008).

Many network analyses (Augusto et al. 2011, Wiszniewski et al. 2009) consider patterns of connections between individuals across all behavioral states or focus solely on associations during social activities. Gero et al. (2005) hypothesized that the plasticity of association in a fission-fusion population, combined with the ability to relocate without substantial energy expenditure (Williams 1999), may allow individuals to maximize social benefits in each behavioral state by shifting associations. Network analysis is especially good at highlighting the differences in these population features in different

behavioral states (Lusseau and Newman 2004). Therefore, a network analysis of the population is likely to produce different results if sorted by behavior. Support for the Gowans et al. (2007) scheme would show that groups are small and rare and associations are not significant. It is still possible to have this type of association pattern if groups were segregated by sex.

*Chapter 3: How do group composition changes in a specialized feeding behavior affect the efficiency of the members of the group?*

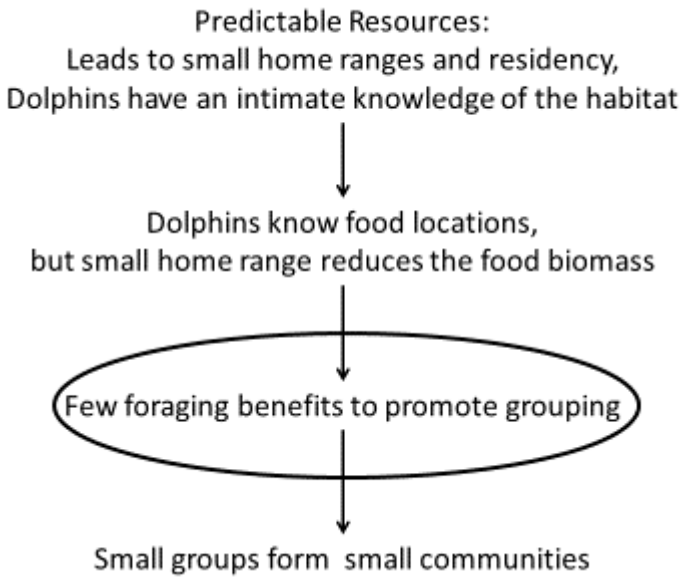


Figure 1.3: Low food biomass predicts that there are few foraging benefits to promote grouping.

The Gowans et al. (2007) scheme predicts that there are few foraging benefits to promote grouping. However, there are still examples of group foraging behavior seen in Cedar Key, Florida. Are there any benefits whatsoever to grouping while foraging?

In 2001, I documented the first known example of a division of labor with role specialization in a marine mammal (Gazda et al. 2005), and only the second in any

mammal species (the first being the African lioness (*Panthera leo*) (Stander 1992)). In the driver-barrier behavior, the driver identity did not change within both groups. Though the driver still remains in the area, the barrier dolphins have disappeared, yet the driving behavior continues.

In 2005 the "TLFN" group had a stable membership of the same three dolphins in all bouts that were observed. The TLFN-group driver, TLFN, captured significantly more fish per bout than the barrier dolphins (Gazda et al. 2005). In 2008 the TLFN group was down to TLFN and one barrier dolphin, and in 2010 TLFN was observed driving alone.

If the behavior is no longer efficient because the barrier dolphins are no longer present, the driver should stop. That driving continues indicates that the behavior may still be a productive way to catch prey for the driver. Since there has been a reduction in the number of participating barrier dolphins since the original study, there is an opportunity to investigate the benefit of barrier dolphins.

The intent is to compare the fish-capture success of the driver by group size, the average capture success of the barriers by group size, and the number of fish available per bout over time as well. If the barrier dolphins are important to the success of the driver, the average fish-capture rate of the driver would significantly decrease with the decrease in barriers. If the barriers are not important to the success of the driver, the capture success of TLFN will not be significantly different or increase as the barrier presence decreases. Barriers may also have an advantage in grouping as well, which can be tested by determining if average catch success increases with increased group size.

*Chapter 4: Are fish relative abundance and species composition correlated to habitat variables? Are these variables, including prey availability, correlated to dolphin spatial structure?*

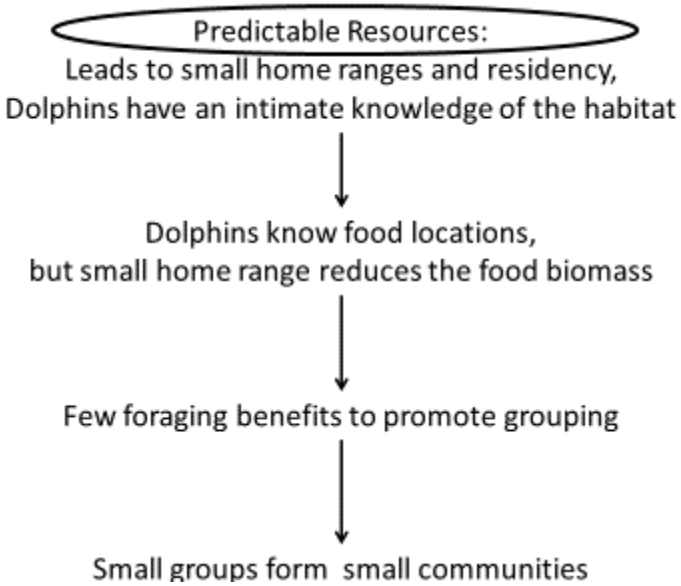


Figure 1.4: The Gowans et al. (2007) scheme for inshore delphinids is based on the underlying assumptions that resources are predictable.

The Gowans et al. (2007) scheme assumes that resources are predictable: not patchy in time or space (food and/or predators). This is the basis for the entire scheme for inshore delphinid societies. Top predators (wolves, sharks, etc.) in both terrestrial and marine ecosystems tend to be highly mobile with large home ranges that encompass multiple habitats. In bottlenose dolphin foraging research, it is often assumed that habitat use is related to prey availability (S. Dawson, personal communication, Torres 2007, Redfern et al. 2006), though this is rarely directly tested. To examine this assumption, predator and prey data need to be on the same temporal and spatial scale, requiring intensive studies of both levels, which is often outside the capabilities of a single research project.

From my collaborative work with the Florida Fish and Wildlife Commission's Fisheries-Independent Monitoring (FIM) program, I am able to integrate data on habitat, prey, and predator, all taken at the same temporal scale. Using the FIM data, I will evaluate the spatial structure of potential prey and their relationship to habitat and other biological and physical variables. I will then evaluate dolphin behavioral sightings (per unit effort, SPUE) for spatial structure and variance. I will correlate these two analyses to fish distribution and habitat variables. The data are on the same fine scale, both temporal and spatial, as the dolphin data I collected, allowing joint statistical analysis.

Dolphin distributions rarely include direct data on prey distribution because prey sampling is more difficult than sampling abiotic variables. In reality, these abiotic variables are usually used as proxies for prey distribution (S. Dawson, personal communication, reviewed in Redfern et al. 2006). Abiotic variables may be correlated with the distribution of dolphins; however, these metrics often have little direct influence on the actual selection of habitats by dolphins (Torres 2007). Therefore, as top marine predators, dolphins are removed from the direct influence of the environmental variability that is commonly used to characterize their habitat (Torres 2007). Dolphin SPUE will be examined in relationship to the fish data for correlations of dolphin behaviors with fish abundance, as well as habitat variables.

If fish species are predictable, per the Gowans et al. (2007) scheme there are two possibilities: Fish would be evenly spread throughout the area and display no spatial structure, or correlation to habitat. Dolphin behavior SPUE would not be correlated with fish abundance distribution since there was no structure to begin with. Alternatively, fish

might display spatial structure and/or variability in species composition because they are only found in certain areas, and this would be correlated with certain habitat variables. Dolphin behavior SPUE could be correlated with fish spatial structure or variability, or habitat variables.

If fish species are not predictable, which would not support the Gowans et al. (2007) scheme, they would appear as randomly spread throughout the area and display no spatial structure or correlation to habitat. Dolphin behavior SPUE would not have a correlation to the fish spatial structure, but they could have a correlation to the variability of the fish since dolphins would be found foraging in locations where fish were.

## STUDY SITE

Cedar Key (29 05’49”N, 83 03’58”W) comprises five major islands, numerous smaller islands, and wetland areas along Florida’s northern Gulf coast (Figure 1.5). In 1995 the legislature of Florida banned gill-net fishing due to severely depleted stocks and bycatch of dolphins and turtles. Starting in 1929, some islands of the Cedar Keys were made protected reserves. The thirteenth, and latest, island was added to the National Wetlands Reserve in 1997. Today, the Cedar Keys are federally protected sanctuaries managed by the Lower Suwannee National Wildlife Refuge, located on the mainland of Florida. The Refuge provides important habitats for many birds, such as bald eagles *(Haliaeetus leucocephalus)*, as well as for *T. truncatus* and West Indian manatees *(Trichechus manatus)*.

Cedar Key is an ideal study site for several reasons. The coastal area is relatively pristine in terms of human development as compared to Tampa Bay and Florida Bay where other studies of bottlenose dolphins are ongoing: The former having a heavily developed shoreline and the latter being hypersaline due to water reclamation (McPherson and Halley 1996, Light and Dineen 1994). Most of the study area is in shallow waters (1-10m depth) so foraging behaviors are readily observed; both specialized and common foraging behaviors have been documented in individual dolphins in the study area (Gazda et al. 2005). There is a large number of dolphins that use the general area, and many of them may be permanent residents (Quintana-Rizzo 1998,

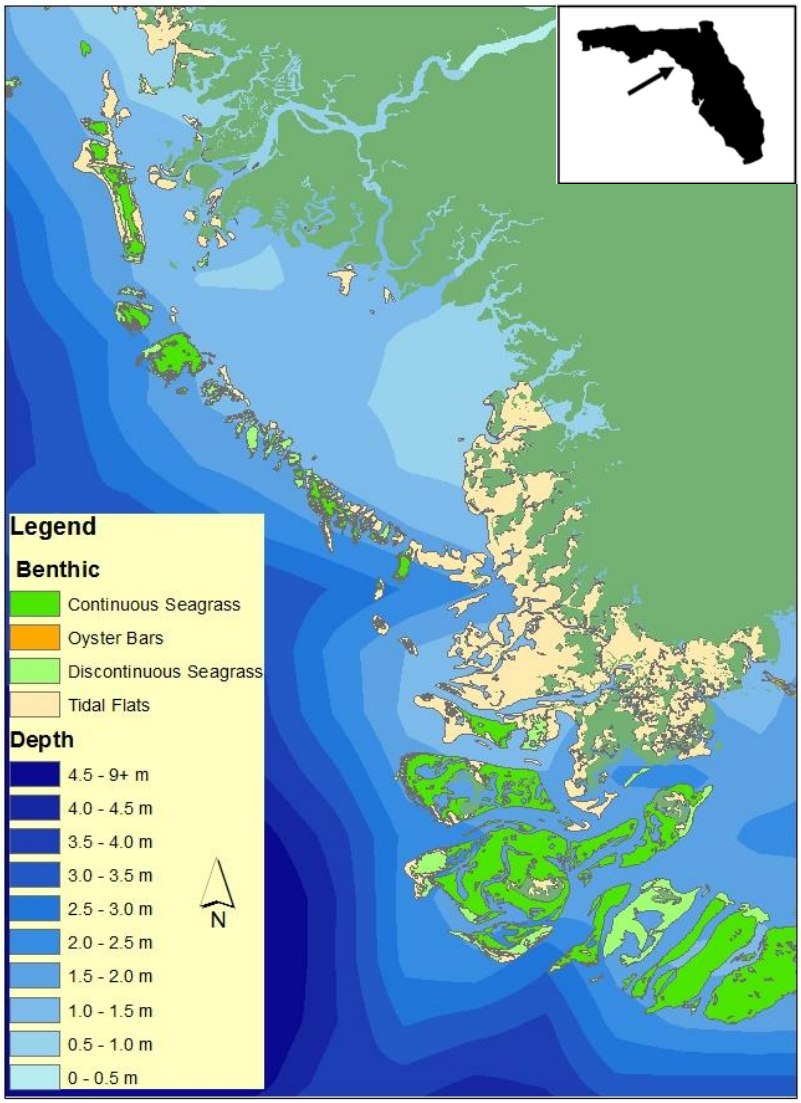


Figure 1.5: Map of the study site. Inset is the state of Florida with an arrow pointing to the general study area of Cedar Key.

Gazda et al. 2005). The current dolphin photo-identification database contains approximately 345 individuals. A remarkable database on fish species and habitat variables collected by the Florida Fish and Wildlife Commission (FWC) overlaps the same coastal area as my sampling sites.

The Cedar Key *T. truncatus* were initially studied by Caldwell (1955). His earlier observations focused on the resighting patterns of an individual dolphin, not on feeding ecology. Quintana-Rizzo (1998) documented the association patterns and habitat use of resident and nonresident Cedar Key *T. truncatus.* She photographically identified 233 dolphins in her approximately 67 $km^2$ study area and estimated the total number observed at 281 using mark-recapture methods. Gazda et al. (2005) reported on a feeding behavior of two groups of bottlenose dolphins in Cedar Key that indicated a division of labor with role specialization. This was the first time this behavior was reported in marine mammals, and only the second example seen in any mammals, the first being the African lioness, (*Panthera leo*) (Stander 1992).

The FWC Fisheries-Independent Monitoring (FIM) program has been collecting monthly fish stock data in 66 locations along the coast from the Suwannee River to Cedar Key, using stratified-random sampling, since 1996. The data are on the same fine scale, both temporal and spatial, as the dolphin data I collected, allowing joint statistical analysis. The FIM data have been made available for my use. Details of this program are described in the Methodology section in Chapter 4. My study area runs from 20 km south of the Suwannee River and from the inshore coastline out approximately 5km; it

encompasses most of the FIM area and all of the study area of Quintana-Rizzo (1998) and Gazda et al. (2005).

## SUMMARY

The aim of this dissertation is to examine a population of bottlenose dolphins for the ecological and sociological factors that may explain its distribution and will add extensively to the literature on behavior and ecology. Analyses of relationships by network analysis have not been differentiated by behavior in the past, but there is evidence (Gero et al. 2005) that it may be oversimplifying to analyze complex organisms with a single network. This work will clarify the different roles of individuals by behavior, which is completely new. The loss of members of the driver-barrier feeding behavior throughout the study period gives a unique opportunity to examine the changes in individual efficiencies over the years, something that has not been done for other feeding behaviors. Lastly, the FIM program has collected extensive data on fish for years and at a level that is not seen in other predator-prey studies (e.g. Torres 2007, Allen et al. 2001) involving bottlenose dolphins, which will allow for a much more in depth examination of the relationships of dolphins, their prey, and the habitat than has been seen before.

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# CHAPTER 2:

# THE IMPORTANCE OF DELINEATING NETWORKS BY ACTIVITY TYPE IN BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN CEDAR KEY, FLORIDA

## INTRODUCTION

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Social animals are by their very nature embedded in a network of relationships. Traditionally in behavioral ecology these relationships are analyzed at the dyadic level, i.e. at the level of pairwise relationships between individuals (Sueur et al. 2011b), but such an approach runs the risk of overlooking those aspects of social relationships which depend on the totality of the network of interactions in which the individuals are enmeshed (Sueur et al. 2011a; Pinter-Wollman et al. 2013; Wey et al. 2008). The fluctuations in the dyadic patterns of behavior can be well captured by network features (Barrat et al. 2012). For this reason, network analysis, which has become an important tool in understanding systems of interacting objects in many areas of biological (May 2006; Barabasi and Oltvai 2004), physical (Watts and Strogatz 1998; Barabasi and Albert 1999), and social sciences (Wasserman and Faust 1994), plays a valuable role in studying the effect of complex patterns of relationships of social organisms (Croft et al. 2004;

Cross et al. 2004; Krause et al. 2007; Lusseau 2003; Lusseau and Newman 2004; Lusseau 2006; Madden et al. 2011; Pinter-Wollman et al. 2013; Sueur et al. 2011a,b; Wey et al. 2008; Wittenmeyer et al. 2005). Networked systems consist of a set of vertices together with a set of edges, each of which connects two vertices (Newman 2006; 2010). In the context of social organisms, the vertices in the network represent the individual animals and the edges represent a connection (for example, direct interactions, home range overlap, or as also in this study associations) between the corresponding animals (Sueur et al. 2011a; Pinter-Wollman et al. 2013; Wey et al. 2008).

Many network analyses of social animals (Wiszniewski et al. 2009; Lusseau and Newman 2004; Augusto et al. 2011) consider patterns of connections between individuals across all behavioral states, or focus solely on associations during socializing activities. However, group members interact in different behavioral contexts, and the interactions in one state may or may not be independent of those in others (Barrett et al. 2012). Gero et al. (2005) showed that dyadic associations between individuals can vary depending on the behavioral state considered and suggested that it may be an oversimplification to analyze complex organisms using a single network. In female Northern long-eared bats, preferred associations and social network metrics vary with reproductive period (Patriquin et al. 2010). Therefore, a network analysis of a population is likely to produce different results depending on the behavioral states of the animals used to construct the network.

There is an extensive literature on the fission-fusion social patterns of mammals (reviewed in Aureli et al. 2008), where group size and composition change daily or even

hourly based on the activity. Examples of such studies include allomaternal care in elephants (Lee 1987), reproductive competition in male bottlenose dolphins (Connor et al. 1992; Scott et al. 2005; Connor and Vollmer 2009), safety in sleeping locations in hamadryas baboons (Stammbach 1987), and congregation in giant mouse lemurs for mating or competing for resources (Schulke and Ostner 2005). Most fission-fusion studies gather data on associations based on the "Gambit of the Group" which assumes that everyone in a group is associating with each other (Whitehead and Dufault 1999). Data from these observations can be combined into networks that are cumulative and then analyzed for non-random features (Croft et al. 2008; Bode et al. 2011). However, presence within a group may not always represent a real association, and observation time is often limited, so the data collected may only be a rough estimate of the entire social structure of the population. Applying a weighted association index removes some sampling bias by filtering out weak associations (Croft et al. 2008; Franks et al. 2010; Whitehead and Dufault 1999). This is still a rough analysis of the population as it does not take the context of the associations that formed the network into account. Creating separate networks in which behaviors are the sorting factor may lead to a much more realistic portrayal of the structure and relationships within the population in question.

Group living is a trade-off between competing factors. Major reasons why individuals form groups are reduction of predation risk, increased access to resources, and when the distribution of these resources promotes grouping. Groups can also reduce foraging efficiency and increase competition, among other costs (reviewed in Gowans et al. 2007). Network analysis in species with fission-fusion grouping patterns can help

develop a more complete explanation of social structure (Ramos-Fernandez et al. 2009), where there are contrasting pressures of predator avoidance and feeding competition (Aureli et al. 2008). Social patterns across different behavioral activities of many fission-fusion populations may be optimally studied using network analysis (Aureli et al. 2008). For example, in male African elephants, controlling for behavioral (sexual) state revealed different patterns in the association networks and demonstrated that they have a much more complex social system than previously thought (Goldenberg et al. 2014). Male zebras have differing association patterns with other males depending on whether they are stallions defending a herd of females or bachelors (Fischoff et al. 2009). When meerkat networks are sorted by behavior, differences in an individual's attributes do not consistently influence association patterns across behavior-specific networks (Madden et al. 2011).

This paper reports on a network-based study of the social patterns across three activity states (socializing, travelling, and foraging) of a population of *Tursiops truncatus* located in Cedar Key, Florida. The null hypothesis is that regardless of activity state, the corresponding networks will be similar to each other and to the overall network that does not take activity into account. There are good reasons to suspect the null hypothesis might be true. For fission-fusion species that disperse to forage in bouts, costs of locomotion will greatly impact the ability to form social groups between foraging bouts (Connor 2000). Bottlenose dolphins (*Tursiops* spp.) have low locomotor costs (Williams 1999), and are well known for their fission-fusion grouping patterns (reviewed in Connor et al. 2000). Because dolphins have such low costs of movement, grouping is much less

likely to be affected by this variable. If the costs or benefits of group formation or partner preferences vary with activity, the different networks should reflect this.

Our predictions for the alternative hypotheses are as follows:

1) Socialize Network: Bottlenose dolphins are highly social animals and often have preferential associations. They express these associations with affiliative behaviors such as physical contact and synchronous movements. Socio-sexual behaviors are also common, and they do not have to be with preferred associates (Connor et al. 2000). Thus, the Socialize network should indicate some preferential associations among individuals. Moreover, dolphins that are connected to a particular dolphin are also expected to be connected to one another.

2) Travel Network: Gero et al. (2005) showed that bottlenose dolphins in Shark Bay Australia (*T. cf. aduncus*) have weaker associations while travelling compared to socializing or foraging groups. Given that cooperation and competition are less prominent aspects of travelling compared to social and foraging interactions, this is not surprising. Accordingly we expect Cedar Key dolphins will have less pronounced preferential travel associations, have few weak associations with others, and as a result travel alone or in small, weakly-connected groups. Also, dolphins that are connected to a particular dolphin are not expected to be connected to each other.

3) Forage Network: Gero et al. (2005) demonstrated that preferred associations in the Shark Bay *T. cf. aduncus* are strongest when socializing or foraging. If this is the case in Cedar Key, the hypotheses for the Forage network would be similar to the Socialize network. However, inshore dolphins that feed predominantly on non-schooling fish may

experience relatively more feeding competition (Gowans et al. 2007), thus the Forage network may be significantly different from the Socialize network. The Forage network may indicate preferential associations among individuals (as seen in Gero et al. 2005) who have few weak associations with others, and as a result forage in small, weakly-connected groups. This also means that unlike the Socialize network, dolphins that are connected to a particular dolphin are not expected to be connected to each other.

4) Overall network: Because the overall network does not take behavior into account, but is built from all of the sightings, it should demonstrate some of the properties of each of the behavioral networks, but will not accurately represent any particular one.

## METHODOLOGY

### *Data collection:*

There are approximately 300 bottlenose dolphins (*T. truncatus*) that inhabit the general area of Cedar Key, Florida (29.0549º N, 83.0358º W), and many of them (approximately 250) are permanent residents (Quintana-Rizzo and Wells 2001; Gazda et al. 2005). Most of our study was carried out in shallow waters (1-10 m deep), where dolphin behaviors are readily observed.

We collected data on the behavioral states of 147 resident bottlenose dolphins in Cedar Key over two different periods: from July, 2008 through December, 2008 and from April, 2010 through August, 2010. When a sighting of dolphins was encountered on a transect survey (Dawson et al. 2008) or opportunistically (Smolker et al. 1992), a slow

approach was initiated. An assessment was made of the predominant behavioral state, defined as the activity of 50% or more of the individuals within the first five minutes of encounter (Acevedo-Gutierrez et al. 2005; Connor et al. 2006; Eierman and Connor 2014). Membership in each sighting was defined by the presence of dolphins during the first five minutes of encounter and within the 10 m chain rule (Smolker et al. 1992). Individual dolphins were photographically identified by comparing the markings on their dorsal fins and bodies (Würsig and Würsig 1977; Defran et al. 1990) with those from an established catalogue (Shane 1990; Gazda et al. 2005). If at any point during the approach or during the sighting, the dolphins changed their behavior to avoid the research vessel or interact with it (for example, if they attempted to bow ride), the sighting was excluded from our analysis.

Occasionally, sightings of dolphin groups of the same or similar composition as those previously sighted during a day were re-encountered. The dynamic nature of dolphin grouping decreases non-independent sampling problems, however, we conservatively excluded sightings if any member had been sighted less than an hour previously, or if all of the members of the sighting were already sighted that day (Smolker et al. 1992).

The behavioral states relevant to this study are: socializing, characterized by repeated incidents of body contact such as rubbing and petting with no consistent direction of movement (Shane 1980; 1990; Ballance 1992); travelling, characterized by spatial progress that is largely regular in terms of speed and consistent in terms of direction (Shane 1990); and foraging, characterized by prey capture or persistent

incidents of prey searching as indicated by long dives or specialized feeding behaviors with direction shifts between surfacings (Shane 1990; Gazda et al. 2005).

The sightings used in the analysis cover 124 sampling days of the study and included 303 sighted groups. The average proportion of identified individuals per group was 0.80 (s.d. 0.21, min proportion 0.2, max proportion 1.0). The average number of sightings per individual was 4.29 (s.d. 4.39, min 1, max 21). Since dependent calves that stay with their mothers and do not forage themselves could bias network associations, they were not included in the analyses.

*Network construction:*

The dolphin sightings data resulted in four networks — an Overall network that does not take behavior into account, and the Socialize network, the Travel network, and the Forage network corresponding to socializing, travelling, and foraging behaviors (Appendix A, Figure A.1). Each sighting contributed vertices corresponding to dolphins in the sighting and an edge connecting each pair of vertices. The number of times that each dolphin was seen across all sightings was recorded as an attribute of the corresponding vertex. For a specified activity type, this construction resulted in a network which was: simple (i.e., no multi-edges or self-edges); undirected (i.e., if A is a neighbor of B then B is a neighbor of A); and weighted, with the weights being the half-weight index (HWI) = the number of times dolphins A and B were seen together divided by the total number of times they were seen together plus half the value of when A was seen without B and B was seen without A, and range from 0 for individuals that are never sighted together in groups to 1 for individuals that are always sighted together (Cairns

and Schwager 1987). The HWI is commonly employed in dolphin studies (Lusseau, 2003), which facilitates comparison (Connor et al. 1992). It should be noted that by construction, the edge weights in the networks are unaffected by variations in the average group sizes in the sightings data.

Following Whitehead (2008; 2009), we pruned the networks by removing the vertices corresponding to dolphins sighted fewer than the threshold value (three in our study) at which the largest number of dolphins would be included in the networks while still allowing significant patterns of association (see the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.4r668).

Having a low threshold for inclusion, or simply including all available association data for all individuals, maximizes the information displayed but increases the sensitivity of the network to seldom-sighted and transient individuals. This may mask or confuse underlying social structure, thus limiting the ability of network analysis to decipher such structures, one of the main benefits of the technique. In contrast, having a high threshold for inclusion, while increasing confidence in displayed associations, decreases the detail of the network. This limits description of the network's overall structure and information regarding interconnections between distal elements of the network. Wey et al (2008) showed that network parameters are robust to different sampling efforts, and removal trials on simulated data have shown that the standard error within each trial was low, meaning the network parameters were measured precisely for different sample sizes (Borgatti et al. 2002). A threshold of three sightings has also been used in other studies in dolphins (Chilvers and Corkeron 2002) and in male zebras (Fischoff et al. 2009).

*Network analysis:*

Network metrics that are pertinent to testing our hypotheses regarding the four networks Overall, Socialize, Travel, and Forage, are listed in Table 2.1 along with definitions of the metrics, their biological significance in the context of the behavioral networks of dolphins, and references to articles where more details on the metrics can be found.

We tested for preferential associations among dolphins in each network using a modified permutation test against a null hypothesis that the dolphins associate randomly (Bedjer et al. 2008; Whitehead 1999). This test was performed using the compiled SOCPROG package 2.4 (available at http://myweb.dal.ca/~hwhitehe/social.htm; Whitehead 2009) with 200,000 permutations per network.

We used a randomization test to evaluate the statistical significance of network measures. The null hypothesis is that a structural measure on the real network is no different from that of a random network. We accepted or rejected the null hypothesis by comparing the observed measure with the frequency distribution of the measure calculated for an ensemble of 10,000 random networks, each generated using edge rearrangement (see the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.4r668) (Croft et al. 2011; Lusseau et al. 2006).

We used the Mann-Whitney U test to test for possible pairwise differences in group sizes (Sueur et al. 2011b). Each network was compared to the others.

## RESULTS

Analysis using SOCPROG show that there are preferential associations between individuals in the Overall network, the Socialize network, and the Travel network, but not in the Forage network (Table 2.2). This is not an artefact of sample size; the number of sightings in the Forage network (153) is greater than that in the Travel network (77) and Socialize network (38).

The main characteristics of the four networks are listed in Table 2.3. In the Socialize network, individuals have strong and repeated connections to many other individuals (highest average degree, highest average strength, highest average edge weight). Socializing happens in large groups (largest group size per sighting, highest size per community), and these groups are not exclusive (least number of communities, fewest connected components). Dolphins that are connected to a particular dolphin are more likely to be connected to one another (highest clustering coefficient).

Dolphins in the Travel network do not have strong and repeated connections to many others except their preferential associates (lower average degree, lower average strength, lower average edge weight). Travelling happens in smaller groups than socializing (smaller group sizes per sighting, smaller community size, larger number of communities, and larger number of connected components). Dolphins that are connected to a particular dolphin are less likely to be connected to each other (smaller clustering coefficient).

The Travel network is comparable to the Forage network in terms of its average strength and clustering coefficient. In many other aspects, such as, average degree,

number of connected components, and number of communities, the Travel network is intermediate between the Socialize network and the Forage network. There is no significant difference in group size between the Overall network and the Travel network (Table 2.3). This indicates that while dolphins do have preferential associations while travelling, they do not travel in groups as large as those they socialize in, or as small as they forage in.

Among the three activity networks, the dolphins in the Forage network have the weakest and least repeated connections to other individuals (lower average degree, lower average strength, lowest average edge weight). Foraging happens in smaller groups than any other activity (smallest group sizes per sighting, smallest community size), and these groups are exclusive with fewer links to other foraging groups (highest number of communities) or they are more likely in groups that never forage together (highest number of connected components). Foraging dolphins that are connected to another foraging dolphin are not as likely to be connected to each other (lowest clustering coefficient) as they are in the Socialize and Forage networks.

A large community overlap between two networks means that dolphins that tend to associate closely with each other in one network also associate closely in the other. Among the three activity networks, the Socialize network and the Travel network have the most substantial community structure overlap (Table 2.4), the Travel network and the Forage network have the least, and the Socialize network and the Forage network have an intermediate value. The overlap between the Overall network and each activity network is less than that of the activity networks to each other.

## DISCUSSION

The results of our study provide clear evidence that the patterns of spatial associations among individuals differ depending on the behavioral state under consideration (Table 2.2). We thus reject our null hypothesis that the four networks are similar to each other. As mentioned earlier, fission-fusion societies are often a response to the competing needs of social interactions (predator protection, social affiliations) and resource availability (Aureli et al. 2008; Schulke and Ostner 2012), and this should be seen in network analysis by behavior. These differences are effectively captured through appropriate network analysis, as we have shown here (Table 2.3). The Overall network masks the differences that are seen in the networks sorted by behavior (Table 2.3). Using an Overall network to describe a population also loses the important information gained by an analysis of community structure overlap. Namely, dolphins that tend to associate closely with each other in the Socialize network also associate closely in the Travel network, there is intermediate overlap of association between the Forage and Socialize networks, and less so between the Forage and Travel networks (Table 2.4). Important network properties that change according to the activity type considered include: the average degree and average strength of vertices, the average edge weight (HWI), the number of communities, the average size of communities, and the average clustering coefficient.

The values of the average clustering coefficients for the three activity networks show that there is a substantially greater likelihood that two dolphins that interact with a common third dolphin will also interact with each other in the socializing behavioral state

than in either the travelling or foraging states. Dolphins engage in strong and frequent associations when socializing, but not when foraging (Table 2.3). The strength and frequency of associations when dolphins are travelling is intermediate between that found when they are socializing or foraging.

These results show that a highly mobile species with extensive fission-fusion relationships may engage in certain inter-individual associations in some behavioral states but not in others. The cost/benefit ratio of interacting with an individual may vary with behavioral state. This may explain some of the features of the Forage network. Bottlenose dolphins in Cedar Key have been observed in small, weakly connected groups (small group size and high numbers of connected components, no preferential associations, Table 2.2; average strength in Forage is not significantly different than a random model, Table 2.3). A likely explanation for such behavior is that prey are distributed singly or in patches small enough that competition generally disfavors the formation of groups. Current evidence in primate research supports this theory (e.g. Shulke and Ostner 2012). For example, Red colobus monkeys that forage in larger groups have reduced foraging efficiency than smaller groups (Snaith and Chapman 2005).

Connor (2000) refers to non-mutualistic clusters of individuals as aggregations, not groups, and notes that smaller aggregations are more likely to resemble mutualistic groups in scale. Non-mutualistic group formation can include aggregations where food is concentrated (Alexander 1974). Other systems have also shown a possible correlation between group structure and food availability. Patchy distributions of prey have been shown to increase rates of fission-fusion in humpback dolphins (Parra et al 2011). Female

baboons have cyclical, qualitative changes in the strength of their associations that depend on resource availability. When food is more abundant, these females do not have strong affiliations of any kind and instead have only connections that are more representative of gregariousness (Henzi et al. 2009). Heithaus and Dill (2002) showed that prey availability for bottlenose dolphins is greater in shallower waters. If this is the case in Cedar Key, then the network structure of the dolphins forms for different reasons than at other sites; Gero et al. (2005) demonstrated that preferred associations are strongest when foraging or socializing in Shark Bay, Australia, and females maintain acquaintance-level associations across behaviors while males maintain affiliate-type relationships. The Cedar Key Forage network shows no evidence of preferred associations (Table 2.2). There was little evidence of cooperative foraging during this study (the cooperative driver-barrier behavior described by Gazda et al. (2005) was observed infrequently). Since dolphins have relatively low costs of locomotion compared to other mammals (Williams 1999), they may be more able to maximize grouping benefits that are behavior-specific (Connor 2000; Gero et al. 2005). We predict that networks will show less change with behavioral state in species with higher costs of locomotion.

Reduction of predation risk is thought to be one of the major factors favoring association across behavioral states in many mammal species (Norris and Dohl 1979; Heithaus 2001; Heithaus and Dill 2002; Schulke and Ostner 2012; Wells et al. 1980). Heithaus (2001) suggests that sharks greater than 3 m in length are the primary predatory threat to immature dolphins. Predation risk is poorly understood in Cedar Key; Quintana-

Rizzo and Wells (2001) mentions seeing a lone bull shark once during the year-long study in Cedar Key, but communication with local fishermen indicates the occasional presence of large sharks. A sufficiently low predation risk in Cedar Key, in contrast to Shark Bay, where over 70% of non-calf dolphins have shark bite scars (Heithaus 2001), may allow foraging in smaller, less connected groups. Dolphins in Cedar Key are occasionally observed foraging in a localized area without obvious signs of interaction or association, but the proximity of other individuals may still reduce predation risk. Reassessing the nature of foraging to delineate situations in which dolphins are foraging in proximity to, but not interacting with, other individuals would require reconsidering the definition of association in the foraging behavioral state. Association in our study was based on a 10 m chain rule. Local enhancement (Pöysä 1992; Turner 1964) offers an explanation for situations in which dolphins are foraging in proximity to, but not interacting with, other individuals. Dolphins may approach and forage near individuals that are catching fish, irrespective of social affiliation. Playbacks of foraging vocalizing dolphins could be used to establish the fish-catch detection distance.

Dependent calves were excluded from the study, and the sexes and ages of the individuals of the population remain largely unknown. Further study of this population in a network context would benefit from this information. In dolphins, males and females have differing association patterns and this would affect network structure (Gero et al. 2005).

In conclusion, we have shown that network analysis successfully captures important differences in the social structure of bottlenose dolphins across different

behavioral states. Individuals do not generally maintain the same level of association in different activity networks and the community structure determined by the network structure changes depending on the activity under consideration. In general it may be important to account for behavioral states when conducting network-based studies of social animals with fission-fusion characteristics.

TABLES

| Network Concept | Definition | Biological Significance | Reference(s) |
|---|---|---|---|
| Average Degree | The degree of a vertex is the number of edges incident on it. The average degree of a network is the average value taken over all the vertices in the network. | High average degree means each dolphin on average interacts with many other dolphins. | Newman, 2010 |
| Average Strength | The strength of a vertex is the sum of the weights of the edges incident on it. The average strength of a network is the average value over all the vertices in the network. | High average strength means each dolphin on average interacts strongly with its neighbours. | Barrat et al. 2004 |
| Average Edge Weight | The average edge weight of a network is the average value of the edge weights over all the edges in the network. | High average edge weight means that on average each pair of dolphins that interact with one another do so strongly. We used HWI values as edge weights. | Barrat et al. 2004; Newman, 2010 |
| Number of Connected Components | The total number of components, where each component is a set of vertices that are linked to each other by paths. | Large number of connected components means that there is a large number of dolphins with possible associations within the component they are in but no associations across. | Newman, 2010 |
| Average Clustering Coefficient | The clustering coefficient of a vertex is the ratio of the number of edges between the vertices connected to it to the number of edges that could possibly exist between them. The average clustering coefficient of a network is the average value over all vertices in the network. | Large average clustering coefficient means pairs of dolphins that interact with a particular dolphin are likely to interact with one another. | Watts and Strogatz, 1998; Barrat et al. 2004; Newman, 2010 |

| Network Concept | Definition | Biological Significance | Reference(s) |
|---|---|---|---|
| Number of Communities | The total number of communities where each community is a collection of vertices that are highly connected among themselves but with few or weak edges to vertices outside the collection. Communities within a network can be identified using the WalkTrap algorithm which is based on the fact that a random walker tends to get trapped in dense parts of a network corresponding to communities. | Large number of communities means large number of groups of dolphins with strong intra-group connections and weak inter-group connections. | Newman, 2006; Pons and Latapy, 2006 |
| Average Community Size | The average number of vertices in a community. | Large average community size means each community on average has many dolphins with connections among themselves. | Newman, 2006 |
| Community Overlap | The distance between the partitions representing communities in networks, measured as the variation of information or shared information distance between the partitions. | Large community overlap means that dolphins that tend to associate closely with each other in one network also associate closely in the other. | Meila 2003 |

Table 2.1: Definitions of network metrics, their biological significance in the context of the behavioral networks of dolphins, and relevant references.

| | | Association Indices | | |
|---|---|---|---|---|
| | | **Real** | **Random** | ***p*-value** |
| ***Overall Network*** | **Mean** | 0.03312 | 0.03558 | ***0.00055*** |
| | **s.d.** | 0.08157 | 0.06967 | 0.99999 |
| | **CV** | 2.46307 | 1.95818 | 1 |
| | | | | |
| ***Forage Network*** | **Mean** | 0.04186 | 0.04181 | 0.53489 |
| | **s.d.** | 0.11154 | 0.09057 | 0.99999 |
| | **CV** | 2.66463 | 2.16634 | 0.99999 |
| | | | | |
| ***Socialise Network*** | **Mean** | 0.18217 | 0.18762 | ***0.03554*** |
| | **s.d.** | 0.20699 | 0.17423 | 1 |
| | **CV** | 1.13628 | 0.92884 | 0.99999 |
| | | | | |
| ***Travel Network*** | **Mean** | 0.0596 | 0.06184 | ***0.0033*** |
| | **s.d.** | 0.1317 | 0.11237 | 0.99999 |
| | **CV** | 2.20953 | 1.81724 | 1 |

Table 2.2: Results from SOCPROG (Whitehead, 2009) analysis of preferential associations among dolphins in the Overall network, the Socialise network, the Travel network, and the Forage network, using an inclusion threshold of three sightings. Real values are compared to random values (permuted 200,000 times per network). The mean, standard deviation (s.d.), and coefficient of variation (CV) of the HWI values are shown along with the *p*-value indicating whether the associations are significant.

| | ***Number of Sightings*** | ***Number of Vertices*** | ***Number of Edges*** | ***Average Group size*** | ***Average Degree*** | ***Average Strength*** | ***Average Edge Weight*** | ***Number of Connected Components*** | ***Average Clustering Coefficient*** | ***Number of Communities*** | ***Average Community Size*** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Overall Network*** | 303 | 147 | 2088 | ***3.991*** (s.d. 3.913) | ***28*** | ***4.835*** | ***0.170*** | ***1*** | ***0.568*** | ***18*** | ***8.167*** |
| ***Socialise Network*** | 38 | 42 | 458 | ***8.359*** (s.d. 5.942) | ***21*** | ***7.469*** | ***0.342*** | ***1*** | ***0.761*** | 4 | 10.5 |
| ***Travel Network*** | 77 | 53 | 302 | ***4.137*** (s.d. 3.099) | ***11*** | ***3.099*** | ***0.272*** | ***2*** | ***0.555*** | ***8*** | 6.625 |
| ***Forage Network*** | 153 | 76 | 462 | ***2.955*** (s.d. 2.993) | ***12*** | 3.140 | ***0.258*** | ***4*** | ***0.539*** | ***17*** | ***4.471*** |

Table 2.3: Basic network quantities for the Overall network, the Socialise network, the Travel network, and the Forage network. Mann Whitney-U tests of group size indicated significant differences in group size between each pair of networks (italics, p-value < 0.003) except for Travel to Overall (p-value > 0.562). Metrics (average degree, average strength, average edge weight, number of connected components, average clustering coefficient, number of communities, average community size) were tested using an edge rearrangement randomisation test. Values in italics are statistically significant (p-value < 0.05).

| | ***Overall Network*** | ***Socialise Network*** | ***Travel Network*** | ***Forage Network*** |
|---|---|---|---|---|
| ***Overall Network*** | 0 | 4.908 | 5.382 | 5.534 |
| ***Socialise Network*** | 4.908 | 0 | 3.031 | 4.686 |
| ***Travel Network*** | 5.382 | 3.031 | 0 | 5.278 |
| ***Forage Network*** | 5.534 | 4.686 | 5.278 | 0 |

Table 2.4: Pairwise community structure overlap for the Overall network, the Socialise network, the Travel network, and the Forage network. The smaller the numeric value the larger the overlap.

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# CHAPTER 3:

# IS THE DECREASE IN THE NUMBER OF BARRIER BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN A DRIVER-BARRIER FEEDING GROUP ASSOCIATED WITH A CHANGE IN FEEDING SUCCESS FOR THE DRIVER AND BARRIERS?

Anderson and Franks (2001) defined a "division of labor" as occurring when individuals, working as a team to complete a task, perform different subtasks. A division of labor with role specialization, where individuals regularly assume different subtasks in a team task, is rare in mammals. A possible case was described in wild dogs: The same individual selects and chases the prey, one or two dogs maintain a distance behind the leader to head off any prey that may escape, and others lag behind (Estes and Goddard 1967). The first definitive case of a division of labor with role specialization in noneusocial mammals was reported in the African lion (*Panthera leo*) (Stander 1992). Females in "center" roles waited for prey to move towards them while those in "wing" positions initiated an attack on the prey (Stander 1992). Hunting success was higher when lionesses occupied preferred stalking positions. Recently, Hurtado *et al.* (2013) described role specialization in mound-building mice: within a group of six mice, two individuals carried most of the materials for building. Additionally, these carrier mice specialized in the type of materials they carried and did not switch. Gazda *et al.* (2005) described an

example of a division of labor with role specialization in a population of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida. Two groups (the A group and B group) were part of this study. In each group, one dolphin herded or drove fish toward other dolphins that appeared to line up and form a barrier. The trapped fish leapt into the air where they were captured by "driver" and "barrier" dolphins. Individuals in each group were consistent in their roles as driver and barrier. Nondriving dolphins were defined as all group members within the 10 m chain rule (all individuals in the group must be within 10m of another individual, Smolker *et al.* 1992) that did not drive. This included the barrier dolphins that were tightly bunched and raised their heads out of the water attempting to catch leaping fishes, as well as any other dolphins in the group that did not drive or form the barrier. In the A but not the B group the driver captured more fish than the barrier dolphins caught, a difference Gazda *et al.* (2005) attributed to the greater stability of the A group.

In the Cedar Keys, bottlenose dolphins display a variety of feeding behaviors including kerplunking (Connor *et al.* 2000, Wells 2001), snacking, tail up/peduncle up dives, "fish whacking" (Shane 1990, Nowacek 1999), and fish chasing onto shore (Quintana-Rizzo 1998, Gazda 2002). In other populations, there are multiple cases of foraging tactics exhibited by a limited subset of dolphins (such as sponge carrying, Smolker *et al.* 1997, Mann *et al.* 2008, Krutzen 2005, Kopps *et al.* 2014; and kerplunking, Connor *et al.* 2000, Wells 2001, Nowacek 2002). For example, in Shark Bay, Australia, a small percentage of mostly female dolphins specialize in deep-water foraging by carrying sponges, a probable tool worn to protect the forager's rostrum

during benthic feeding (Krutzen 2005, Mann *et al.* 2008, Mann *et al*. 2012, and Kopps *et al.* 2014).

The driver-barrier behavior in the Cedar Keys is another example of a behavior used by a limited subset of individuals. Only a small portion (approximately 6.7%) of the approximately 325 dolphins identified in the Cedar Keys have been observed to engage in driver-barrier feeding. At least four groups have been identified: the A and B groups from the Gazda *et al.* (2005) study and two other groups for which there are only a few sightings.

The B group consisted of three to six individuals; membership was not consistent per bout and they have not been seen in the study area since 2001. During the initial study in 2001, the A group consisted of the same three individuals. Over time, its group membership has changed from three to two to just one individual dolphin, the original driver "TLFN" (2001: 56 driver-identified driver-barrier bouts, 52 with three dolphins (one driver, two barriers), 4 with two (one driver, one barrier); 2008: 101 driver-identified bouts, 93 with two dolphins (one driver, one barrier), 8 with one driver (no barriers); 2010: 110 driver-identified bouts, all with one driver dolphin (no barriers)). Since the A group barrier dolphins were last seen in the group, they have not been sighted in the study area.

The A group driver TLFN has only been observed to drive fish and has not been seen using any other feeding method (28 total sightings: 2001, 9 sightings, 6 driver foraging and 4 socializing; 2008, 9 sightings, 5 driver foraging, 1 traveling and 3 socializing; 2010, 9 sightings, 7 driver foraging and 2 traveling). While the proportion of

individuals that use this behavior is small, it is clear that the A group driver TLFN specializes in this method of feeding.

This change in group size provides a unique opportunity to examine questions about the feeding success of the driver dolphin and the role of the barrier dolphins. In the initial study, one of the barrier dolphins from the B group was observed to drive fish alone, and significantly fewer fish jumped per bout. Accordingly, Gazda *et al.* (2005) suggested that the barrier role may not be essential but nonetheless important for trapping fish. An alternative hypothesis for this behavior was that the barrier dolphins were scroungers in a producer-scrounger system (P-S model; Barnard and Sibly 1981; Hamilton and Dill 2002).

Therefore, the objective of this note is to determine if the decrease in the number of barrier dolphins in Group A was associated with a change in feeding success for the A group driver and with respect to barrier dolphin success. Measures of feeding success examined are 1) number of fish caught, 2) the number of fish leaping per bout, 3) bout duration, and 4) the proportion of completed bouts.

Methods followed closely those described in Gazda *et al.* (2005). The study area encompassed most of the Cedar Keys (29º05'49" N, 83º03'58" W), which comprise five major islands, numerous smaller islands, and wetland areas connected to the mainland off the northwest coast of Florida. Briefly, observations were made from a 14-foot boat from June through August 2001, July through December 2008, and March through August 2010. In 2001, individuals were photographed using a Nikkormat camera fitted with an 80-250 zoom lens. In 2008 and 2010, a Nikon D300 camera with a 400 mm Nikkormat

zoom lens was used. Once a dolphin was encountered, the dorsal fin was photographed for individual identification (Caldwell 1955) using the methods described by Defran *et al*. (1990). Individuals were included in the group if they were within 10 m of any other group member (Smolker *et al.* 1992).

Feeding behaviors were recorded with a camcorder (2001: a Panasonic digital zoom S-VHS; 2008 and 2010: SONY HDR-HC1 HDV Handycam 1080i Digital Camcorder), and the dorsal fin of the driver was photographed during each bout. Blank photographs were taken between bouts to demarcate sequential feeding bouts. In addition, observers on board identified the driver verbally for the video camera. A feeding bout began when the driving dolphin began swimming rapidly in tight circles—either with or without fluke slaps—and was considered to be complete when the participating dolphins put their heads back under water and rolled upright. An incomplete bout was defined as a bout where the driver began swimming in tight circles—with or without fluke slaps—but stopped before fish started jumping out of the water and no participating dolphins put their heads above water. No fish jumped during incomplete bouts.

Only aerial fish capture was recorded, and only dolphins that had their heads up (*i.e.*, drivers and barrier dolphins) were used to calculate capture success. Fish-capture success was determined by counting the number of fishes each dolphin caught in air, indicated by either observing the fish in the dolphin's mouth or observing the dolphin's lunge followed by repeated biting motions. A lunge that was not followed by biting motions was not counted because dolphins sometimes missed fishes that they lunged at.

Recording the capture rates of individual barrier dolphins was not possible because the dolphins frequently changed positions and their dorsal fins were often submerged. Therefore, for each bout, an average number of fishes captured by the barriers was calculated from the number of barriers and the total number of fishes that they captured (Gazda *et al.* 2005). Fish that jumped were identified by eye as mullet (*Mugil cephalus*).

Fish-capture success might relate to the number of leaping fishes; therefore, the number of fishes leaping per feeding bout was counted from the videotape. Some leaps occurred after a leaping fish fell back into the water and thus could have been a fish leaping for a second time. These cases were not included in the total of fishes leaping per bout (Gazda *et al.* 2005).

Seventy driver-barrier bouts of the A group were seen in 2001 (56 bouts with an identified driver; 80% identification rate), 116 in 2008 (101 bouts with an identified driver; 92% identification rate), and 110 in 2010 (110 with an identified driver; 100% identification rate). All data were analyzed using SPSS Statistics (Version 19). The data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$ for all tests) nor did groups have similar variances (Levene's test for equality of variances, $P > 0.05$ for all tests). Differences in catch success between driver and barrier dolphins (overall and by number of dolphins per group) were analyzed via a paired samples *t* -test. Welch's *t*-tests were used for the remaining analyses; it does not assume equal variance or sample size between the two samples being tested (Ruxton 2006). Each table lists the number of bouts that were used for a given analysis.

TLFN was the driver in every identified bout. This finding of a consistent driver is significantly different from a distribution derived from a hypothesis that the driving individual is randomly selected for each bout (Binomial test, n = 163, $P < 0.001$). Bouts where a driver was not identified were due to poor video or photo quality. Any bouts where fish could not be counted due to poor video quality were removed from the analysis.

When analyzing complete bouts only, the driver did better than the barrier dolphins regardless of group size (group size of two, mean driver catch 0.70 (± 0.62 SD), mean barrier catch 0.50 (± 0.53 SD), $t = 2.572$, $P = 0.012$; group size of three, mean driver catch 1.07 (± 0.69 SD), mean average barrier catch 0.70 (± 0.56 SD), $t = 2.469$, $P = 0.02$),. There was no indication that group size was related to driver fish-capture success (Table 3.1, complete bouts only, no significant differences in TLFN catch rates between group sizes). There was a significant difference in barrier catch rates in complete bouts across group sizes (group size of two, n = 72, mean barrier catch 0.51 (± 0.56 SD), group size of three, n = 29, mean average barrier catch 0.72 (± 0.56 SD), $P < 0.001$). Based on these results, it seems that the driver dolphin does not benefit from an increased catch success with differing numbers of barrier dolphins participating, but the barrier dolphins do.

The number of barrier dolphins did not have a significant relationship with bout duration (Table 3.2) or in fish jumping per bout (Table 3.3). It should be noted that the decrease in driver-barrier group size is very closely correlated with change in year (N = 267, Pearson correlation -0.912, $P > 0.001$). This means that any change in success could

be a measurement of time and of group size or that one may mask the other. It is possible that TLFN improved with time, which may be why number of fish per bout and bout duration did not change with group size.

There is a significant difference (2X2 contingency table, Table 3.4) in the proportion of incomplete bouts between group sizes of one (one driver, no barriers) and three (one driver, two barriers; $P < 0.05$), as well as marginal significance between groups of two (one driver, one barrier) and three ($P = 0.07$). There is no significant difference in the proportion of incomplete bouts between group sizes of one and two ($P = 0.11$).

Of the four measures considered here (number of fish captured, leaping, bout duration and proportion of completed bouts), the number of barrier dolphins was associated only fish captured per barrier dolphin and with the proportion of completed bouts. The number of completed bouts had not been considered in the original study. I estimated the reduced feeding success of the driver in small groups by running a general linear model (Poisson loglinear) using all of the bouts: incomplete (no fish jumped therefore no captures) and complete (fish jumped therefore captures were possible). The increase in incomplete bouts as group size decreases may mean that the driver catches less fish per bout. I tested for catch success of the driver by group size. There was a significant decrease in the number of fish caught by the driver from a group size of three (one driver, two barriers) to a group size of one (only the driver; B = -0.448, $P = 0.039$). There was also a significant decrease in the number of fish caught by the driver from a group size of three to two (one driver, one barrier; B = -0.454, $P = 0.046$).

Having a group size of three means that there are fewer incomplete bouts, which increases the foraging efficiency for both driver and barriers. In incomplete bouts, there are no fish captures, though the driver does start driving and the barriers start to line up. It is possible that the driver or barriers catch fish below the surface, which would make it a different feeding technique, but there is no evidence (such as jerking motions from dolphins as they bite and chew their prey) that this is the case.

Evidence suggests that specialists in a foraging task outperform those that do not have a specialization in the same task (reviewed in Vickery *et al.* 1991, Tinker *et al.* 2008). This study has shown that a driver dolphin does have greater catch success than the barrier dolphins regardless of group size. This is different than what was initially predicted (Gazda *et al.* 2005). Because the barrier dolphins disappeared from the study site, it is difficult to determine if they were specialists at being barriers. Focal follows of barrier dolphins to clarify this are needed.

This study does not provide convincing evidence that the driver-barrier behavior fits a producer-scrounger model. In the P-S model, producers can experience a reduction, an increase, or no change in payoff due to the change in frequency of scroungers (Giraldeau and Dubois 2008). The driver does not have a significant difference in catch success related to the number of barrier dolphins when only accounting for complete bouts, but when accounting for both types, success significantly decreases from a group size of three to two or one. Further, barrier dolphins do better when there are more of them. In all scenarios of the P-S model the increase in frequency of scroungers leads to a decrease in payoff to the scroungers (Giraldeau and Dubois 2008Cooperation with role

specialization still remains the best explanation for this behavior. Connor (2010) defines cooperative behavior as "cooperative behavior as that which provides a benefit to another individual (recipient), and which is selected for because the actor's behavior yields a direct benefit from the receiver." There are two cooperative interactions occurring: one between the barriers and one between barriers and the driver.

The first cooperative interaction is between the barrier dolphins themselves. There is a significant difference in barrier catch rates across group sizes (Welch's *t* test, $P < 0.001$) and two barriers were more successful at fish capture than one barrier. The barriers increase foraging benefits by coordinating their behavior with the other group members (, by-product mutualism, Connor 1995).

The second cooperative interaction is between the barriers and the driver. Barriers in groups of three provided a benefit to the driver by reducing the number of incomplete bouts. Additionally, when accounting for incomplete bouts when testing for driver fish-capture success, there is a significant decrease in success rate as the group size decreases. Group size does not significantly relate to the number of fish leaping per bout, which combined with the increased catch success in a larger group, means that barriers and the driver catch a higher percentage of available fish leaping per bout. Fish may jump away from one individual but towards another.

The variable of the proportion of incomplete bouts was ignored in the initial study (Gazda *et al.* 2005). If this was not accounted for here, it would lead to a conclusion that this behavior was not necessarily cooperative, but one where barrier dolphins were opportunists. A similar shift in interpretation with the inclusion of a previously ignored

variable was found in a study of African wild dogs. Hunting was not found to favor group formation until the cost of locomotion was taken into account (Creel and Creel 1995). Larger packs had more successful and shorter hunts. It is widely assumed that mullet (*Mugil cephalus*) jump to avoid predation. Larger driver-barrier groups may be able to corral fish more efficiently, and there may be some sort of "threshold" of fish school size that has to be reached before a bout can be completed. Determining how barrier dolphins relate to foraging efficiency in different sized groups (and what an appropriate measure of efficiency is) is critical to understanding the role of barriers within this behavior, as well as the impact of their removal from the system. Studies on a larger number of groups that vary in the number of barrier dolphins and where time effects can be removed are needed to clarify these issues.

TABLES

| Group Size | n | Mean (±SD) | *t* | *P*-value |
|---|---|---|---|---|
| 1 | 104 | 0.78 ± 0.64 | 0.488 | 0.63 |
| 2 | 79 | 0.73 ± 0.59 | | |
| 2 | 79 | 0.73 ± 0.59 | -1.802 | 0.08 |
| 3 | 27 | 1.07 ± 0.92 | | |
| 1 | 104 | 0.78 ± 0.64 | -1.577 | 0.12 |
| 3 | 27 | 1.07 ± 0.92 | | |

Table 3.1: Welch's *t*-test of catch success of TLFN compared to group size. Only completed bouts were used in this analysis. Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin) or one dolphin (one driver, no barrier dolphins). N is number of bouts used for each analysis; *t* is *t*-value. There are no significant differences between groups (*P*-values > 0.05).

| Group Size | n | Mean bout duration, seconds (± SD) | *t* | *P*-value |
|---|---|---|---|---|
| 1 | 94 | 21.16 ± 12.71 | 0.928 | 0.35 |
| 2 | 90 | 22.47 ±11.37 | | |
| 2 | 90 | 19.76 ±8.45 | -1.180 | 0.25 |
| 3 | 22 | 21.96 ± 7.67 | | |
| 1 | 97 | 21.16 ± 12.71 | 0.392 | 0.70 |
| 3 | 22 | 21.96 ± 7.67 | | |

Table 3.2: Welch's *t*-test of bout duration. Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin) or one dolphin (one driver, no barrier dolphins). n is number of bouts analyzed, *t* is *t*-value. There are no significant differences between groups (*P*-values > 0.05).

| Group Size | n | Number Fish Jumping Per Bout (± SD) | *t* | *P*-value |
|---|---|---|---|---|
| 1 | 67 | 17.95 ± 15.71 | 0.419 | 0.68 |
| 2 | 75 | 16.75 ± 18.41 | | |
| 2 | 75 | 16.75 ± 18.41 | 0.329 | 0.743 |
| 3 | 32 | 15.63 ± 15.09 | | |
| 1 | 67 | 17.95 ± 15.71 | 0.706 | 0.48 |
| 3 | 32 | 15.63 ± 15.09 | | |

Table 3.3: Welch's *t*-test of number of fish jumping per bout. Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin) or one dolphin (one driver, no barrier dolphins. n is number of bouts used for each analysis, *t* is *t*-value. There are no significant differences between groups (*P*-values > 0.05).

| Group Size | Complete Bouts | Incomplete Bouts | *P*-value |
|---|---|---|---|
| 1 | 118 | 16 | 0.11 |
| 2 | 97 | 6 | |
| | | | |
| 2 | 97 | 6 | 0.07 |
| 3 | 52 | 0 | |
| | | | |
| 1 | 118 | 16 | *0.009* |
| 3 | 52 | 0 | |

Table 3.4: Contingency tables analysis of the proportion of expected vs. observed for complete and incomplete bouts. Incomplete bouts do not have any aerial fish catch (no fish jumped). Group size of one has only TLFN the driver; group size of two has one driver, one barrier; and group size of three has one driver, two barriers. Significant *P*-values are in italics.

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# CHAPTER 4:

# USING SPATIAL ANALYSIS TO DETERMINE IF ABIOTIC AND BIOTIC VARIABLES, INCLUDING PREY AVAILABILITY ARE CORRELATED TO DOLPHIN SPATIAL STRUCTURE

## INTRODUCTION

### *Background:*

A significant theme in ecology is the identification and explanation of spatial patterns of species distributions, composition, or diversity (Legendre 1993). The fundamental thought behind ecological studies is that distributions of species are not random. Species can select habitat areas for multiple (and sometimes conflicting) reasons. There is often a trade-off between predator avoidance and resource abundance. For example, for bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, groups were larger in the more dangerous shallow habitats and larger during resting than during foraging. When sharks were absent, dolphins had the same distribution as their food. When sharks were present, they deviated significantly from their food distribution, with fewer dolphins foraging in shallower areas than expected (Heithaus and Dill 2002). Similar trade-offs have been found in guppies (Abrahams and Dill 1989) and primates (Hill and Lee, 1998).

Additionally, species do not function alone; individual species can display spatial structure, which means that community composition is usually not random and will also display spatial patterns (Dray et al. 2012). Complicating this is the fact that there is no single scale at which processes occur (Agrawal et al. 2007, Fortin et al. 2002).

Ecological data sets are frequently summarized by multivariate analyses such as Principal Components Analysis (PCA). One type of PCA is based on correlation analysis and is a way to summarize a data set of many variables into a few dimensions. It is usually the first step in a facto analysis. It detects structures in the data that are associated with the strongest variance (Marengo 2010). However, PCA does not take spatial relations directly into account and cannot be used to identify spatial structures (Arrouays et al. 2011).

Many ecological data sets have some sort of spatial data associated with them, and traditional multivariate analyses are not designed to identify spatial structures (Dray et al. 2008). Traditionally, the simplest approach has been to analyze data sets using PCA and then apply univariate spatial statistics individually to the PCA scores for each axis (reviewed in Dray et al. 2012). This is an indirect approach and does not test for spatial autocorrelation (Dray and Jombart 2011).

Spatial autocorrelation measures both the proximity of sampling locations and the similarity of the attributes of these points at their locations. The data are not isolated as the locations are analyzed in relationship to their neighbors (Marengo 2010). It can be used to identify patterns across a study site at both a local and global scale. When sampling sites that are closer together display abundance values that are more similar

than distant sites, they have positive autocorrelation. It means that species aggregate, cluster together, or are clumped, and there is a high variation in density across the site (over dispersion). When sampling sites have density values that are either equally spread out (avoidance) or different from their closest neighbors, this can result in negative autocorrelation (under dispersion or even dispersion; Dray et al. 2012).

There are multiple options to analyze spatial patterns (reviewed in Dray et al. 2012). These patterns can be measured in a univariate (variance of a single variable) or a multivariate (variance of several variables) way. Univariate spatial methods include Moran's *I* and Geary's *c*. A Moran's *I* correlogram measures the extent to which a variable is spatially concentrated (positive spatial correlation; sites near to each other are similar) or spread out (negative correlation; sites near to each other are dissimilar). It does this by computing the degree of correlation between the values of a variable as a function of spatial lags by calculating the deviation between the values. Values close to zero mean that there is no spatial autocorrelation (Fortin et al. 2002). Geary's *c* is distance type function and measures the difference among values of a variable at nearby locations (Fortin et al 2002). Values vary from 0 (positive autocorrelation) to larger than 1 (negative autocorrelation). While univariate analyses are helpful for determining individual species spatial structure, they do not take the whole community into account.

Multivariate spatial analyses take advantage of the multidimensional nature of community ecological data (e.g., species that may interact with each other). The appropriate analyses to use also depends on the intent of the research (exploration, inference, or mapping) and how the data were collected (a complete census, regular

spacing, or irregular spacing; Fortin et al. 2002). The data collected for this study were collected randomly (irregular spacing), and all three intents will be examined here. Therefore, based on Fortin et al. (2002), the methods that are appropriate for irregular spacing and exploration and inference include those that use Moran's *I*, Geary's *c*, or Mantel tests. Methods that are appropriate for mapping include trend surface analysis, kriging, splines, or Voronoi polygons.

Spatial analyses based on Mantel tests have been shown to have very low power to distinguish spatial patterns (Legendre et al. 2005). Mantel tests themselves are not spatial in nature and only find the significance level of autocorrelation, which may or may not be related to spatial structure. Geary's *c* based methods are sensitive to outliers (Fortin et al. 2002). More recently, GDM (generalized dissimilarity modeling) methods have been suggested, but they have not been evaluated sufficiently yet (Dray et al. 2012). Analyses based on spatial weighting matrices (SWM; a symmetric site-by-site matrix that expresses the strengths of the potential relationships between the spatial units; Dray et al. 2012) can be tested using Monte Carlo permutation tests, and were made popular in landscape ecology (Cliff and Ord, 1973). SWM use either Moran's *I* or alternatively Geary's *c* (Wagner 2003) to measure spatial dependence. These spatial autocorrelation coefficients are computed for the entire study site, which produces global statistics (Dray et al. 2012). Geary's *c* based methods are sensitive to outliers (Fortin et al. 2002), so methods that use Moran's *I* are preferred.

For this study I chose to use the MULTISPATI function for spatial analysis found in the *ade4* package in R (Dray and Dufour 2007). It is a multivariate spatial analysis that

uses Moran's *I* to calculate global statistics. It also incorporates a spatially weighted matrix (SWM) and as a result, MULTISPATI results can be tested for significance using Monte Carlo permutation tests.

Wartenberg (1985) proposed the first attempt at depicting multivariate spatial patterns using Moran's *I*. Wartenberg's M matrix is not positive semidefinite because the main diagonal elements can be negative (negative spatial autocorrelations). Wartenberg's (1985) . MSC can be done by doing an eigenanalysis of the M matrix. However, his analysis is restricted to normalized variables (Dray and Jombart 2011).

Dray et al. (2008) proposed a generalization of Wartenberg's method. It involves two measures of spatial association: Moran's *I* values of the variables and a row-sum standardized spatial weighted matrix (row-sum standardized SWM). This matrix is an *n*-by-*n* matrix where *n* are the locations where the data were collected. It is considered to be row-sum standardized when all of the rows are standardized to equal one (Wartenberg 1985). This multivariate spatial analysis based on Moran's *I* is known as MULTISPATI (Dray et al. 2008). The analysis seeks coefficients to obtain a linear combination of variables that maximizes the product of the classic multivariate analysis and a generalized version of Moran's coefficient (Arrouays et al. 2011, Dray 2008). It allows analysis of all of the variables at once (as opposed to univariate analysis, which deals with one variable at a time) and preserves all of the information in the SWM (Dray et al. 2012). If a normalized PCA is used, MULTISPATI is equivalent to Wartenberg's approach (Dray 2008). The advantage of MULTISPATI is that it maximizes the spatial autocorrelation between sites, whereas PCA maximizes the variance. Therefore, the MULTISPATI

scores show the strongest spatial structures on the first few axes, while PCA scores can show variance on any axis (Arrouays et al. 2011). A Monte Carlo permutation test can be used to determine the statistical significance of the spatial structure.

MULTISPATI uses the approach developed by Anderson and Legendre (1999) for redundancy analysis/CANOCO. In order to use MULTISPATI, two items are required: a PCA of the species variables and a row-sum standardized SWM. PCA is calculated via a statistical triplet (three matrices **X**, **Q**, and **D**), where **X** is a table with *n* (observations) rows and *p* (variables) columns, **Q** is a *p*-by-*p* diagonal matrix with the weights of the *p* columns of **X** used to measure the relationships between the variables, and **D** is an *n*-by-*n* diagonal matrix containing the weights of the *n* rows of **X** matrix used to measure the differences between the sites (Dray et al. 2008, Dray and Dufour 2007). In PCA one can use either the covariance matrix or the correlation matrix to determine the components. If **X** is a set of normalized quantitative variables the triplet is identical to a principal component analysis on a correlation matrix. An example of normalizing **X** is mean centering: the mean for each variable is calculated from the data set and then subtracted from the variable values for each observation (Geladi and Kowalski 1985).

MULTISPATI determines the relationships between several variables and their spatial structures by including a row-sum standardized weighted matrix (of spatial information from the observations *n*) **W** in the statistical triplet **X**, **Q**, **D** (Dray et al. 2008).

Despite the potential power of this analysis, its uses have been mostly limited to analyses, soils, bacteria, and landscape classification: Most recently, MULTISPATI has

been used to determine spatial components of soil and terrain variables, which were then clustered using fuzzy k-means cluster analysis to define different management zones for differential nitrogen fertilizer applications (Peralta et al. 2015). Fuzzy clustering allows variables to be put in more than one cluster (it is not “hard” clustering). Significant spatial structure using allele frequencies has been found in goat, sheep, and cattle breeds across Europe, which seem to be related to the dispersal patterns of these species as they are introduced as livestock into new areas (Laloe et al. 2010). Standard multivariate techniques are often used on geo-referenced data sets and often with success (Dray et al. 2008). An example where this is not the case is with patterns of vegetation composition. MULTISPATI results shows that there are spatial patterns of vegetation composition, and these patterns are not obvious in the mapping of Canonical Analysis scores alone (Dray et al. 2008). Soil characteristics of topsoil in France have strong spatial structure that can be attributed to natural processes. While classical PCA and MULTISPATI produced similar results on the first two axes, MULTISPATI was better at detecting large regional trends (Arrouays et al. 2011). Bacterial composition of soils in France indicate that the distribution may be more related to local factors (soil type) than global ones such as climate (Dequiedt et al. 2009). The Scottish landscape can be adequately described by 50 different variables, and each of these variables has a spatial component (Marengo 2010). Lastly, MULTISPATI has been used to reanalyze Guerry’s 1833 moral statistics data set. Guerry gathered data on “moral statistics” such as crime, suicide, and literacy for different counties in France, called “Essai sur la Statistique Morale de la France.” This was the first social data analysis; he used maps to summarize the data set, which is

multivariate and georeferenced. Similar results were found compared to other spatial and nonspatial multivariate analyses; however MULTISPATI method retains all of the spatial information, which is ideal in spatial pattern analysis (Dray and Jombart 2011).

Based on Fortin et al. (2002), the methods that are appropriate for irregular spacing of spatial data and mapping include trend surface analysis (estimates of the variable are obtained by a regression model calibrated over the entire study area; Legendre and Legendre 2012), kriging (assumes that the distance or direction between sample points reflects a spatial correlation that can be used to explain variation; Isaaks and Srivastava 1989), splines (kriging with a fixed covariance; Dubrule 1984), or Voronoi polygons (values of unsampled locations are exactly equal to their neighbors; Tatalovich et al. 2006). Trend surface analysis is acceptable for describing broad-scale spatial trends, but fine-grained maps are not accurate (Legendre and Legendre 2012). Voronoi polygons are not ideal for scattered data points, as the values of unsampled areas depend on neighboring polygons (Sirovich et al. 2002). With kriging, unsampled locations are not considered to be equal to their neighbors as in Voronoi polygons (Tatlovich et al. 2006). Because splining does not perform an analysis of the variable being examined and instead uses a fixed covariance, there is a loss of accuracy (Dubrule 1984). Kriging is therefore the best option for this data.

*Goals of the Study:*

Marine fish species are not randomly distributed but have a distribution that is structured in space and time (Pape and Vaz 2014, Mello and Rose 2005). This structure is usually the result of several combined forces: external ones (e.g., environmental variables

and/or food availability) and internal ones (such as breeding timing) to the species, population and/or community (Aarts et al. 2013). Questions asked are: Are there spatial patterns in the relative abundance of fish species in the Cedar Keys? If fish have a spatial structure, is this structure correlated to habitat variables? Can fish that have spatial structure be clustered into groups?

Dormann (2007) reviewed 21 studies that each compared a traditional analysis of their data such as a generalized linear model with a spatial model. Of those 21 studies, only 3 were on mammals (bank voles *Clethrionomys glareolus*, Keitt et al. 2002; mammalian species richness in South America, Tognelli and Kelt 2004; and red deer *Cervus elaphus*, Augustin et al. 1996). In all of these studies the results showed that spatial modeling was much more accurate in describing species dispersion.

Examining spatial autocorrelation in animals, specifically mammals, is still relatively rare, though there are several studies on rodents. For example, spatial autocorrelation of Australian bush rats (*Rattis fuscipes*) showed that in general they live in high-density groups with areas of low density in between (Peakall et al. 2003). More frequently, studies on mammals have looked at spatial autocorrelation in genetics. The brush-tailed rock-wallaby (*Petrogale penicillata*) has strong female philopatry (Hazlitt et al. 2004), and this was determined by strong spatial genetic autocorrelation (females that were more related to each other were closer spatially).

Univariate measures such as Moran's *I* have been used in marine mammal research. Redfern et al. (2013) calculated a Moran's *I* value for each of the species that were at risk for ship strikes in the study site. Most of the species had high positive

autocorrelation, and specifically humpback whales (*Megaptera novaeangliae*) and blue whales (*Balaenoptera musculus*) have opposing areas of higher density, which means that creating shipping channels to minimize risk to one will increase risk for the other. Another study used individual Moran's *I* values on 12 seabird species and 8 marine mammal species. These were correlated with bathymetry. The results demonstrated that resident and migrant marine birds and cetaceans are associated with bathymetric features and shallow-water topographies, though the responses varied across species and time (Yen et al. 2004).

Most bottlenose dolphin research on habitat and prey is based on correlating sighting efforts to habitat makeup. In the Bahamas, bottlenose dolphins use habitats disproportionately more where potential prey can be found (Eierman and Connor 2014). The opposite has been found in Shark Bay, Australia, but this is because of increased predation risk (Heithaus and Dill 2002). Other studies have used univariate analyses such as Moran's *I*, but in one study that showed seasonal changes in habitat use, it was to confirm that sampling cells were not spatially correlated (they were not; Bearzi et al. 2008). Spatial autocorrelation studies of bottlenose dolphins seems to be relatively rare and related to testing for correlation between genetic similarity and geographic distance between samples (Natoli et al. 2008, Wiszniewski et al. 2009).

In bottlenose dolphin foraging research, it is often assumed that habitat use is related to prey availability (S. Dawson, personal communication, Torres 2007, Redfern et al. 2006), though this is rarely directly tested. To examine this assumption predator and prey data need to be on the same temporal and spatial scale, requiring intensive studies of

both levels, which is often outside the capabilities of a single research project. The FWC-FIM program makes this analysis possible: monthly fish relative abundance sampling has been ongoing in the study area since 1996. Dolphin sightings per unit effort (SPUE) will be classified by behavior. PCA partitions and graphically displays the variance in the data (in this case, what behaviors have the most variability in SPUE) whereas MULTISPATI partitions and graphically displays the patterns of spatial auto- and cross-correlation (what behaviors have a spatial structure or are distributed through the study site nonrandomly). The questions asked here are: Does dolphin behavior SPUE have spatial structure? What are the differences in results between PCA and MULTISPATI? Can fish relative abundance and habitat variables be correlated to dolphin spatial structure or variance in behaviors?

Dolphin distributions rarely include direct data on prey distribution because prey sampling is more difficult than sampling abiotic variables. In reality, these abiotic variables are usually used as proxies for prey distribution (S. Dawson, personal communication, Torres 2007, as reviewed by Redfern et al. 2006). Abiotic variables may be correlated with the distribution of dolphins; however, these metrics often have little direct influence on the selection of habitats by dolphins (as reviewed by Torres 2007). Therefore, as top marine predators, dolphins are likely to be removed from the direct influence of the environmental variability that is commonly used to characterize their habitat (Torres 2007). This analysis will close this gap by correlating dolphin SPUE variability and spatial structure to potential prey species and environmental variability. There is no single scale at which species interactions and processes occur. I am analyzing

this data based on a fine scale (the 0.2 $nm^2$ microgrids from the FWC FIM program), and this study will indicate if dolphins function at this scale.

## METHODOLOGY

### *Overview:*

I examined the relative abundance of fish species in Cedar Key using data collected from the Florida Fish and Wildlife Commission (FWC) long-term Fisheries Independent Monitoring Program (FIM). I first ran this on the fish collected by seines and by month, field season, and field seasons combined. Based on these results and those of the dolphin spatial analysis (below), I examined more closely a subset of these data. I correlated the MULTISPATI axes (Dray and Dufour 2007, R Core Team 2015, Wei 2013) that explain the most spatial autocorrelation to habitat variables (biotic such as substrate and abiotic such as pH and temperature) to determine whether spatial patterns can be explained by these variables. Because MULTISPATI incorporates the relative weights of neighbors when calculating spatial autocorrelation (Marengo 2010), I used cluster analysis to determine if the sampling locations can be clustered into groups and if these groups are logical given any possibly correlated environmental variables. I repeated these steps on the fish collected by trawls.

I analyzed dolphin SPUE by both methods to highlight the differences between the two techniques and determine what behaviors contribute the most to each. Using the FWC FIM fish data, I correlated the relative abundances of fish species to the PCA and the MULTISPATI axes and for environmental variables as well. This indicated if certain

species of fish can be used to explain either the variation in SPUE (PCA) or spatial structure in the behaviors (MULTISPATI). The FWC-FIM program fish data are collected in 0.2 $nm^2$ (nautical mile squared) microgrids, and correlations to dolphin data were analyzed on this same scale. The scale of a sampling design for a spatial study should be determined from what the ecological question is being addressed (Dungan et al. 2002), and no structure can be detected that is smaller than the unit being sampled or larger than the extent of the study (Legendre and Legendre 2012).

*Fish Data:*

From my collaborative work with the Florida Fish and Wildlife Commission's Fisheries-Independent Monitoring (FIM) program, I was able to integrate data on habitat (abiotic factors) and fish relative abundance, all taken at the same spatial and temporal scale. The FIM program has divided the survey region into three zones based on logistical and hydrological characteristics—two geographically defined bay zones and one riverine zone. Each zone is divided into grids and then into microgrids (0.2 $nm^2$). Each microgrid is characterized by its habitat (depth, percent cover of seagrass beds, and if applicable, shore type). FIM conducts stratified random sampling each month: 66 are sites randomly selected from the microgrids available in each zone (see Figure 4.1 for a map of the sampling sites by gear type, as well as the zones). Smaller fish are collected with a 21-meter seine (depths of 1.8 m or less), either set on shore or by boat, or a 6.1-meter otter trawl (depths greater than 1.8 m). Larger subadult and adult fishes are collected using 183-meter haul and purse seines. Over 100 parameters are taken at each site, including water quality and detailed habitat data. Some of these parameters are listed

in Table 4.1. The FIM data are processed and stored in a database. These data are available for researchers to access with prior approval. From the database, I selected all of the data that overlapped with the field seasons (August through December, 2008 and April through August, 2010). It is commonly accepted by the FIM program that catch is a measure of relative abundance, rather than absolute. Fish collection was standardized using FIM protocols to catch per 100 $m^2$ for each sampling site for each species collected. The catch by the shore set 21-meter seine fishes approximately 140 $m^2$; the boat set 21-meter seine fishes approximately 68 $m^2$. The 183-meter seines fishes approximately 4120 $m^2$. Effort for the otter trawl is calculated by speed and distance towed. The trawl is dragged for approximately 10 minutes and covers 0.02 nm per minute. The coverage of the trawl is approximately 1853 $m^2$. Because the trawl methodology is very different than those of the seines, I analyzed these separately.

*Habitat Data:*

While the FIM program takes data on the habitat at each site, I wanted to use GIS maps to get a more detailed breakdown of habitat makeup in each microgrid (Torres 2007). The Florida Geographic Data Library (http://www.fgdl.org/metadataexplorer/explorer.jsp) has extensive and current data layers for public use. Using ArcGIS 10.1, I rasterized a bathymetry layer of depth for the field site. I overlaid GIS maps of the microgrids on top of this depth raster, as well as a Cedar Key Benthic shapefile (Cedar Key Benthic2, data source: Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute). This shapefile classifies the ocean floor by different variables (defined by the Florida Land Use, Cover and Forms

Classification System handbook, 1999; see Figure 4.2 for a detailed map of the benthic habitats):

- Seagrass: Areas where there are seagrass beds. The beds are separated into discontinuous (patchy) or continuous seagrass.
- Oyster bars: Areas where there are oyster bars (typically natural formations) or oyster beds (typically aquaculture sites).
- Tidal flats: Areas of sand or mud that do not have vegetation. They are protected by wave action and are exposed at low tides.
- Bays and estuaries: Inlets or arms of the sea that extend into the land. They are only classified as such when they are included within the mainland of Florida.
- Major body of water: Parts of the sea that does not go into the mainland of Florida.
- Not classified: Habitat areas that do not fall into any of the other descriptors or have not been surveyed. Most of these areas are more inshore and in freshwater inputs such as the Suwannee River.

I used the Tabulate Intersection tool, which computes the intersection between two feature classes and tabulates (in this example, the microgrids and the benthic shapefile) the area of the intersecting features. I converted this result to a percentage of each habitat type within each microgrid that was sampled for fish. This is the habitat data that I used for the spatial analysis.

*Dolphin Data:*

Dolphin sightings per unit effort (SPUE, standardized by km of transect driven) and distribution data was collected in the field in 2008 (August through December) and in 2010 (April through August). The dolphin study area is divided into three roughly equal sized zones, each with a different directionality of shoreline (Figure 4.3). The purpose of these zones is to divide up the study area into sections according to the directionality of the shoreline. Zone 1 extends from the mouth of the Suwannee River to the northern point of Deer Island (10.5 km) and 5.5 km offshore. This zone is characterized by input of multiple large freshwater creeks. Zone 2 extends from the southern edge of Zone 1 to the northern edge of Zone 3, the entrance to channel 3 (9.8 km), and 6 km offshore. Zone 2 has a shoreline that is angled differently from the other two areas, and has a mix of islands and freshwater creek inputs. Zone 3 extends from the entrance of channel 3 to the northern side of Corrigan Reef (6.9 km) and 7.5 km offshore. Zone 3 consists of the Cedar Key islands.

A combination of offshore and inshore transects lines were used. Offshore transect lines run at a 45 degree angle to shore, thus capturing alongshore density gradients, and are spaced at 1 km intervals following Dawson et al. (2008 and Du Fresne et al. 2006). Transects provide unbiased data as to the locations of dolphins across microhabitats. Zone 1 has 7 lines, Zone 2 has 6, and Zone 3 has 8 (Figure 4.4). Offshore lines vary from 1.6 km to 7 km long, and extend from the outer edges of the zones to 250 m from the shoreline. Transects were conducted on a 16-foot boat with an 80 hp 4-stroke engine. The starting location (south or north, inshore or offshore) for each daily block of

transects was randomly picked. During transects, two observers sat on an elevated polling platform at the front of the boat facing their respective viewing angles. The driver piloted the boat from a center console and looked ahead for dolphins. During transects the left observer scanned from 9 to 12 o'clock, and the observer on the right scanned from 12 to 3 o'clock. Boat speed was depth dependent—in waters over 1 m, the boat traveled at approximately 7 knots/hour (Dawson et al. 2008, Hiby 1982); in waters shallower than 1 m depth, speed was at 3 to 5 knots/hour. Any dolphins sighted within a 250 m range either sides of the boat were noted. The transect location of the boat was marked with a GPS point. The boat was steered to the dolphin sighting location, and another GPS waypoint was marked; the team switched to survey mode (see below). Once the survey was complete, the boat returned to the transect location where the dolphins were first sighted, and the line was resumed with time and location noted with a GPS waypoint. Transects were conducted in a Beaufort Sea State of 2 or less.

I ran separate alongshore transects in each zone (Figure 4.5). Due to the shallowness of the study area, as well as underwater obstacles such as oyster bars that make straight-line transects close to the shore treacherous, these lines follow the general contours of the shoreline of the mainland and larger islands. Alongshore transects were run 250 m from shore, and an observer at the front of the boat scanned from the boat to the shore. The methodology to approach sighted dolphins and record data was the same as for offshore transects.

Surveys are brief encounters (typically 10–20 minutes) with groups of dolphins during which predominant group activity (> 50% individuals), individual identification,

location, and environmental variables are recorded. Surveys provide data on who associates with whom and the behaviors of individuals and where/what microhabitat such behaviors may occur. Membership in each survey was defined by the presence of dolphins during the first 5 minutes of encounter and within the 10 m chain rule (each individual must be within 10 m of another to be considered part of the group, Smolker et al. 1992). Individual dolphins were photographically identified by comparing the markings on their dorsal fins and bodies (Würsig and Würsig 1977, Defran et al. 1990) with those from an established catalogue (Shane 1990, Gazda et al. 2005).

Group sightings were classified by behavior. Behaviors used were: Socializing, characterized by repeated incidents of body contact such as rubbing and petting with no consistent direction of movement (Shane 1980, 1990; Ballance 1992); Traveling, characterized by spatial progress that is largely regular in terms of speed and consistent in terms of direction (Shane 1990); and Foraging, characterized by prey capture or persistent incidents of prey searching as indicated by long dives or specialized feeding behaviors with direction shifts between surfacings (Shane 1990, Gazda et al. 2005). If the initial behavior could not be determined, we classified it as Unknown.

*Statistical Analysis: Weighted Neighborhood Matrix*

For the analysis I used the program R, a free open source statistical computing program (R Core Team 2015). I used the *sdpep* (Bivand and Piras 2015) and *ade4* (Chessel et al. 2004) packages. The first step in determining if there is a spatial relationship in the fish species is to create a neighborhood network of the sampling points (spatial weighting matrix, SWM). There are two main ways of defining a neighbor

relationship: adjacency or distance. The literature reviewed is relatively limited about the use of method and criteria for defining the neighborhood relationships, so based on previous works (Marengo 2010) I decided to use the k-nearest neighbors method, which states that the user-defined number of points (four in this analysis; also based on Marengo 2010 who used four, and Dray 2008, who suggested the numbers of neighbors remain constant) are the nearest neighbors. This is also appropriate because the sampling areas in each microgrid, while randomly selected, often do not share boundaries, therefore an adjacency criterion would return few neighbors. This returns a matrix of *n* rows (observations) weighted by *k* neighbors. The matrix was then row-sum standardized so that the influence of each neighbor is the same (Dray et al. 2008). This is done by standardizing the weights of each row to equal one. This creates proportional weights in the cases where sites may have an unequal number of neighbors. This is also appropriate where one wants to compare spatial structures across different scales of data sets, which was the intent for the initial analysis of the seine data by month, field seasons, and field seasons combined. I used the same methodology to create a neighborhood network of sampling points for the trawl data and then for the dolphin behavior data.

*Statistical Analysis: Fish MULTISPATI*

The total number of potential fish species that could be caught per time period is very high (approximately 155 species), but many species are extremely rare or were not captured during the field season. Alternatively, there may be some species, such as the broad stripe anchovy (*Anchoa hepestus*) that are captured quite frequently at regular densities and therefore do not have a clear spatial pattern. Based on the time span of the

analysis (month, field season, or combined field seasons), I removed the fish species that were not caught at all during that timeframe. Additionally, because my intent was to analyze the data for spatial structure, I assessed the data for "noise": the species that did not have any significant spatial pattern. Dray et al. (2012) also states that the first step is to test the data for spatial significance. I did this by using the package *spdep* in R to perform a permutation test for the Moran's *I* statistic (suggested by Dray et al. 2012) for each species by using 1000 random permutations of the species weighted by the weighted neighborhood network mentioned above. The Moran's *I* is simulated in each time permutation for each species under an assumption of no spatial pattern, and the actual value is compared to the simulated distribution to obtain the *p*-value. For each species, a rank of the observed statistic in relation to the simulated values and a *p*-value is returned. Any species with a *p*-value greater than 0.05 can be assumed to have no spatial relationship and therefore was removed from the analysis. These pared-down species abundances were used for the MULTISPATI analysis. Table 4.2 lists the number of species used for each analysis after the "noise" was removed. I repeated this same methodology for the trawl sampling data using both field seasons combined.

MULTISPATI is an application that carries out a multivariate analysis (PCA) and a spatial autocorrelation analysis by calculating Moran's *I* on the basis of the weighted neighbor matrix. PCA analysis is sensitive to non-normal data. For both the seine and trawl data, the Shapiro-Wilk test for normality was highly significant ($p < 0.001$). Log transformation requires adding a 1 to the zero values, and zeroes themselves can be important, as they may be indicators of over-dispersion (Cunningham and Lindenmayer

2005). Additionally, it has be found that for count data (which the fish data are count data standardized to effort) it performs poorly under log transformation (O'Hara and Kotze 2010). I therefore used mean centering, which is also the default in the *dudi.pca* function. The mean for each variable is calculated from the data set and then subtracted from the variable values for each observation (Geladi and Kowalski 1985). Mean centering ensures that the first axis of PCA explains most of the variation in the data. For each set of species data, I carried out a PCA with mean centering (*dudi.pca* in R).

The statistical triplet of the PCA is then weighted by the neighbor matrix (*multispati* in R). I then ran a permutation test of the MULTISPATI analysis (*multispati.rtest*; 1000 repetitions) to detect significant patterns of spatial structure. This permutation test does not rely on any hypotheses of distribution (Arrouays et al. 2011).

I retained the first two positive axes from the MULTISPATI analyses for the correlation analyses. I chose these axes because the scores of MULTISPATI show strong spatial structure (global structures) on the first few axes. For seines, the first and second axes explain 19.26% and 12.01% of the variance in the data (Figure 4.5). The scores from the MULTISPATI site were correlated to the environmental variables using the corr.test function in the *psych* package in R (Revelle 2015) using Kendall's tau and adjusted for multiple tests using the False Discovery Rate test (FDR; Benjamini and Hochberg 1995; "fdr" in R). Traditional Bonferroni adjustments can become prohibitive in situations where there are dozens of repeated tests. Garcia (2003) noted that the more detailed the analysis, the less likely that a significant result will be found. False Discoveries are erroneously rejected null hypotheses (Benjamini and Hochberg 1995). Controlling for the

FDR allows for increased power in repeated tests. The correlations are performed on up to 10 variables per axis, so the FDR is appropriate for this analysis.

For seines, I separated the fish data by month and field season (2008: August through December, 2010: April through August). I also combined the two field seasons and analyzed this in its entirety. However, based on the results of the dolphin analysis (see *Statistical Analysis: Dolphins* below), I chose to concentrate on the combined field seasons for all remaining analyses. For the trawl data, I followed the same procedure as above, for both field seasons combined, after standardizing the fish abundance data to catch per unit effort (CPUE). For trawls, the first and second axes explain 22.9% and 21.0% of the variation in the data (Figure 4.5).

Lagged vectors are the weighted averages of the neighboring values (weighted by the spatial weighting neighbor matrix, explained above). That is, a value at a particular location is replaced by the average value computed on neighboring locations. Dray et al. (2008) suggest that lagged scores from MULTISPATI analysis could be used to perform spatial classifications of the sites, as the scores are a reflection of how similar sites are to their neighbors. Using the *NbClust* package in R (Charrad et al. 2014), I performed a cluster analysis on the lag scores of the seine and the trawl sampling sites separately using kmeans clustering. This is a method where *n* observations are partitioned into *k* clusters; each observation belongs to the cluster with the nearest mean (MacQueen 1967). The *NbClust* package uses 30 indices for determining the best number of clusters and returns a suggestion of the best partition based on majority rule. I then coded the seine and then trawl sites to their suggested cluster and mapped the clusters using ArcGIS.

*Statistical Analysis: Dolphins*

For each set of dolphin data (month, field season, and combined field seasons), I created a spatial weighting matrix based on the neighborhood network of sampling points. I used four as the user-defined number of points that are the nearest neighbors. I chose four based on previous work (Marengo 2010) and because I used this number in the fish analysis. I then carried out a mean-centered PCA (*dudi.pca* in R) and used the resulting triplet with the spatial weighted matrix in the MULTISPATI analysis. I then ran a permutation test on the MULTISPATI analysis (1000 repetitions) to detect significant patterns of spatial structure. The results of the MULTISPATI analysis indicated that there was only significant spatial structure in dolphin sightings for both field seasons combined ( Table 4.3). Therefore, for the remaining analyses (determining if dolphin spatial structure is correlated to fish species or habitat variables), I only focused on the combined data set of both field seasons.

The FWC fish data were not necessarily taken at the same locations as the dolphin sightings. Therefore, I needed to interpolate these variables across the study site. I treated the seines and trawls separately but followed the same procedure for both: I used the combined fish data from both field seasons and selected the species of fish that showed a significant spatial structure in each data set (significant Moran's *I* value, see above for more details). There were 50 species caught by seines (Table 4.4) and 34 species caught in trawls (Table 4.5) that had significant spatial structure. I kriged each of these species abundances to the study site in ArcGIS 10.1. Kriging is a method that assumes that the distance or direction between sample points reflects a spatial correlation that can be used

to explain variation (Isaaks and Srivastava 1989). It is the most appropriate of the methods recommended by Fortin et al. (2002; reviewed in the Introduction of this chapter). I used the Extract Value from Raster tool to get the kriged values of each species abundance at each dolphin survey site (Tittensor et al. 2010). To confirm that kriging was the appropriate interpolation method, I also used the inverse distance weighting (IDW) tool (Shephard 1968) and compared the two results. IDW is based on the assumption that objects that are closer to each other spatially are more similar than those that are farther away. It is similar to kriging, but the difference is that in kriging, the weights applied to the points are not standardized inverses of the distances. The weights are based upon the covariances on a variogram model (describes the degree of spatial dependence; Legendre and Legendre 2012). It estimates the values of an unsampled area as a weighted average based on neighborhood points or areas. The weight assigned decreases the further from the neighbor point it gets (Isaaks and Srivastava 1989). The results from IDW were similar to kriging; the methodology was not sensitive to the different tools.

I did not take abiotic data during dolphin sightings but instead relied on the abiotic data from the FWC fish database. This is because the FWC takes much more data (and with higher quality instruments) than I could (Table 4.1), though not at the same sites as dolphin sightings. Using ArcGIS I kriged each of the FWC abiotic (temperature, pH, salinity, and Secchi disk depth) variables across the study site (Redfern et al. 2013) using the microgrids as the spatial scale. This means that I used kriging to fill in the empty microgrids. Habitat type variables were taken as percent makeup of the microgrid

(using ArcGIS 10.1, Tabulate Intersection tool) that the dolphin sampling point was in. Depth was recorded as an average value of the microgrid.

*Statistical Analysis: Fish and Dolphins*

PCA partitions and displays the major patterns of variance in the data (in this situation, the variance in dolphin behavior SPUE), whereas MULTISPATI examines spatial structure (if dolphin behaviors occur with spatial patterns). I am interested in both of these, so I did an in-depth analysis of both tools. For PCA, I retained the first 2 axes (which explain 22.8% and 21.3% of the variance of behavior SPUE, respectively; see Figure 4.6). I retained the first 2 and last axes (which explain 37.90%, 22.21%, and 28.06% of the variance in spatial structure, respectively) from the MULTISPATI analyses of the dolphin data for the correlation analyses. I retained the last axis because in MULTISPATI, large negative axes can indicate local areas of dissimilarity or under dispersion. The scores from the MULTISPATI axes were correlated with the environmental variables and with the kriged fish values (from seines and then from the trawls) using the corr.test function in the *psych* package in R (Revelle 2015). Correlation plots were created using the corrplot package in R (Taiyun 2013).

PCA explains variance in SPUE rather than spatial structure. Therefore, when correlating the PCA axes to the fish species, it is less critical that only the fish that have spatial structure are used. I added the fish species that dolphins have been known to preferentially consume (Berens McCabe et al. 2010). These fish species were common snook (*Centropomus undecimalis*), sand weakfish (*Cynoscion arenarius*), spotted

seatrout (*Cynoscion nebulosus*), ladyfish (*Elops saurus*), lane snapper (*Lutjanus synagris*), kingfish spps. (*Menticirrhus* spp.), Gulf toadfish (*Opsanus beta*), black drum (*Pogonias cromis*), and red drum (*Sciaenops ocellatus*). All were caught in the seines, though the sand weakfish and the Gulf toadfish did not have a significant Moran's *I* value and were not in the MULTISPATI analysis, therefore they were added to the PCA correlations. Common snook and ladyfish were not caught in the trawls. The other species were caught in trawls but did not have a significant Moran's *I* value and were not in the MULTISPATI analysis, therefore they were added to the PCA correlations.

The cluster analysis of the fish data (described above) may show defined areas that can be explained both spatially and from the variance in relative abundance of species. Dolphins may use the study site based on these total differences rather than individual species. To determine if dolphin behaviors correlate to the cluster areas determined by fish sampling sites, I created polygons around each cluster type for seines and then for trawls using the Minimum Bounding Geometry tool in ArcGIS. I used the convex hull polygon method, which creates the smallest polygons by connecting the outer points of the clusters. I used a spatial join to determine which dolphin sightings were in which cluster. The behavioral SPUEs were not normally distributed (Shapiro-Wilks tests, $p$-value $< 0.05$), so I performed a nonparametric Kruskal-Wallis test on the distributions of the means by cluster.

## RESULTS

*Fish Data:*

Table 4.2 shows the number of species and number of sites used for each MULTISPATI analysis (after initially removing the species that did not have a significant Moran's *I* autocorrelation *p*-value), as well as the *p*-value for the Monte-Carlo analysis. Monte-Carlo permutation tests of MULTISPATI were highly significant (at least *p*-value <0.02 for all tests): This means that spatial structures were strong in all of the temporal scales and not attributed to random variations. The list of species that were used in the combined field seasons for the seines and trawls can be found in Tables B.1 and B.2 in Appendix B.

The loadings of species to the axes (contributions of the species to the MULTISPATI axes) varied by month and field season. Since the dolphin data only indicated significant spatial structure when the two field seasons were combined (Table 4.3), the results of the monthly and field season analyses for the seines can be found in Appendix B (Figures B.1 to B.24). The results from both field seasons combined are discussed at length in this chapter.

I kept the first 2 axes of the MULTISPATI per the eigenvalue bar plots (Figure 4.6). The first two axes combined explain 33.41% of the variance for seines and 46.80% for trawls. Loadings represent the relative weight of each species in each retained axis, scaled by the amount of variance expressed by the axis. However, these values are absolute so it does not delineate between species that load positively or negatively to the axes. These can be found in Appendix B (Figures B.25 and B.26).

Figure 4.8 (for seines) shows the coefficient of the variables (fish species) on the first two MULTISPATI axes. Top loading species are labeled. The cosine of the angle between vectors provides an estimate of the Moran's I cross correlations among species. The seines show that the top loading species are in three groups: one that is negative on the first axis, and two groups that oppose each other on the second axis. Spatial autocorrelation can be seen as the link between one variable and the lagged vector. Figure 4.9 is a plot of the scores and the lagged scores, connected by an arrow. The bottom of the arrow is the score and the head is the lagged score. The lag score is the averages of the neighbors weighted by the spatial connection matrix (Dray et al. 2008). A long arrow means that there is spatial discrepancy (the site is not similar to its neighbors), while a short one means that there is local spatial similarity. Arrows are labeled by their cluster group number; three clusters based on the lag scores were suggested by the *NbClust* analysis. Clustering based on lag scores means that sites that are similar to their neighbors will cluster together. By looking at both of these figures together, the variables that are positive on the first axis correspond to cluster 3. The variables that oppose each other on the second axis belong to the first (positive) and second (negative) clusters. The second cluster is along the first axis. The map of the seines coded by cluster (Figure 4.10) shows clearly that there are three distinct clusters of sites. Cluster one is alongshore, and the top loading species are a mix of freshwater and brackish species (Table 4.4). Cluster two opposes cluster one on the second axis (Figure 4.8) and is more offshore (Figure 4.10), and the top loading species (Figure 4.8) that correspond to this cluster are all saltwater species (Table 4.4). Cluster three is negative along the first axis and is mostly

freshwater and brackish species (Table 4.4). This cluster is almost entirely within the Suwannee River, which is freshwater (Figure 4.10).

Correlations of the MULTISPATI site scores on the first and second axes to abiotic and environmental variables can also help explain the MULTISPATI axes. This figure is a correlation matrix of the site scores to environmental variables for both field seasons. High site scores on the first axis of fish spatial structure for seines (Figure 4.11) are linked to higher pH, higher salinity, and larger proportions of continuous and discontinuous seagrass beds and tidal flats, as well as deeper waters. The higher site scores are linked to lower proportions of nonclassified benthos (negative correlations; Figure 4.11). For example, there is a significant positive correlation ($p$-value = 0.001) between site scores on the first axis and pH. This means that sites with higher scores on this axis are found in higher pH environments. However, the species with high loadings on the first axis are negative, which means that they are correlated with lower pH, salinity, cooler waters, and lower proportions of seagrass beds and tidal flats, as well as higher proportions of nonclassified benthos and shallower waters. Cluster three is correlated to the first axis of MULTISPATI (Figures 4.8 and 4.9) and is more inshore than the other two clusters (Figure 4.10). These sites would have lower pH, conductivity, salinity, cooler waters and fewer seagrass beds and tidal flats than the more offshore areas because they are more freshwater. Nonclassified benthos is typically in the inshore freshwater inputs, so it is logical that they are correlated to an increase in this type of environmental variable. This cluster is further inshore, so it is also logical that it is correlated with shallower waters.

The second axis for seines has essentially the opposite correlations: High positive site scores are linked to lower salinity, pH, and seagrasses (continuous), but higher proportions of nonclassified benthos and shallower depth (Figure 4.11). High negative site scores are linked to higher salinity, pH, and seagrasses, but lower proportions of non classified benthos and deeper waters. The species that fall along the second axis (Figure 4.8) are in clusters one and two (Figure 4.9), which are along shore (cluster one) or more offshore (cluster two). Those species in cluster one have the higher positive site scores, and are alongshore. Those in cluster two have negative site scores are more offshore, and have more saltwater. This may seem like the two axes report similar results, but this is not necessarily true. Cluster three is very different in spatial location than the other two sites and branched out on its own axis as a result.

The trawls show equally clear results. Figure 4.12 shows the coefficient of the variables (fish species) on the first two MULTISPATI axes. Top loading species are labeled. The trawls (Figure 4.12) show that the top loading species are in three groups: Two oppose each other on the second axis and another group is positive on the first axis. Figure 4.13 is a plot of the scores and the lagged scores, connected by an arrow. Arrows are labeled by their cluster group number (*NbClust* analysis suggested three clusters). By looking at both of these figures together, the variables that have obtuse angles on the second axis belong to the first and second clusters. The third cluster is along the first axis. The map of the trawls coded by cluster (Figure 4.14) shows clearly that there are three distinct clusters of sites. Cluster one is in the Suwannee River, and the top loading species are a mix of freshwater and brackish species (Figure 4.12). Cluster two opposes

cluster one negatively on the second axis (Figure 4.12) and is along the shoreline (Figure 4.14). This area has a significant freshwater input from the Suwannee River, and the top loading species (Figure 4.12) that correspond to this cluster are a mix of marine and freshwater species (Table 4.5). Cluster three is along the first axis (Figures 4.12 and 4.12), is made of trawl sites further offshore (Figure 4.14) and the top loading species are marine and brackish (Table 4.5).

Trawl data correlations are almost as easily interpretable. High positive site scores on axis one are correlated to higher proportions of tidal flats and bay and estuaries benthos, but negatively correlated to marine benthos and to Secchi depth (which means that high site scores are in more turbid waters). Cluster three falls along the first axis (Figures 4.12 and 4.13) and is more offshore than the other cluster. High positive site scores on axis two are correlated to a decrease in salinity, pH, Secchi depth, and average depth. They are positively correlated to an increase in not classified benthos. Cluster one falls along the positive of axis two, which is in the Suwannee River. The Suwannee River is very turbid and visibility is minimal, which means Secchi depth is decreased. Cluster two is negative on axis two, which means site scores are correlated to an increase in salinity, pH, marine benthos, and Secchi depth. They are also correlated to a decrease in nonclassified benthos and deeper waters. Cluster two is more alongshore, which would indicate more salt water.

*Dolphin Data:*

Table 4.6 summarizes the differences between the classic PCA approach and the MULTISPATI analysis for dolphin behaviors for both field seasons combined. There is a

loss of variance from PCA to MULTISPATI (for example, PCA axis 1, 1.13 vs. MULTISPATI axis 1, 1.05), but there is an increase in spatial autocorrelation (PCA axis 1, 0.02 vs. MULTISPATI axis 1, 0.19 (Figure 4.7). PCA eigenvalues are related to the variance in behavior SPUE, whereas eigenvalues of MULTISPATI are a product between the variance and spatial autocorrelation of the site scores. The first two axes of the PCA analysis, traditionally the ones that are retained, explain 44.0% of the variance (Figure 4.7). The eigenvalues of the PCA analysis decrease much more quickly than the gradual decrease of the PCA analysis. One of the benefits of MULTISPATI analysis is that there is usually a clearer distinction in what axes explain the most variance, so the selection of the retained axes is less arbitrary. Dray et al. (2008) recommend retaining the last negative axis, as large negative eigenvalues can explain local spatial dissimilarity. In this situation, the first two and last axes of MULTISPATI explains 88.2% of the variance (Figure 4.7).

The Monte Carlo permutation test of the MULTISPATI analysis was significant in only one test, when both field seasons were combined (Table 4.3). These are the only cases where the spatial analysis of dolphin behavior analysis of dolphin behavior . From this point onwards, I only discuss the results from data with dolphins when both field seasons are combined.

Since MULTISPATI explains more of the spatial structure and PCA explains more of the variance, plotting the axes of the PCA analysis onto the first two axes of MULTISPATI can provide further information about the structure of the data (Figure 4.16). PCA axis two is more closely correlated with axis one of MULTISPATI, and PCA

axis one is more closely correlated with axis two of MULTISPATI. If the axes were aligned with each other, this would mean that the variance in PCA would be similar to the spatial autocorrelation in MULTISPATI.

This is supported by the loadings plots of the behaviors to the first and second axes of PCA and the first, second and last axes of MULTISPATI (Figures 4.17 and 4.18). Forage and Socialize are the top loading behaviors on the first and second axes, respectively, for PCA (Figure 4.17). For MULTISPATI, the top loading behaviors are Socialize and Travel for the first and second axes, and Forage for the last (Figure 4.18). Plots of the top loading behaviors for the other three axes of both analyses are in Appendix B (Figures B.27 and B.28).

Figures 4.17 and 4.18 are graphical displays of the first two axes of the PCA and of the MULTISPATI analysis for both field seasons combined. The PCA graph of the first and second axes shows that there is a correlation between Rest, Unknown, and Socialize (Figure 4.17; negatively correlated to the second axis), and that Travel (explained by a negative relationship to the first axis and a positive relationship to the second) indirectly opposes Forage (most correlated positively with the first axis). Travel, Forage, and Socialize have similar import in explaining the variance in the first two axes, while Rest and Unknown have lesser importance. This means contributes strongly to PCA axis one. Graphs of PCA axis one vs. axis four and PCA axis one vs. axis five can be found in Appendix B (Figures B.29 and B.30). The MULTISPATI graph is different, where a relationship between Forage and Unknown is directly opposed to Travel. Socialize (on the first axis) and Travel (on the second) are most important to explaining

spatial structure, and Rest, Forage, and Unknown are not as important (Figure 4.18). However, Forage is very strongly aligned with the fifth axis of MULTISPATI. High negative eigenvalues can mean that there is local dissimilarity or under dispersion. MULTISPATI results indicate that there are local hotspots of foraging. From these three graphs and the map of the dolphin sightings, Forage explains most of the variance in the SPUE data, and there are areas where foraging happens locally at an intense level. Socialize explains most of the global spatial structure, as it is the primary contributor to the spatial structure on axis one to MULTISPATI. Maps of the behavior types also support this result: Forage happens throughout the study site, but Socialize happens in certain areas (mostly around the islands; Figure 4.19).

*Dolphin and Fish Data:*

Correlations of dolphin behavior MULTISPATI site scores to biotic variables, (kriged) abiotic variables, and (kriged) fish relative abundances for species with significant spatial structures (in seines and in trawls) were performed. There are no correlations of dolphin behaviors to abiotic or biotic variables (Figure 4.20), fish relative abundance from seines (Figure 4.21), or fish relative abundance from trawls (Figure 4.22).

Only three fish species that dolphins consume are species that contribute the most to the loadings of spatial structure in the seines (Table 4.4). Seven species that dolphins consume were top loading species in the trawls (Table 4.5). These are noted, as is whether they are preferentially consumed (P) or negatively selected for consumption (N) based on results in Sarasota Bay, Florida (Berens McCabe et al. 2010). Sand weakfish

(*Cynoscion arenarius*) is the only preferential forage species found in both seines and trawls.

There is a loss of variance in dolphin behavior SPUE from PCA to MULTISPATI, but there is an increase in spatial autocorrelation (Table 4.6). If fish abundance does not correlate with dolphin SPUE site scores that have spatial structure, it is possible that variance (PCA) is a better explanation for dolphin behaviors. Most of the global spatial structure in dolphin SPUE can be explained by nonforaging behaviors, whereas the variance in SPUE itself and local spatial structure can be explained by foraging. Since there were no correlations to local spatial structure, it is possible that a correlation analysis to the PCA site scores may be more informative than to MULTISPATI, because variance in dolphin behavior SPUE may be more important to describing the population rather than spatial structure.

There are no significant correlations of any of the five PCA axes to biotic and abiotic variables (Figure 4.23), to the fish collected in seines (including dolphin prey that have nonsignificant spatial structure; Figure 4.24), or to the fish collected in trawls (including dolphin prey that have nonsignificant spatial structure; Figure 4.25).

Dolphin SPUE variance or spatial structure did not correlate to fish species or environmental variables. However, dolphins may use the areas differently based on a suite of different species rather than individual ones. The cluster analysis of the MULTISPATI results of the seines and the trawls suggested three clusters for each, which are based on the spatial variance as well as the variation in the species abundances. I created polygons based on the outer points of the clusters (convex hull) and coded each

sighting to the cluster that it fell inside. Maps of the seine cluster areas can be seen in Figure 4.26 and trawl clusters can be seen in Figure 4.27.

There are no dolphin sightings in the Suwannee River cluster determined by the seine data. Mann-Whitney *U* tests for the seines showed that there is no significant difference in the distribution of Forage SPUE across the clusters (*p*-value > 0.05). There are significant differences in the distribution of Travel SPUE across the clusters (*p*-value = 0.043); more Travel was found in the offshore areas than alongshore. The other behaviors were only found in one cluster (the offshore cluster): Rest, Socialize, and Unknown. Mann-Whitney *U* tests for the trawls showed that there is no significant difference in the distribution of Forage, Socialize, or Travel SPUE across the clusters (*p*-value > 0.05). Rest and Socialize were only found in one cluster (the offshore cluster).

## DISCUSSION

### *Fish Data:*

This work showed that MULTISPATI is an effective tool to determine spatial structure of fish species in the study area. Marine fish species are not randomly distributed but have a distribution that is structured in space (Pape and Vaz 2014, Mello and Rose 2005). Using MULTISPATI has elucidated what species of fish contribute most to spatial variation (Tables 4.4 and 4.5). The species that contributed most to the variation for seines and for trawls did not overlap, other than sand weakfish (*Cynoscion arenarius*) and pinfish (*Lagodon rhomboides*). Therefore it is important, when analyzing the FIM

data, to consider which species are relevant to the question at hand, as the techniques target different species.

Dray et al (2008) had suggested that lagged scores (weighted averages of the neighboring values) should be used for spatial classification of the sites, as the scores are a reflection of how similar sites are to their neighbors. Cluster analysis for the seines and the trawls suggested three clusters each (Figures 4.10 and 4.14). MULTISPATI results effectively incorporated both the spatial structure and the fish abundance variation in the seine and trawl data, and top loading species grouped out into three distinct groups (Figures 4.8 and 4.12).

Correlations of the MULTISPATI axes to environmental variables indicated that there are habitat variables that can explain the spatial structure in fish. Variables that were significant for both trawls and seines were salinity, pH, Secchi depth, and average depth. More saline waters have a higher pH, and areas with low Secchi depth correspond to areas with higher freshwater input because of sedimentation in the Suwannee River (Mason 1991). Additionally, the area of the Cedar Keys is relatively shallow. Because of the large freshwater input from the Suwannee River (a blackwater river that discharges about 4.7 million gallons per minute, on average; Bledsoe and Phlips 2000), nearshore areas that are shallow are also heavily sedimented and also have low Secchi disk depth. These correlated environmental variables explain the clusters well: freshwater, brackish, and saltwater areas.

*Dolphin Data:*

From this analysis it is likely that significant spatial structure in behavior SPUE

were found in only one test (Table 4.3) because the number of sightings per month and per field season were too low to have power. It is clear that there are differences in a classic PCA test vs. MULTISPATI when the field seasons are combined. Forage is the dominant contributor to the last negative axis in MULTISPATI. The last axis can show local structure such as dissimilarity or avoidance. Therefore, Forage can be seen as the primary contributor to the variance in SPUE in the data, whereas Socialize is the primary contributor to global positive spatial autocorrelation. The large negative autocorrelation for Forage indicates that dolphins can forage intensely in one location but not as much in areas next to it, i.e., that there are high local variations in SPUE due to foraging. The PCA eigenvalues, which explain proportions of the variance, do not have a clear cutoff point where one can make a decision on how many axes to retain (Figure 4.7). Forage still has the highest explanation of the variance on axis one, though: in the graphical representation of the second and third axes of PCA (Figure 4.17). Forage has very little variance on axis two and has more so on axis three. Therefore, the conclusion remains that Forage explains most of the variance in SPUE.

*Dolphin and Fish Data:*

There was no correlation between dolphins and the kriged habitat variables (Figure 4.21) or kriged relative abundances of fish species (Figure 4.14) for the seines or for the trawls (Figures 4.22 and 4.23) using either PCA or MULTISPATI to explain the dolphin behaviors. There are several reasons this could be the case.

Foraging is scattered throughout the site, but Social and Travel are clustered more in areas around the islands in Zone 3 (Figure 4.19). Therefore it is likely that there is no

correlation to fish because most global spatial variation in dolphins is due to nonforaging activities.

In the case of the habitat variables, this could be a situation where spatial scale is important. The benthic area of the study site is clearly heterogeneous (Figure 4.1), and locations of sightings can have very different characteristics depending on the scale used to measure the habitat data (the point, 0.2 $nm^2$ grid, or larger). Dolphins have low costs of locomotion (Williams 1999), therefore they have the ability to travel large distances daily. The scale at which the variables were taken were at a 0.2 $nm^2$ (nautical miles squared) grid. It is possible that the spatial scale was too fine to reveal meaningful detail. The abiotic habitat variables (pH, salinity, temperature, etc.) were measured over the whole field seasons but when this data was combined, it likely muddled the analysis. For example, the water temperature in December 2008 averaged 15.8 C, but in August 2008 it averaged 29.0 C. This is nearly a twofold increase, and because sampling sites are randomly sampled, the spatial pattern of temperature when the field seasons are combined would also present as random. However, there was no significant spatial structure in any temporal period other than when the field seasons were combined. This is probably due to lower sightings per month, and the data only became significant when the sample size issue was resolved by combining the data. In order to do a seasonal analysis, multiple field seasons would be required to increase the sample size. Additionally, Torres (2007) did find that despite the spatial scale issues with dolphin and fish abundances, the temporal scale of the water quality sampling she did was enough to be able to predict dolphin distribution. This was because she took data at each dolphin

sighting as well as fish sampling locations. Therefore, fine scale variability was possible and the interpolated maps of water quality sampling had higher resolution than in this study. However, she did not do a spatial statistics analysis (she used generalized additive models).

Scale-dependent relationships between predator and prey are not unique. Aside from Torres' (2007) study of Florida Bay bottlenose dolphins, it has been studied in multiple other species. In the yellow-nosed albatross (*Thalassarche carteri*) habitat use differed depending on the spatial scale. At the macro-scale (oceanic basin), birds foraged in pelagic, subtropical waters. Birds traveled to areas where primary productivity was enhanced at large scale, but at a smaller scale, they increased search effort based on sea surface height and chlorophyll concentrations (Pinaud and Weimerskirch 2005). Female Antarctic fur seals (*Arctocephalus gazella*) respond to small scale changes in habitat variables, but they tend to forage within large areas that have high primary productivity, even though this positive relationship is not present at the smaller scale (Guinet et al. 2001). Murres (*Uria* spp.) actively track their prey (capelin) at different scales (Fauchald et al. 2000) and at the smallest scales (less than 3 km) there is no overlap of predator and prey. In all of these studies, the spatial scale of the predator and prey affected whether a relationship was found.

In the case of the fish species, this too may be a scale issue, as well as a habitat preference on the part of the fish. Smaller fish (the seines and trawls tend to be biased towards catching smaller fish) cannot travel as far as dolphins, and as seen in the results, all of the temporal scales measured showed significant spatial structure. Torres (2007)

found that the predictive capacity of dolphin habitat use did not increase by including prey species and concluded that it was likely due to the too-small scale of the fish collection (50 $m^2$ grids). Expanding the relative abundance of fish and dolphin SPUE to a coarser spatial scale (larger than 0.2 nm2 grids) may show spatial patterns. One option is to use the zones I used to create the transect lines. They were created to accommodate the directionality of the shoreline, but do have different general features (Figure 4.2).

Of the 50 species for seines and 34 for trawls that had significant spatial structure for both field seasons combined (Appendix B, Tables B.1 and B.2), only 11 are known to be consumed by dolphins, and of those 11, only 2 are preferentially consumed (Berens McCabe et al. 2010). Some of the fish species dolphins are known to consume are not caught in the seines or trawls, or they do not have significant spatial structure. Mullet species (*Mugil* spps) are an example of this. They are caught in seines but not consistently in trawls. Mullet are commonly known for having a jumping reflex and jump out of the gear. Jack (*Caranx hippos*) is another tightly schooling fish that is consumed by dolphins. They are also very fast and escape nets. Schooling fish can reduce the effect of the abundance estimates in the study area, as they are in high abundance contributions when caught, but can also give false negatives if they are not set on by the gear. The large negative autocorrelation in the MULTISPATI results for Forage indicates that dolphins forage intensely in a given location but not near it. This could be because dolphins are foraging on schooling fish, which are not well represented in the fish-collection methods. Guinet et al. (2001) found a negative relationship between the occurrence of forage fish and the number of individual fish sampled per species, despite the fact they sampled in

the same area and during the same time of night as the fur seals. They suggest that one reason this is so is because the catchability of fish species was biased, therefore the sample population was not truly representative of their relative abundance.

Aside from spatial and temporal scale considerations, many of the top loading species of fish (Tables 4.4 and 4.5) are freshwater, and while the inshore surveys covered freshwater inputs (Figure 4.5), dolphin sightings were not nearly as frequent there (Figure 4.19). These fish species were not found in marine water samples and therefore had zero values when kriged to dolphin survey points.

Correlating dolphin behavior to the polygons created by the cluster areas also had similar results. For both seines and trawls there was no significant difference in the distribution of Forage SPUE across the clusters. The only significant difference was with Travel SPUE in the seine clusters; most Travel happened in the offshore cluster (Figure 4.27). Rest and Socialize were only found in one cluster for the seines and for the trawls: the offshore clusters (Figures 4.26 and 4.27). What I can determine from this is that there are areas where dolphins gather for socializing, traveling, and resting, and they seem to be in the areas surrounding the islands. Again, this does support both the PCA and MULTISPATI analyses, which showed that Forage is not positively spatially structured, but Socialize and Travel are. The clusters are determined both spatially and by variance in the fish abundance.

Benoit-Bird and Au (2003) used an echosounder to take data on spinner dolphins (*Stenella longirostris*) and prey densities at the same time. While fish species cannot be determined this way, it may be a more accurate way to quantify the fish densities where

dolphins are found and to see if there is a relationship rather than relying on kriging catch data. Additionally, my study simply kriged the fish relative abundances across the study area. Because fish select for habitats based on multiple parameters, it may be more accurate to use ArcGIS to calculate the relative abundance of fish based on the habitats they are found over (e.g., if they are in seagrass beds more than tidal flats, the interpolation method should take this into account and interpolate higher relative abundances in seagrass beds than tidal flats) and use that information to interpolate across the field site. Therefore the number of fish at a site would equal the contributions of different habitat combinations to the total population size (Pape and Vaz 2014; Dahlgren et al. 2006 calls this the effective fish habitat).

Bottlenose dolphins do not choose prey based on taxonomy but on functional traits (e.g., the energetic costs of foraging strategies can drive prey selection, including caloric content; Spitz et al. 2014). Functional traits are those that affect the how the species function in an ecosystem by influencing the performance of the species (Menzes et al. 2010). These species traits are not independent of each other, and it has been suggested to group species instead by complex adaptations such as life-history strategies (Verberk et al. 2008). Parsing the fish-collection data to categorize species by these traits rather than their taxonomy may be more relevant to interpreting predator-prey relationships. Spitz et al. (2014) did this with several different marine mammal predators: Prey were classified due to morphological characteristics, and prey of marine mammals were linked to these characteristics. They also found that prey quality—caloric content—is more important than quantity (Spitz et al. 2014). The FWC FIM program does take

some data on the health of fish species, but they usually only do this for commercially or recreationally important ones. It is possible that the fish species, when grouped by traits, may show correlations to dolphin spatial structure. However this requires much more information about the fish species, and not all of this information is known. Caloric content of fish is obtainable in future studies.

This analysis separated the fish by species. It is possible that a better approach would be to calculate relative abundances based on functional traits. Basing information on trait morphology rather than species can get show who is sensitive to bottom-up forcing events (Spitz et al. 2014). Biotic and abiotic factors can drive species choice of habitats and different scales (Gruss et al. 2011, Aarts et al. 2013). There are several ways to determine functional traits, two of which are as follows:

1) Winemiller (1989) suggests seven parameters to categorize functional traits. Some of these are collected by the FWC, but several are not, and while some may be found in the literature, there are some species that not all information is known. Some of these traits would be relevant to dolphins, such as size at maturity, or maximum size, as they can relate to caloric content or other relevant parameters, such as catchability.

2) Environmental variables could be retained in relation to species and what life stage they are in. Calculating the density based on biotic/abiotic factors would be more accurate. The ”number“ of fish would reflect the relative contributions of different habitat combinations (Pape and Vaz 2014).

## CONCLUSIONS

In conclusion, this study showed that MULTISPATI is a valid tool for describing spatial autocorrelation in fish distributions, but spatial scale is important to consider when analyzing the data for larger more mobile species such as dolphins. Additionally, while combining data sets to change the temporal scale can lead to significant spatial structure in dolphins, this may be the opposite case for abiotic factors. The use of abiotic factors or potential prey distribution to describe dolphin distribution must be approached cautiously, as the incorrect scale may lead to erroneous conclusions.

A future goal is to identify the most appropriate scales that account for species-environmental variations, and this could change with the scale of the observations (Dray et al. 2012, Dungan et al. 2002, and Legendre et al. 2009). Testing spatial structures at multiple scales allows hypotheses about how species diversity is maintained or evolves (Dray et al. 2012).

Future work should include increasing the spatial scale of the analyses for fish, abiotic and biotic variables, and dolphin distribution. It is possible that increases in spatial scale may lead to elucidation of possible reasons for why dolphins distribute themselves the way that they do. Fish abundances should be interpolated to dolphin points using biotic and abiotic factors as weights. It may also be beneficial to group fish into relative abundances by functional traits rather than taxonomically, since traits are undoubtedly how dolphins choose their prey.

TABLES

| BIOLOGICAL | PHYSICAL | HABITAT |
|---|---|---|
| Unique numeric identifier for every species that FIM might encounter | Average dissolved oxygen in water at sampling site | Bottom type over which the sample was taken |
| The number of a particular species collected | Average salinity at sampling site | Bottom vegetation over which the sample was taken |
| The sex of the species collected | Average water pH at sampling site | Gross overview of bottom habitat and substrate type |
| Length measurement of Xth specimen | Average water temperature at sampling site | Gross overview of shore habitat type |
| Number of animals measured at a given size class | Latitude and longitude where the sample was taken | Tidal phase when sample was collected |
| Size class designator when multiple size classes of a species were measured | Depth where the sample was taken when sampling ended | Percent composition of specific bottom vegetation |
| Amount of bycatch (nonfish species) in the sample | Depth where the sample was taken when sampling started | Percentage of the bottom covered by any type of bottom vegetation |
| Bycatch type collected (nonfish species) | Gear used to collect that sample | The habitat stratum sampled during stratified-random sampling |

Table 4.1: A subset of the variables measured at each fish sampling point. Data are collected by the FWC FIM program.

| Gear Type | Year | Time Scale | Number of Species | Number of Sites | *p*-value |
|---|---|---|---|---|---|
| Seines | 2008 | August | 24 | 49 | *0.001* |
| | | September | 29 | 49 | *0.001* |
| | | October | 15 | 44 | *0.001* |
| | | November | 8 | 44 | *0.019* |
| | | December | 6 | 29 | *0.001* |
| | | Field Season | 41 | 222 | *0.001* |
| | 2010 | April | 6 | 33 | *0.001* |
| | | May | 6 | 37 | *0.001* |
| | | June | 11 | 30 | *0.001* |
| | | July | 11 | 25 | *0.001* |
| | | August | 19 | 49 | *0.001* |
| | | Field Season | 41 | 235 | *0.001* |
| | 2008 and 2010 | Both Field Seasons | 50 | 474 | *0.001* |
| Trawls | | Both Field Seasons | 34 | 143 | *0.001* |

Table 4.2: Number of species and sites used for each MULTISPATI analysis of temporal scale for seines and for trawls after using Moran's *I* to reduce the data to significant species. Significant *p*-values in italics indicate that the analysis indicated strong spatial structures within the data.

| Year | Temporal Scale | Sightings | *p*-value |
|---|---|---|---|
| 2008 | Field Season | 48 | 0.285 |
| | August | 1 | NA |
| | September | 28 | 0.939 |
| | October | 19 | 0.182 |
| 2010 | Field Season | 97 | 0.421 |
| | April | 12 | 0.203 |
| | May | 41 | 0.287 |
| | June | 25 | 0.233 |
| | July | 19 | 0.684 |
| 2008 and 2010 | Both Field Seasons | 145 | *0.032* |

Table 4.3: *p*-values of the MULTISPATI analysis by temporal scale on dolphin data. Sightings is the number of dolphin sightings, on effort, for the time scale. Significant *p*-values are in italics. In November and December 2008, transects and inshore surveys were conducted but no dolphins were seen on effort. There was only one sighting on effort in August 2008 (we started transects and surveys the last half of the month); therefore there wasn't enough data to conduct a spatial analysis.

| Scientific Name | Common Name | Cluster | | | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | Marine | Freshwater | Brackish | |
| *Anchoa mitchilli* | Bay anchovy | Y | Y | Y | Y | Y | Y | |
| *Ariopsis felis* | Hardhead catfish | | | | Y | | Y | |
| *Bairdiella chrysoura* | Silver perch | Y | Y | | Y | Y | Y | |
| *Callinectes sapidus* | Blue crab | Y | Y | Y | Y | | | |
| *Chilomycterus schoepfii* | Striped burrfish | | Y | | Y | | | |
| *Cynoscion arenarius* | Sand weakfish | Y | Y | | Y | | Y | P |
| *Eucinostomus harengulus* | Tidewater mojarra | Y | Y | Y | Y | | Y | |
| *Eucinostomus spp.* | Mojarra spps. | Y | Y | Y | Y | | Y | |
| *Fundulus grandis* | Gulf killifish | Y | Y | | | Y | Y | |
| *Fundulus seminolis* | Seminole killifish | Y | Y | Y | | Y | Y | |
| *Gambusia holbrooki* | Eastern mosquitofish | Y | Y | Y | | Y | Y | |
| *Gobiosoma bosc* | Naked goby | Y | Y | Y | Y | | Y | |
| *Labidesthes sicculus* | Brook silverside | Y | | Y | | Y | | |
| *Lagodon rhomboides* | Pinfish | Y | Y | Y | Y | Y | Y | N |
| *Leiostomus xanthurus* | Spot croaker | Y | Y | | Y | | Y | N |
| *Lepomis auritus* | Redbreast sunfish | | | Y | | Y | | |
| *Lepomis macrochirus* | Bluegill sunfish | Y | | Y | | Y | | |
| *Lepomis microlophus* | Redear sunfish | | | Y | | Y | | |
| *Lepomis punctatus* | Spotted sunfish | | | Y | | Y | | |
| *Lepomis spp.* | Sunfish spps. | | | Y | | Y | | |

| Scientific Name | Common Name | Cluster | | | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | Marine | Freshwater | Brackish | |
| *Menidia spp.* | Silverside spps. | Y | Y | | Y | Y | Y | |
| *Menippe spp.* | Stone crab spps. | Y | Y | | Y | | | |
| *Micropterus salmoides* | Largemouth black bass | Y | | Y | | Y | | |
| *Monacanthus ciliatus* | Fringed filefish | | Y | | Y | | | |
| *Pomoxis nigromaculatus* | Black crappie | Y | | Y | | Y | | |
| *Syngnathus floridae* | Dusky pipefish | | Y | | Y | | | |
| *Trinectes maculatus* | Hogchoker | Y | Y | Y | Y | Y | Y | |

Table 4.4: Fish species that have the highest loadings for the first two MULTISPATI axes in the two field seasons combined for seines. Habitat information (what type of water they inhabit) is from www.fishbase.org. In the column "Seen in Dolphin diet?" from Berens-McCabe et al. (2010), P indicates positive selection, and N indicates negative selection for the species based on research in Sarasota Bay, Florida. Blank spaces indicate no information is available as to whether bottlenose dolphins consume these species. Cluster number refers to in what cluster of sampling sites the species were found.

| Scientific Name | Common Name | Cluster | | | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | Marine | Freshwater | Brackish | |
| *Acanthostracion quadricornis* | Scrawled cowfish | | Y | Y | Y | | | |
| *Ameiurus catus* | White catfish | Y | | | | Y | | |
| *Anchoa hepsetus* | Broad-striped anchovy | Y | Y | Y | Y | | Y | |
| *Chaetodipterus faber* | Atlantic spadefish | Y | Y | Y | Y | | Y | |
| *Citharichthys macrops* | Spotted whiff | | | Y | Y | | | |
| *Cynoscion arenarius* | Sand weakfish | Y | Y | Y | Y | | Y | P |
| *Dasyatis sabina* | Atlantic stingray | Y | Y | Y | Y | Y | Y | |
| *Etropus crossotus* | Fringed flounder | Y | Y | Y | Y | | Y | |
| *Farfantepenaeus duorarum* | Marine shrimp | Y | Y | Y | Y | | Y | |
| *Ictalurus punctatus* | Channel catfish | Y | | | | Y | | |
| *Lagodon rhomboides* | Pinfish | Y | Y | Y | Y | Y | Y | N |
| *Menticirrhus americanus* | Southern kingcroaker | Y | Y | Y | Y | | Y | N |
| *Ogcocephalus cubifrons* | Batfish | Y | Y | Y | Y | | | |
| *Oligoplites saurus* | Leatherjacket | Y | | | Y | | Y | |
| *Orthopristis chrysoptera* | Pigfish | | Y | Y | Y | | Y | N |
| *Prionotus scitulus* | Leopard searobin | | Y | Y | Y | | | N |
| *Prionotus tribulus* | Bighead searobin | Y | Y | Y | Y | | Y | N |
| *Synodus foetens* | Inshore lizardfish | | Y | Y | Y | | Y | N |

Table 4.5: Fish species that have the highest loadings for the first two MULTISPATI axes in the two field seasons combined for trawls. Habitat information (what type of water they inhabit) is from www.fishbase.org. In the column ”Seen in Dolphin diet?” from Berens-McCabe et al. (2010), P indicates positive selection, and N indicates negative selection for the species based on research in Sarasota Bay, Florida. Blank spaces indicate no information is available as to whether bottlenose dolphins consume these species. Cluster number refers to in what cluster of sampling sites the species were found.

| | Axis | Variance | Moran's I |
|---|---|---|---|
| PCA | 1 | 1.14 | 0.019 |
| | 2 | 1.06 | 0.090 |
| | 3 | 1.04 | 0.031 |
| | 4 | 1.01 | -0.012 |
| | 5 | 0.74 | 0.048 |
| | | | |
| MULTISPATI | 1 | 1.06 | 0.191 |
| | 2 | 1.01 | 0.117 |
| | 3 | 0.87 | 0.038 |
| | 4 | 1.01 | -0.030 |
| | 5 | 1.05 | -0.142 |

Table 4.6: Demonstration of the difference between traditional PCA and MULTISPATI using Dolphin behaviors. Values are relative. Between the axes of the different analyses, there is a loss of variance in MULTISPATI but a gain of spatial autocorrelation.

FIGURES

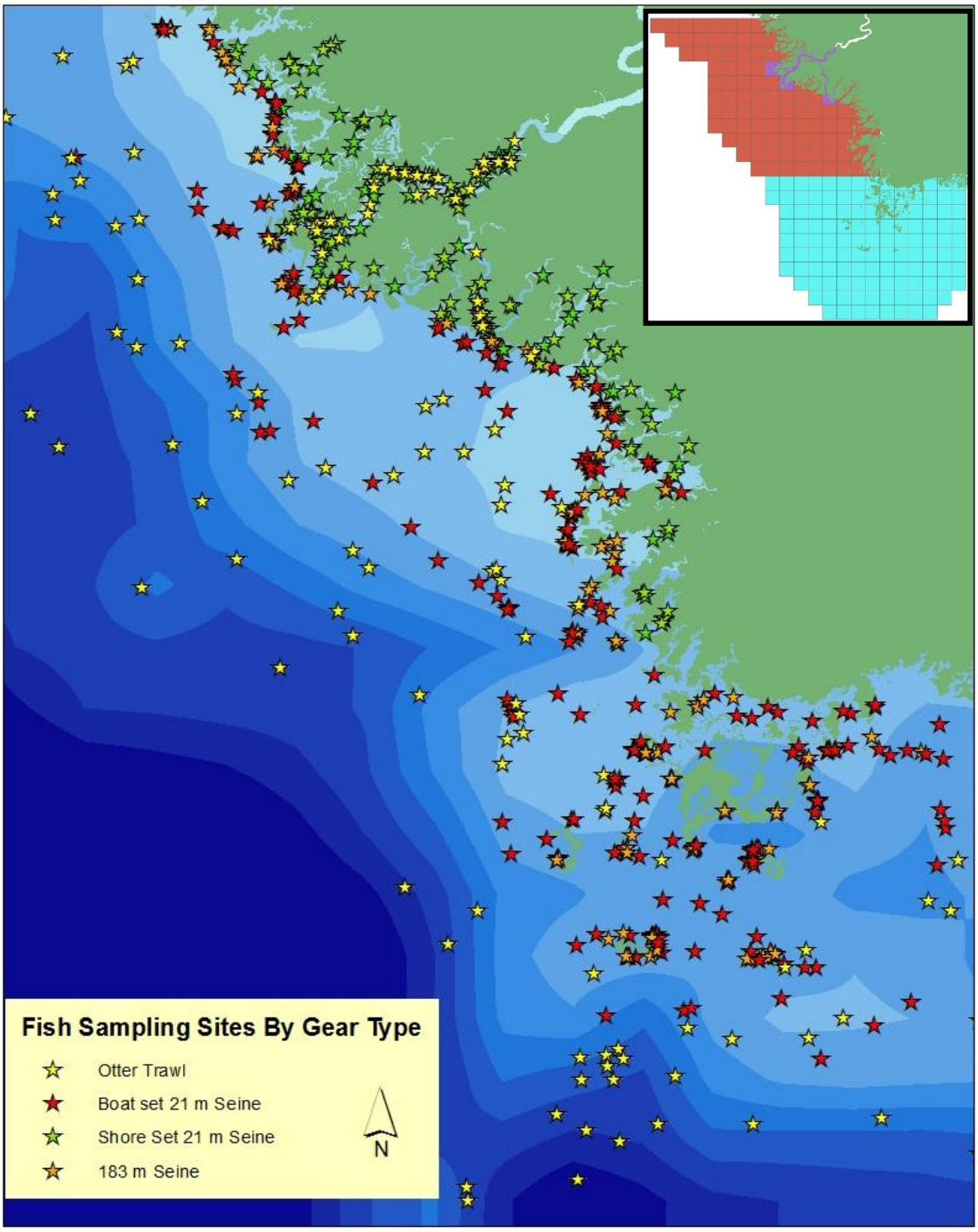



Figure 4.1: Map of the FIM fish sampling sites by gear type for both field seasons combined. Inset is the sampling sites with the three sampling zones determined by the FIM program: purple is the inshore area, and the blue and red areas are geographically defined bay areas.

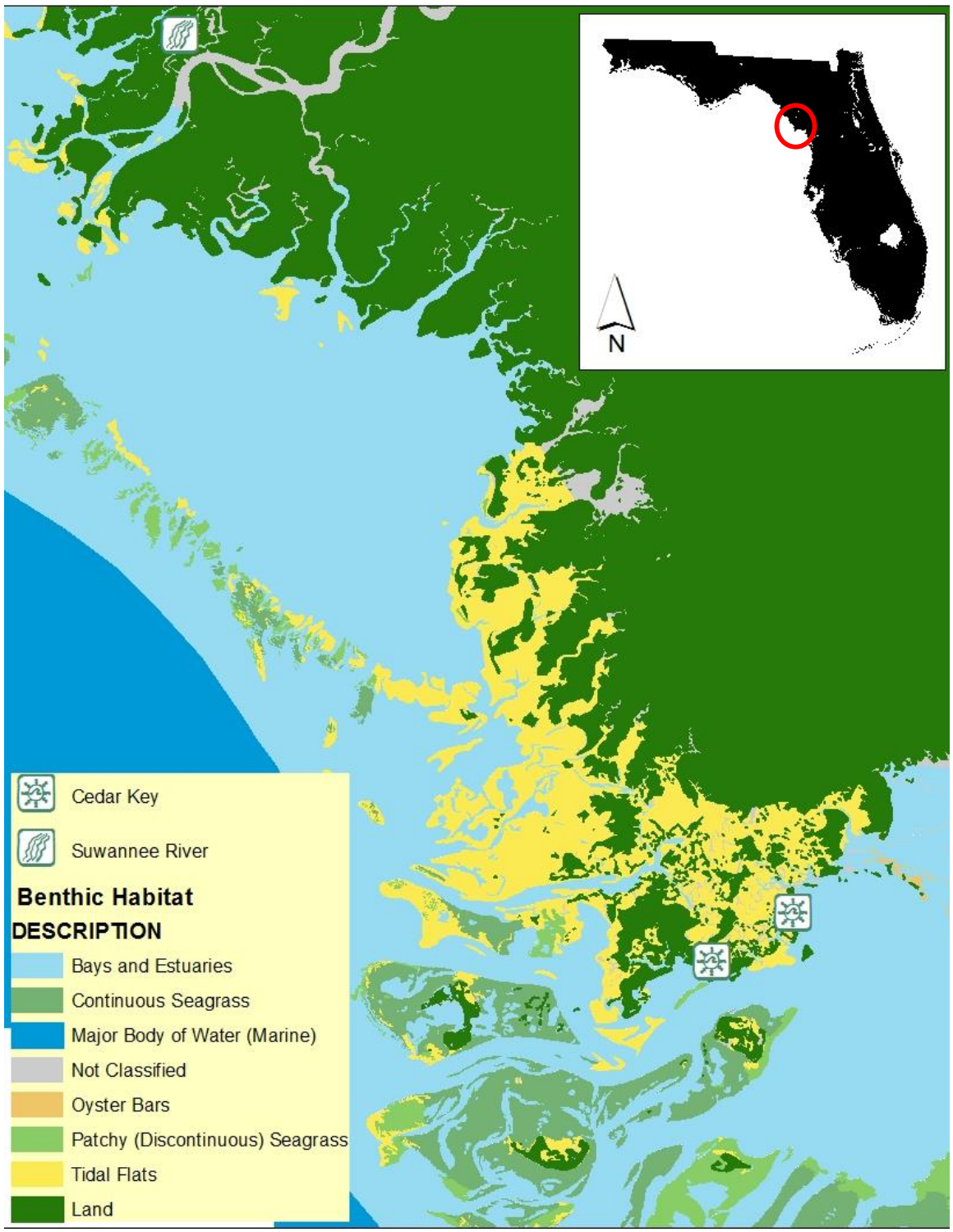



Figure 4.2: Map of study area with benthic areas defined from the Cedar Key Benthic 2 shapefile. Inset is the state of Florida with the general area of the study site circled in red.

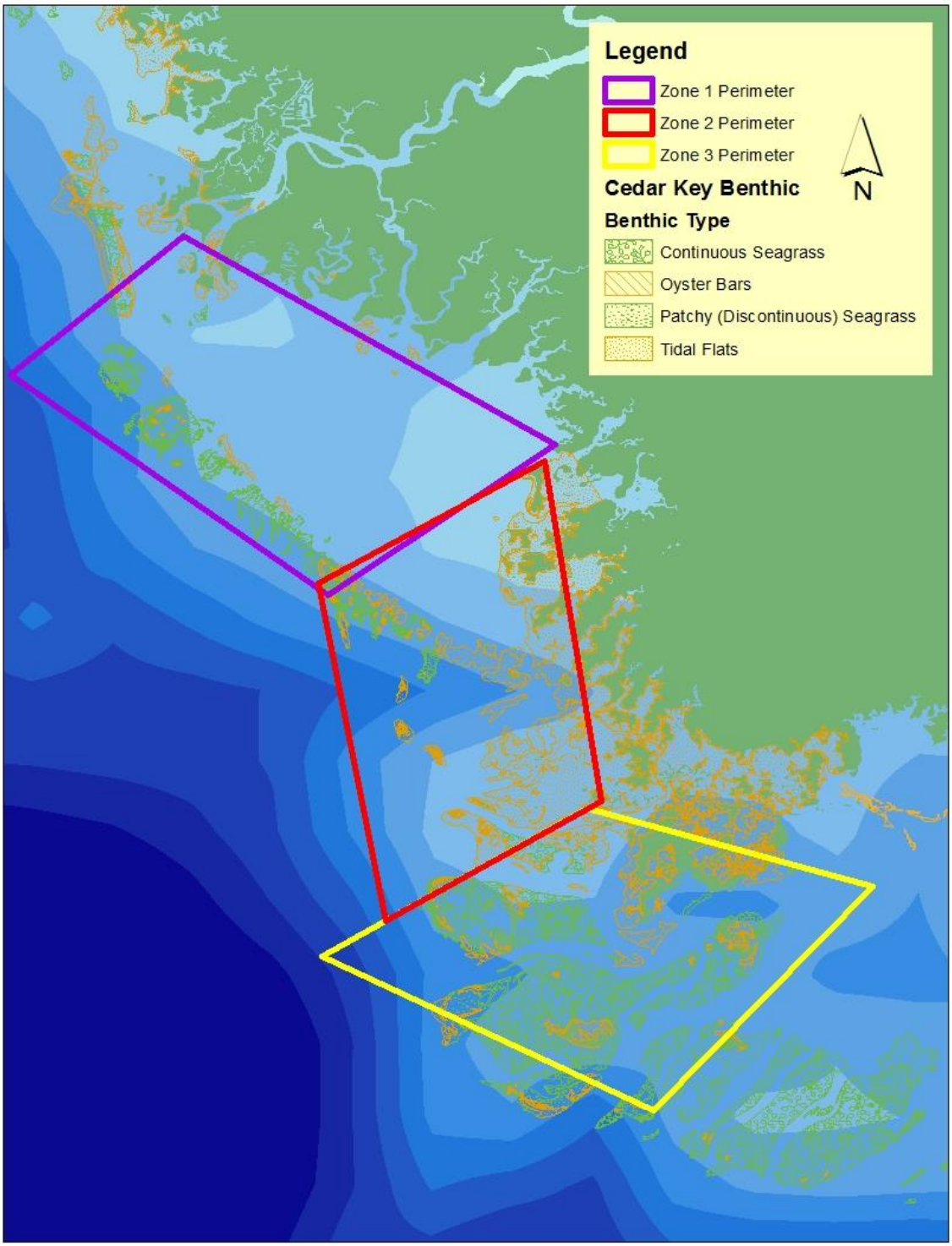



Figure 4.3: Zones of the study area for dolphin surveys. Zone 1 is most northern and includes the Suwannee River. Zone 3 is most southern and includes most of the islands of the Cedar Keys. Zone 2 is in the middle and is a mix of freshwater inputs from creeks and islands.

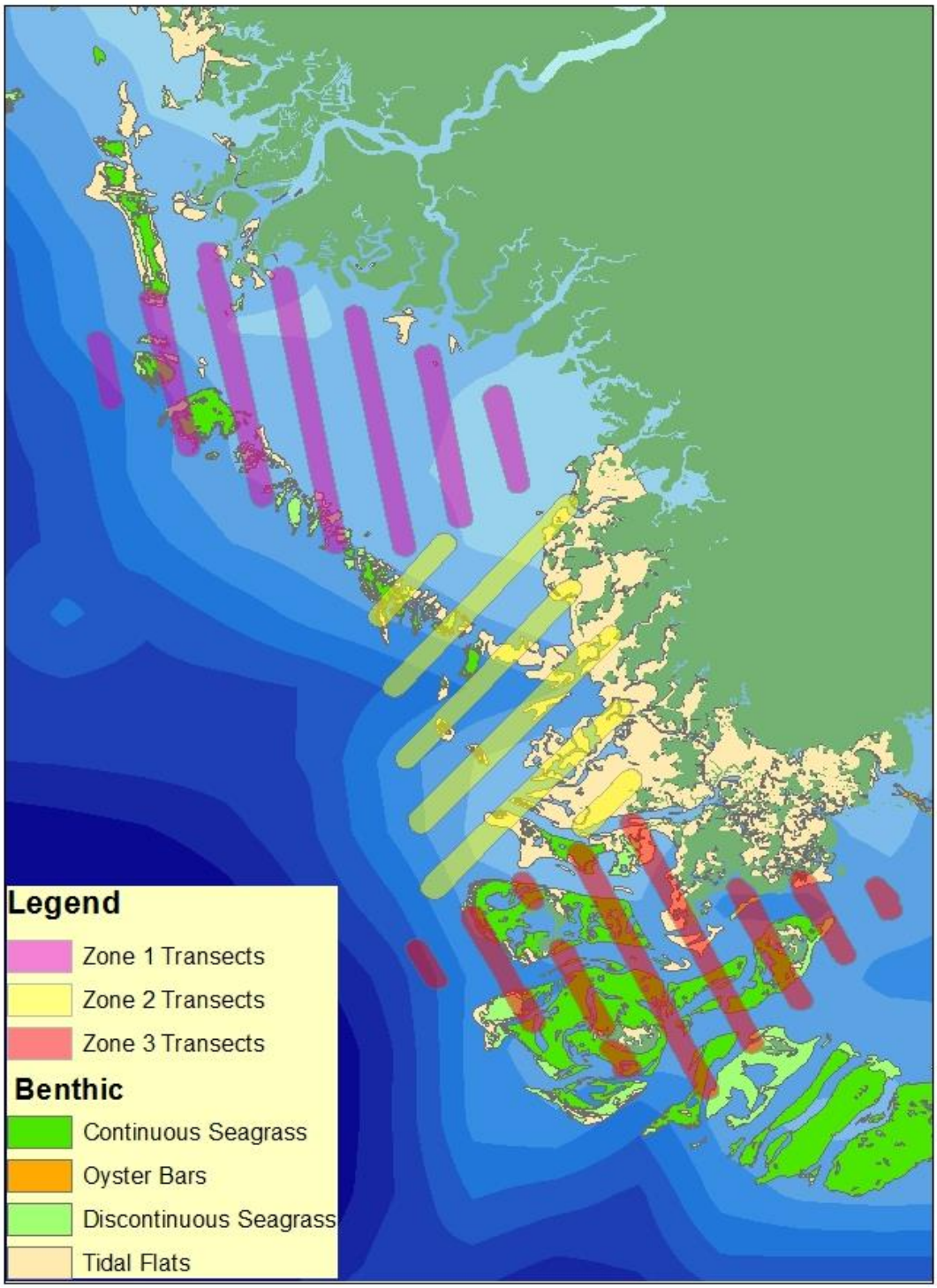



Figure 4.4: Transects divided into Zones (1, 2, and 3) in the study site. Transects were run with a 250 m sighting distance on each side of the line. Transects were run at a 45 degree angle to the directionality of the shoreline. Here this sighting area is represented by bands.

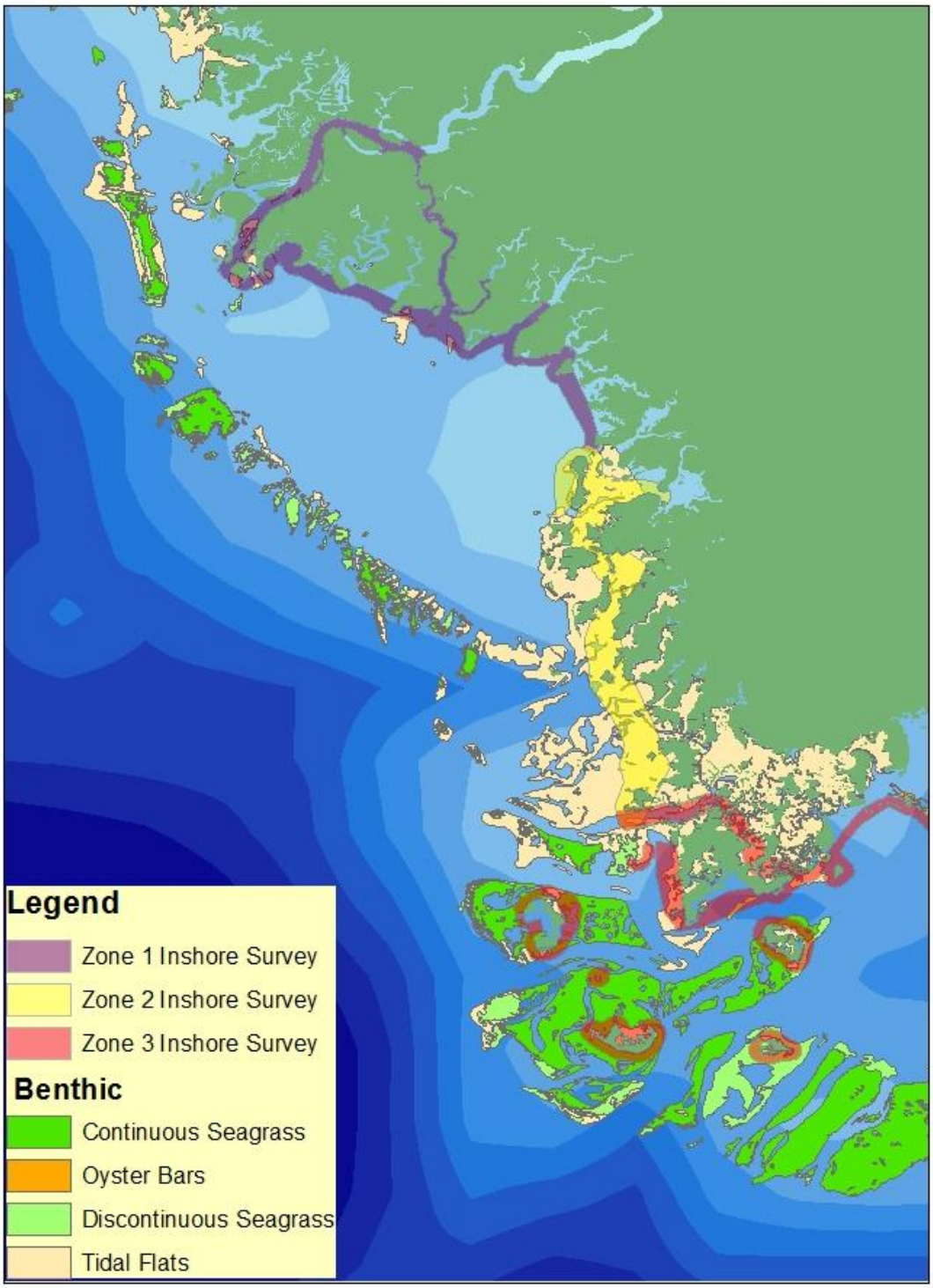



Figure 4.5: Systematic Inshore Survey (SIS) coverage area for the three zones. A SIS ran 250 m from shore with one observer looking in towards the shore. The 250 m survey area is represented here with bands.

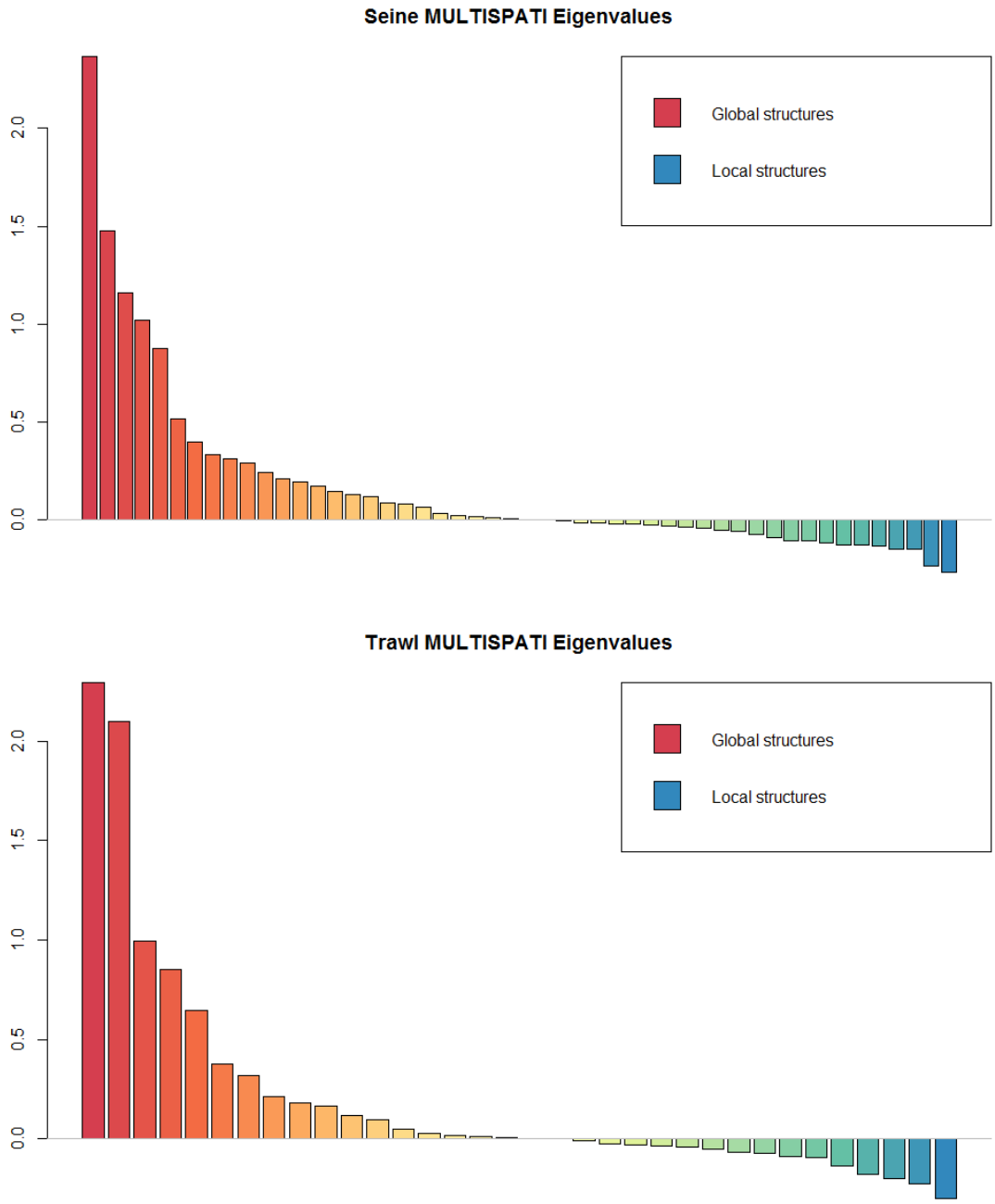



Figure 4.6: Eigenvalue bar plots from MULTISPATI of seines (top) and trawls (bottom). Values are relative. Global structures (positive spatial autocorrelation) are found on the first positive axes. Local stuctures (negative spatial autocorrelation) are found on the last negative axes. For seines, the first and second axes explain 19.26% and 12.01% of the spatial variance in the data. For trawls, the first and second axes explain 22.87% and 20.96% of the spatial variation in the data.

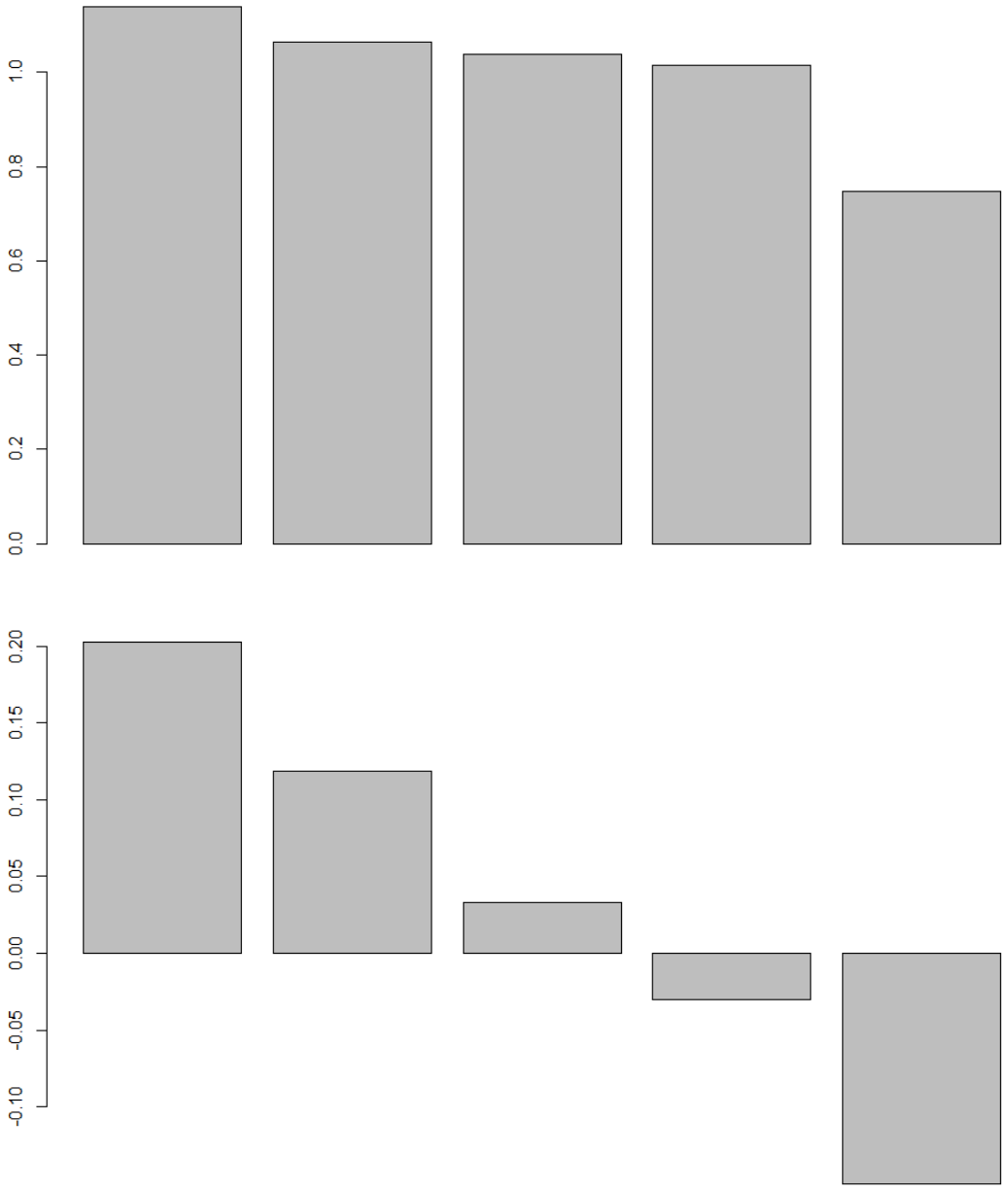



Figure 4.7: Eigenvalue bar plots from PCA analysis (top) and MULTISPATI analysis (bottom) of the five axes for dolphin behavior SPUE. For PCA, in order of axis, the percent variance explained is 22.77, 21.26, 20.75, 20.29, and 14.93. For MULTISPATI, in order of axis, the percent variance explained is 37.90, 22.21, 6.13, 5.68, and 28.06.

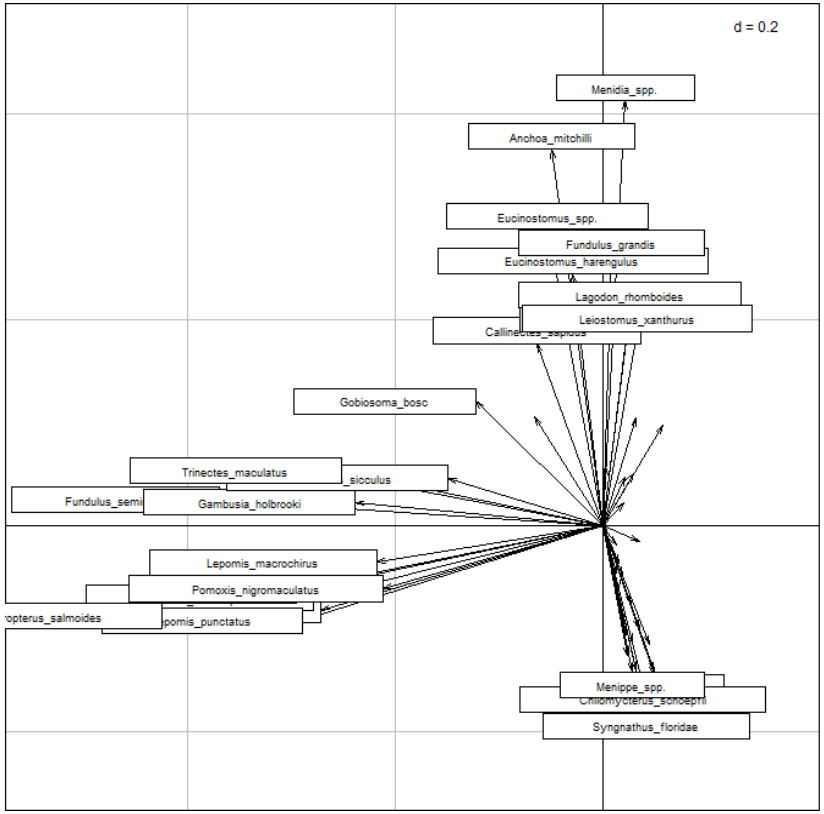



Figure 4.8: Coefficients of variables (fish species) on the first two axes of MULTISPATI both field seasons combined for seines. The first and second axes explain 19.26% and 12.01% of the spatial variance in the data. Only top loading species are labeled. Mesh size of the grid is indicated by "d."

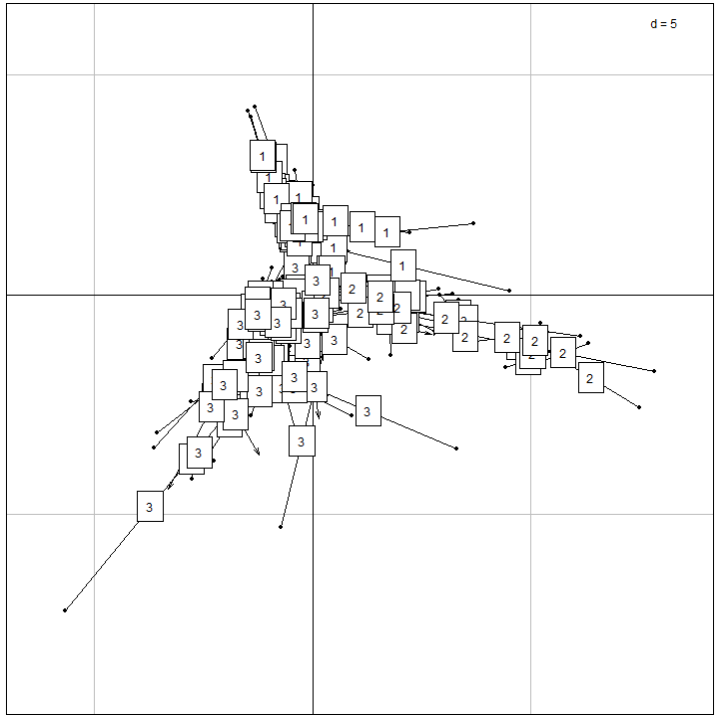



Figure 4.9: Link between scores and lagged scores for seine sites. The bottom of the vector is the score and the head is the lagged score. A long vector means that there is spatial discrepancy while a short one means that there is local spatial similarity. Sites are coded by suggested cluster number, which is based on the lag score of the site. Lag scores are scores of the site averaged with the nearest neighbor scores and weighted by the spatial connection matrix. Mesh size of the grid is indicated by "d."

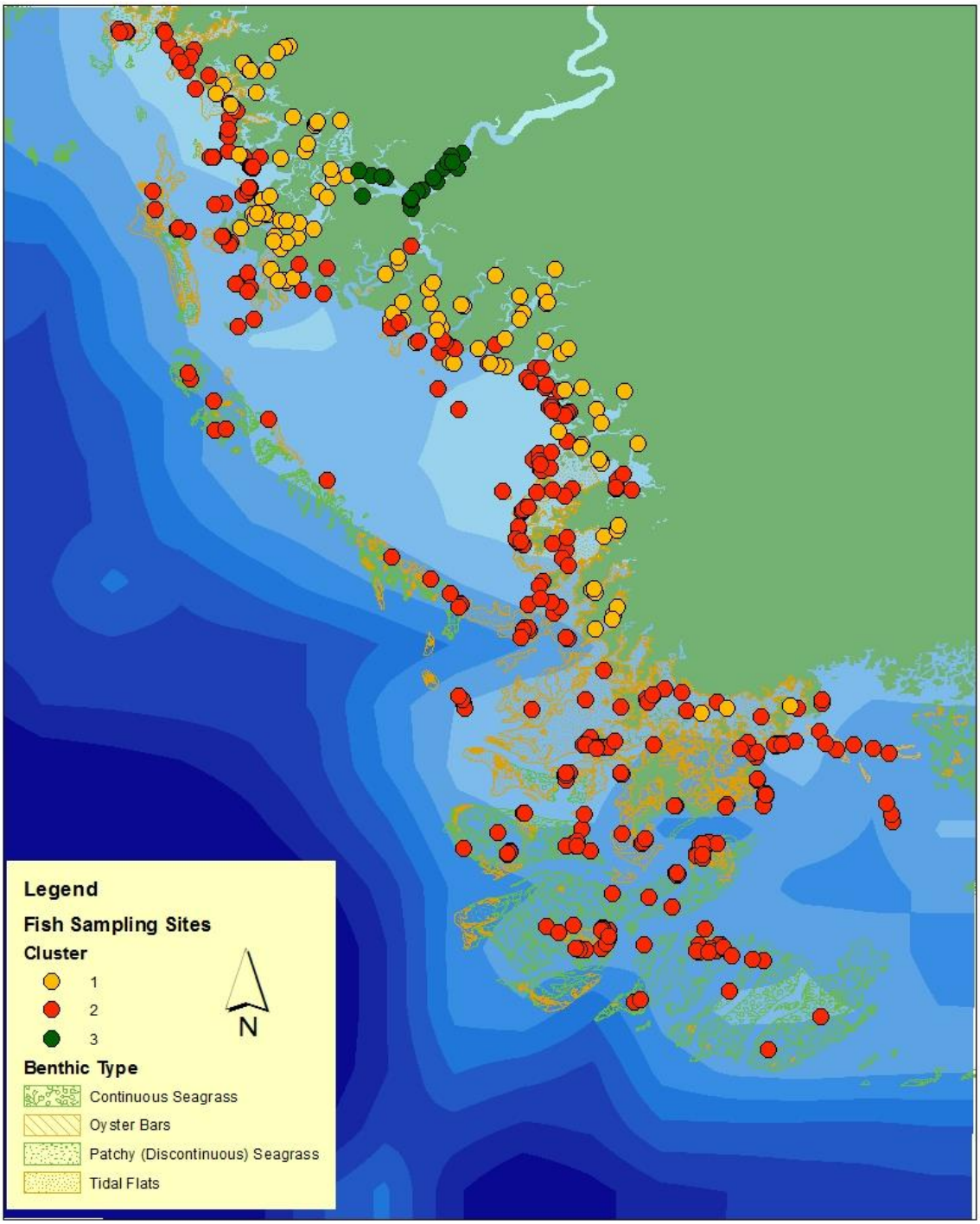
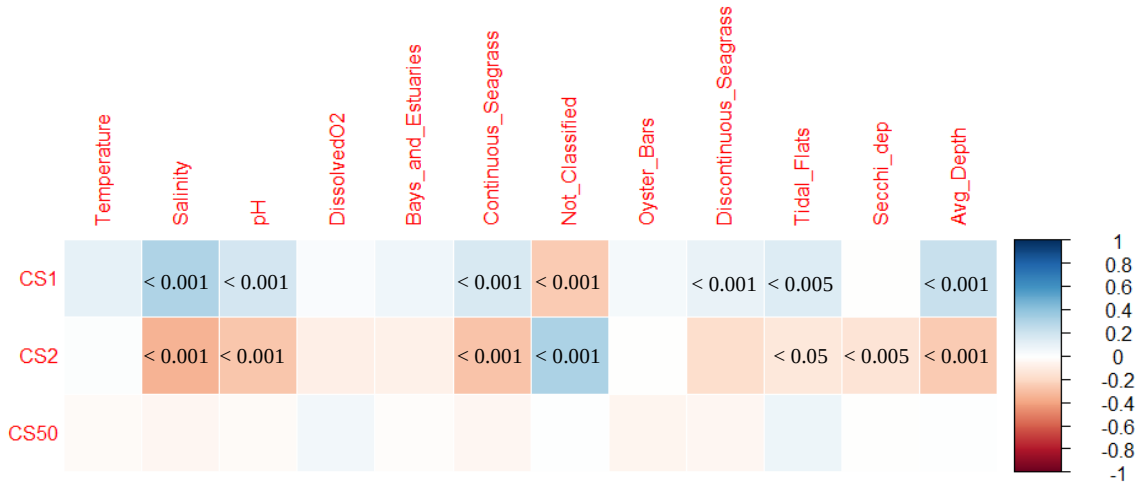



Figure 4.10: ArcGIS map of seines clustered by the kmeans method with *NbClust* in R. Green sites are almost entirely in the Suwannee River. Yellow sites are alongshore; orange sites are more offshore.




| MULTISPATI Axis to Variable | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-Salinity | 0.217 | 0.301 | 0.381 | 2.16E-10 |
| CS2-Salinity | -0.419 | -0.342 | -0.261 | 5.12E-13 |
| CS1-pH | 0.092 | 0.181 | 0.267 | 0.000306 |
| CS2-pH | -0.352 | -0.271 | -0.185 | 1.86E-08 |
| CS1-Continuous Seagrass | 0.077 | 0.166 | 0.252 | 0.000888 |
| CS2-Continuous Seagrass | -0.362 | -0.282 | -0.197 | 3.33E-09 |
| CS1-Not Classified | -0.339 | -0.258 | -0.172 | 6.89E-08 |
| CS2-Not Classified | 0.231 | 0.314 | 0.393 | 4.12E-11 |
| CS2-Discontinuous Seagrass | -0.265 | -0.179 | -0.091 | 0.000306 |
| CS1-Tidal Flats | 0.055 | 0.144 | 0.231 | 0.004364 |
| CS2-Tidal Flats | -0.216 | -0.129 | -0.039 | 0.012643 |
| CS2-Secchi Depth_ | -0.234 | -0.148 | -0.059 | 0.003709 |
| CS1-Avg_Depth | 0.142 | 0.229 | 0.313 | 1.88E-06 |
| CS2-Avg_Depth | -0.334 | -0.252 | -0.166 | 1.27E-07 |

Figure 4.11: Plot of correlations using Kendall's tau and table of significant correlations for the first two axes of the site scores (variance in fish relative abundance) to environmental variables for seines. Lower confidence interval, r, upper confidence interval, and *p*-value are reported. Blue indicates positive correlation; red is negative.

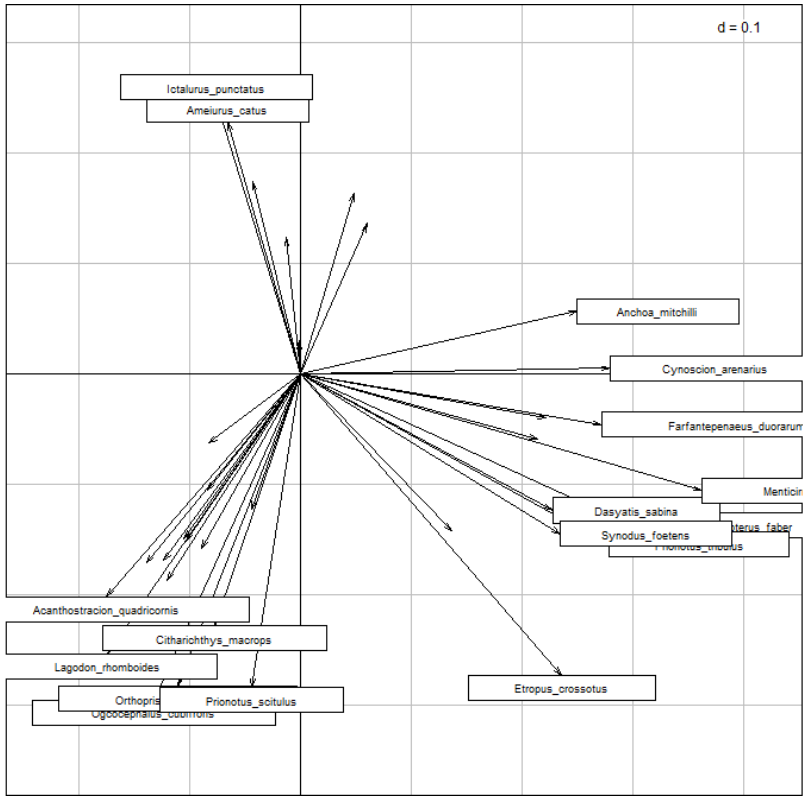



Figure 4.12: Coefficients of variables (fish species) on the first two axes of MULTISPATI for trawls. The first and second axes explain 22.87% and 20.96% of the spatial variation in the data. Only top loading species are labeled. Mesh size of the grid is indicated by "d."

Figure 4.13: Link between scores and lagged scores for trawl sites. The bottom of the vector is the score and the head is the lagged score. A long vector means that there is spatial discrepancy while a short one means that there is local spatial similarity. Sites are coded by suggested cluster number, which is based on the lag score of the site. Lag scores are scores of the site averaged with the nearest neighbor scores and weighted by the spatial connection matrix. Mesh size of the grid is indicated by "d."

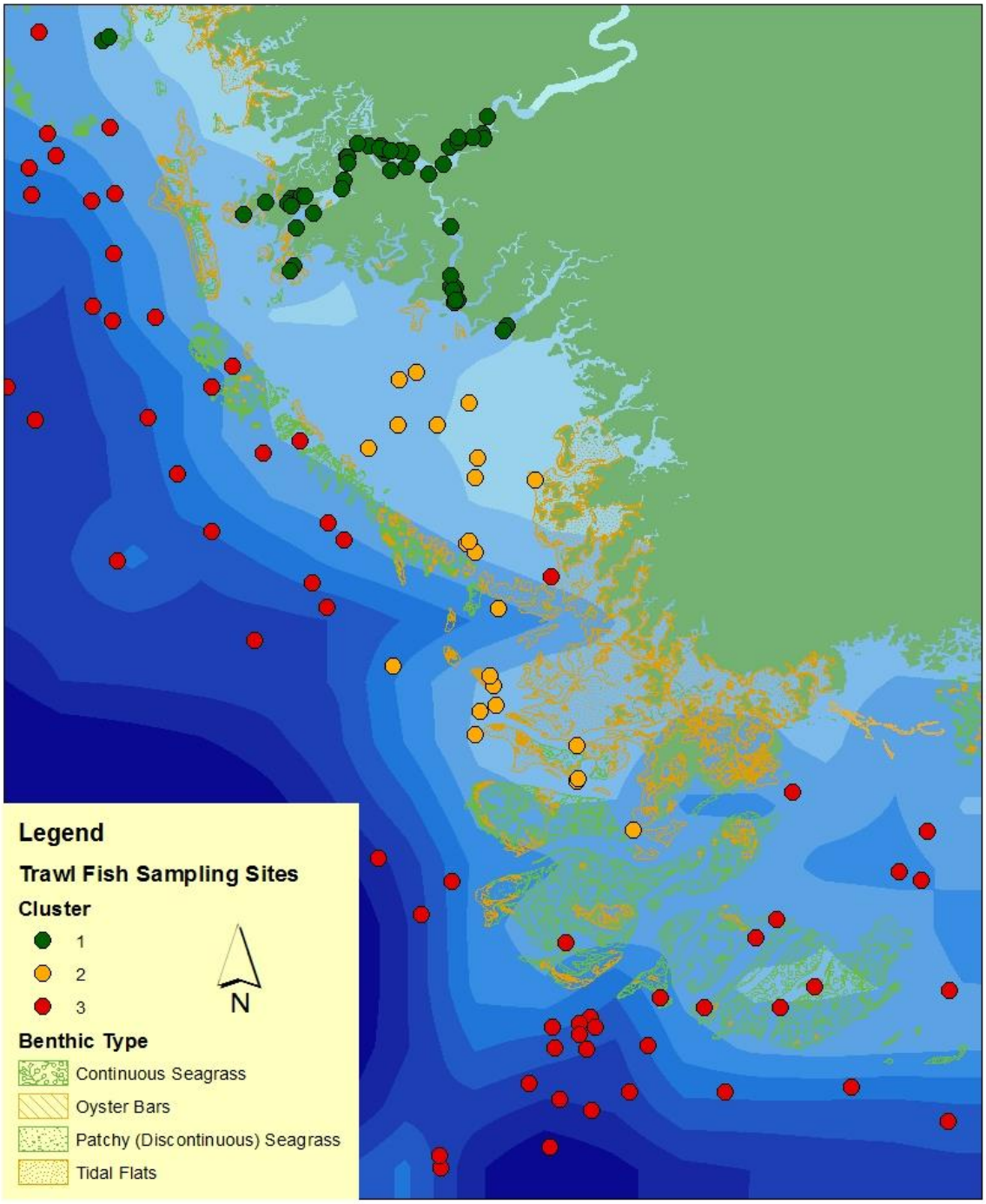
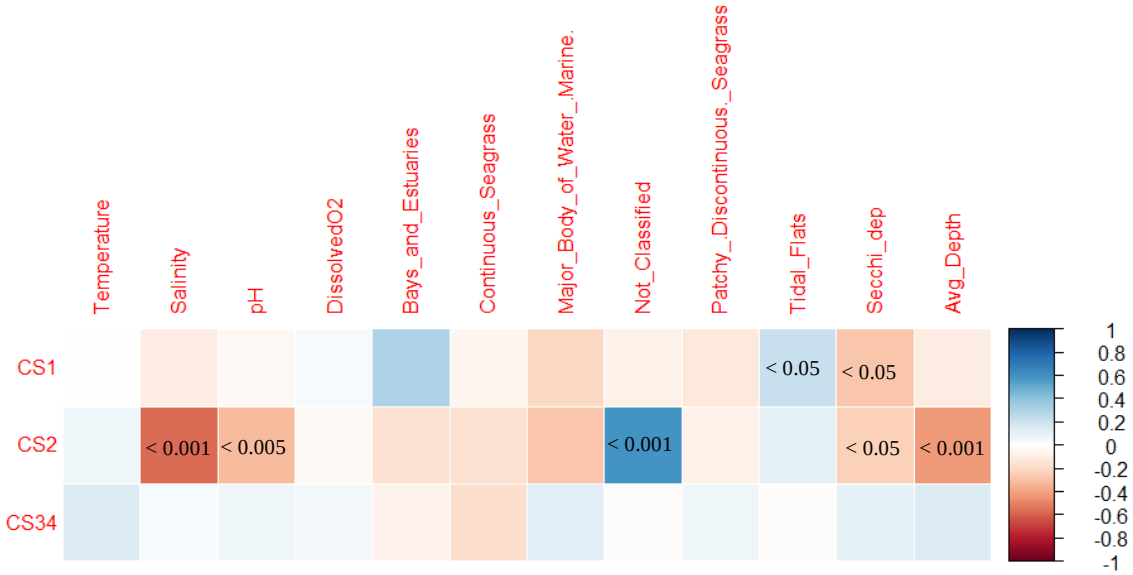



Figure 4.14: ArcGIS map of trawls clustered by the kmeans method with *NbClust* in R. Green sites are almost entirely within the Suwannee River or the main offshoots of the river. Yellow sites are more alongshore; red sites are offshore.




| MULTISPATI Axis to Variable | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS2- Salinity | -0.67006 | -0.56843 | -0.44589 | 2.36E-12 |
| CS2-pH | -0.45136 | -0.31019 | -0.15387 | 0.001405 |
| CS1-Bays and Estuaries | 0.150069 | 0.306664 | 0.448248 | 0.001405 |
| CS1-Major Body of Water | -0.35975 | -0.20788 | -0.04528 | 0.045815 |
| CS2-Not Classified | 0.4789 | 0.596182 | 0.692555 | 1.44E-13 |
| CS1-Tidal Flats | 0.059229 | 0.221226 | 0.371871 | 0.0317 |
| CS1-Secchi Depth | -0.41615 | -0.27047 | -0.11127 | 0.005667 |
| CS2-Secchi Depth | -0.38586 | -0.2367 | -0.07549 | 0.019905 |
| CS2-Average Depth | -0.54956 | -0.42362 | -0.27886 | 1.62E-06 |

Figure 4.15: Plot of correlations using Kendall's tau and table of significant correlations for the first two axes of the site scores (variance in fish relative abundance) to environmental variables for trawls. Lower confidence interval, r, upper confidence interval, and *p*-value are reported. Blue indicates positive correlation; red is negative.

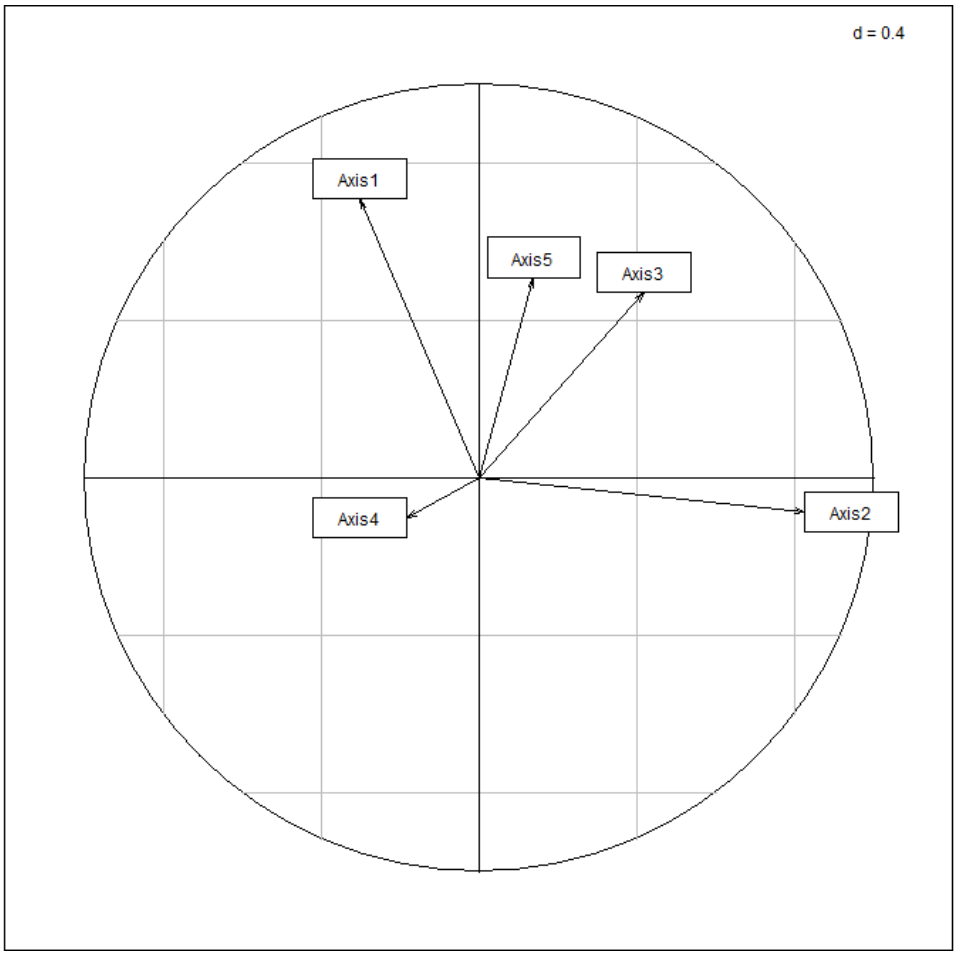



Figure 4.16: Plot of the five PCA axes onto the first two axes of MULTISPATI. The two methods are extracting similar patterns of data in the first two axes. Mesh size of the grid is indicated by "d."

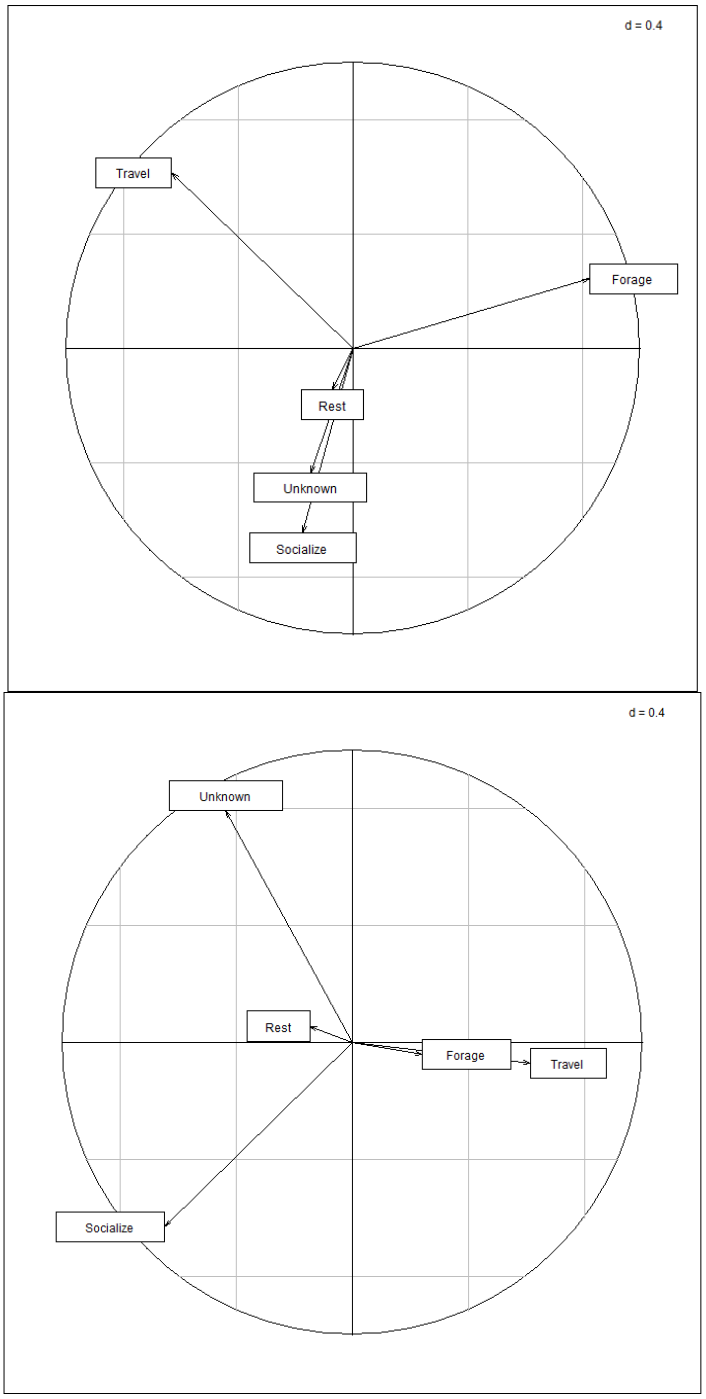



Figure 4.17: Graphical representation of the first two axes of PCA of dolphin behaviors (top) and the second and third axes of PCA (bottom). First and second axes: Rest, Unknown, and Socialize are all correlated to each other. Travel, Forage, and Socialize have the longest lines and therefore are most important in the PCA analysis. Second and third axes: Forage has very little variance CPUE on axis two, more so on axis three. In order of axis, the percent variance explained is 22.77, 21.26, 20.75, 20.29, and 14.93. Mesh size of the grid is indicated by "d."

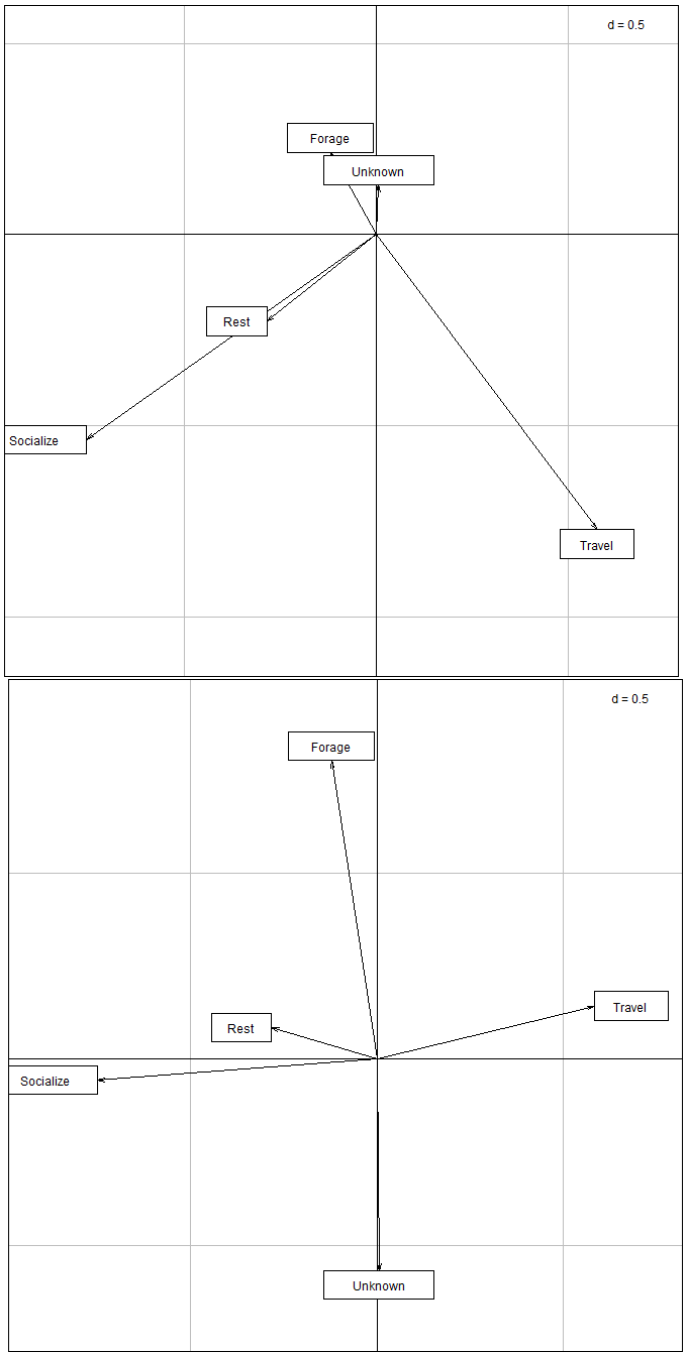



Figure 4.18: Graphical representation of the first two axes (top) and the first and fith axes (bottom) of MULTISPATI of dolphin behaviors. On the first two axes, Forage and Unknown are correlated to each other, as well as Rest and Socialize, but the two groups are not correlated. Travel is directly opposite to Forage and Unknown, which means it has negative correlation. Bottom, Forage is very closely aligned with the fifth axis. In order of axis, the percent variance explained is 37.90, 22.21, 6.13, 5.68, and 28.06. Mesh size of the grid is indicated by "d."

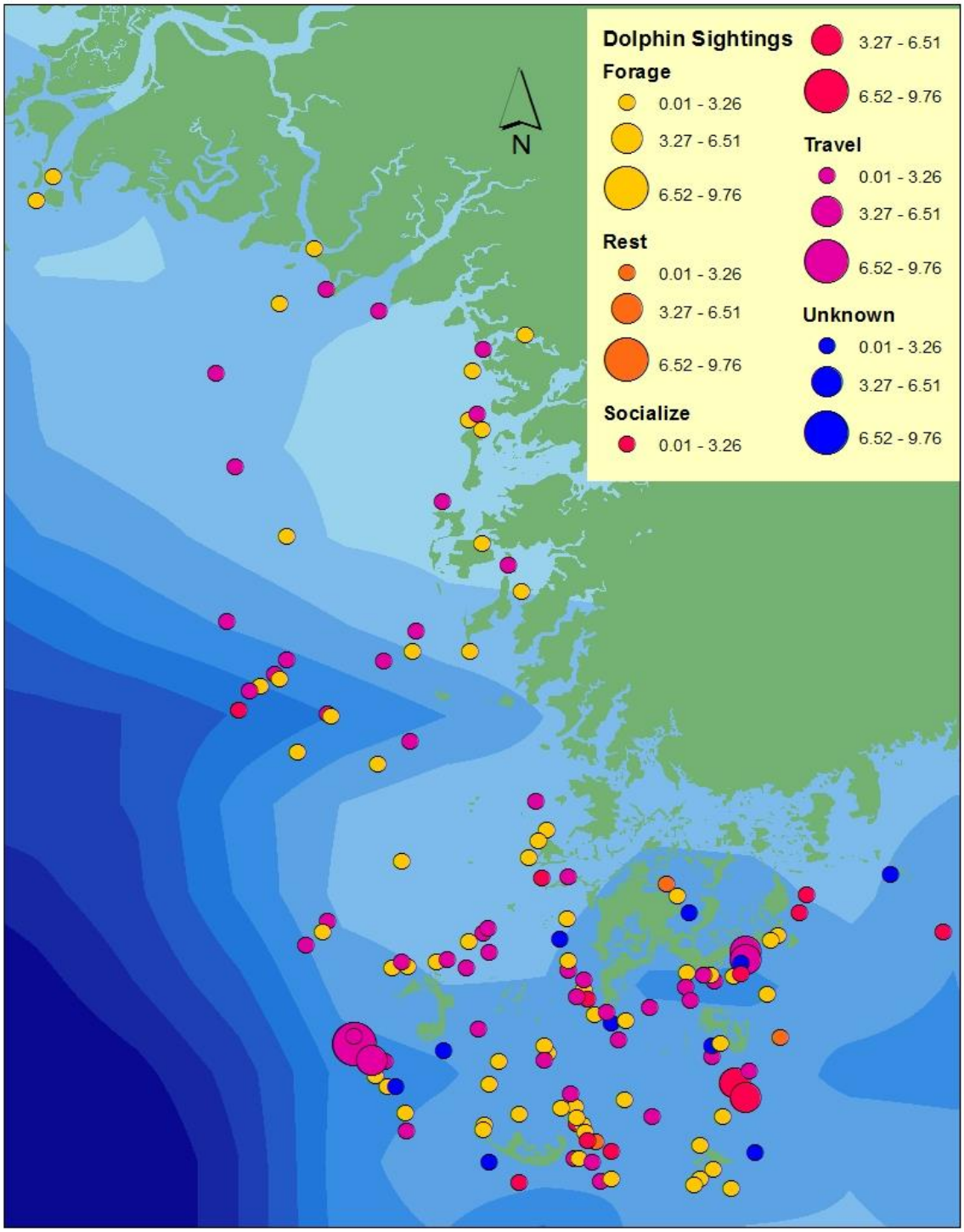



Figure 4.19: Map of the study area with dolphin behavior coded by color. Sightings are standardized by sightings per unit effort (SPUE). Forage happens throughout the study site, whereas the other behaviors happen in more distinct places.

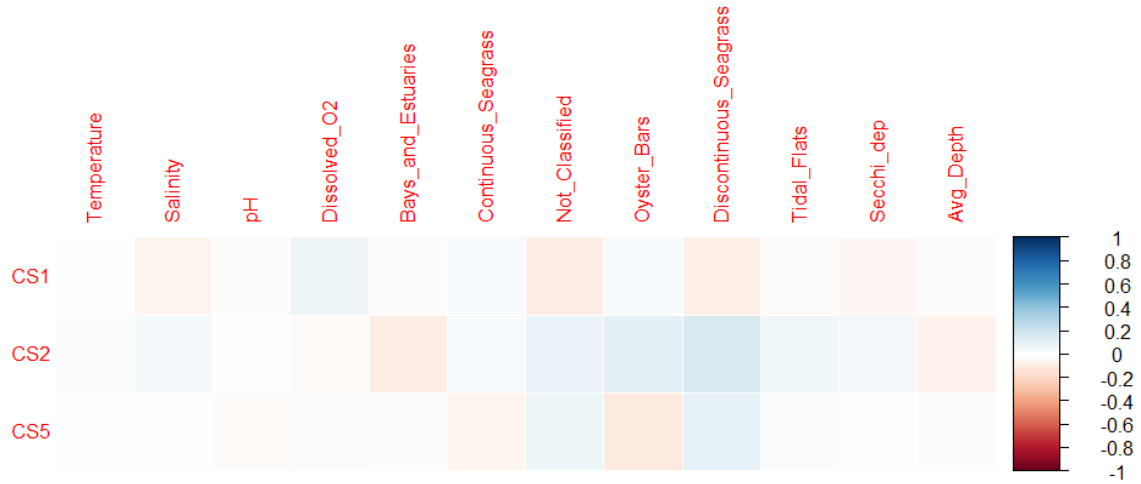



Figure 4.20: Correlations using Kendall's tau of the MULTISPATI axes of site scores of dolphin behaviors to environmental variables (kriged across the study site using ArcGIS). There are no significant correlations.

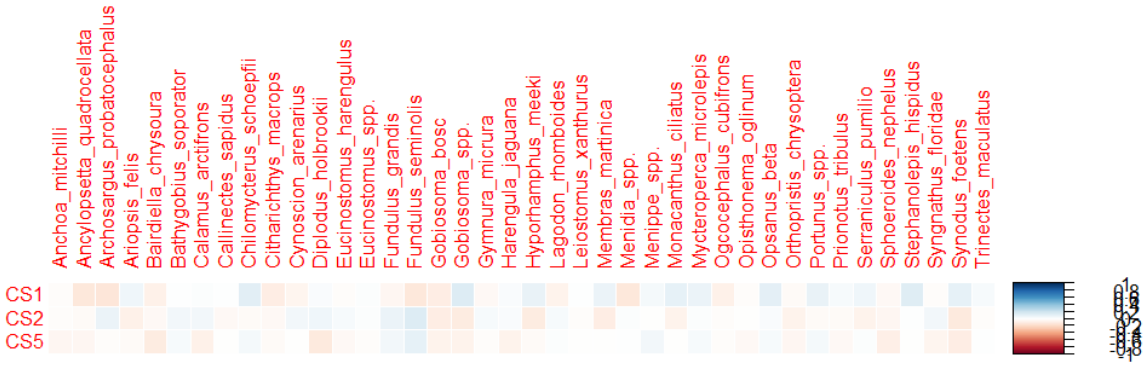



Figure 4.21: Correlations using Kendall's tau of the MULTISPATI axes of site scores of dolphin behaviors to fish relative abundance from seines (kriged across the study site using ArcGIS). There are no significant correlations.

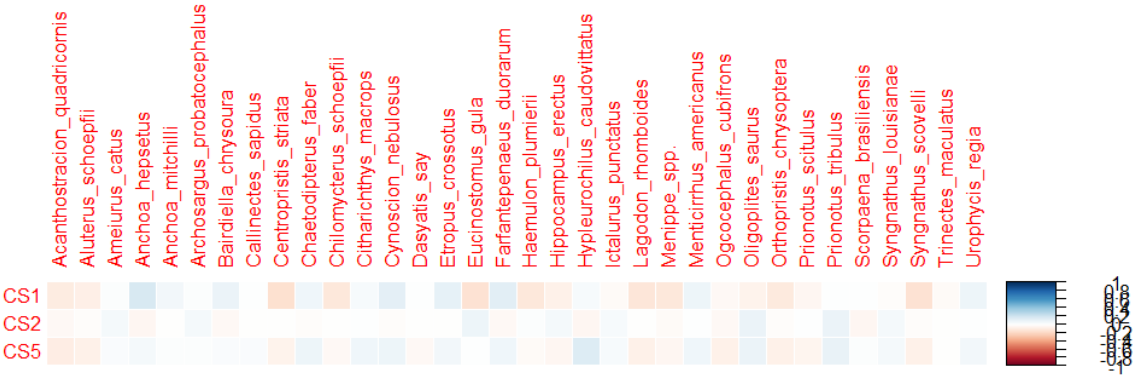



Figure 4.22: Correlations using Kendall's tau of the MULTISPATI axes of site scores of dolphin behaviors to fish relative abundance from trawls (kriged across the study site using ArcGIS). There are no significant correlations.

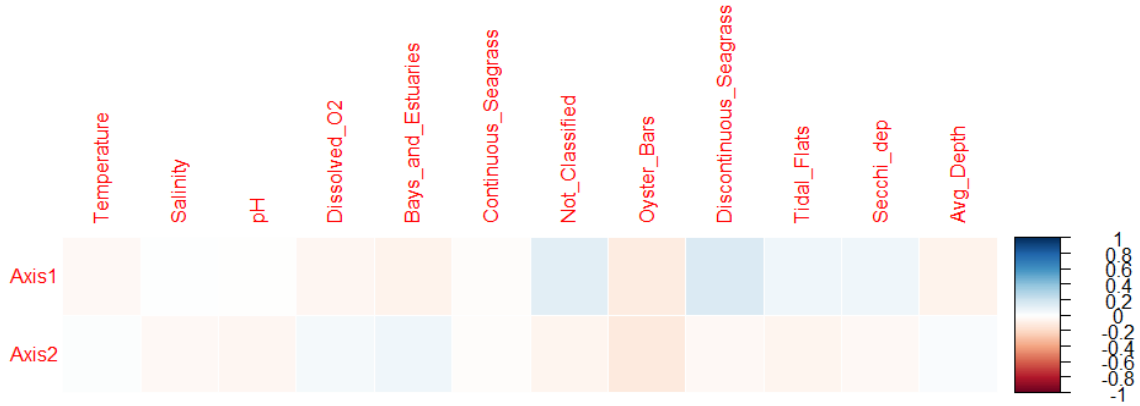



Figure 4.23: Correlations using Kendall's tau of the PCA axes of site scores of dolphin behaviors to environmental variables (kriged across the study site uusing ArcGIS). There are no significant correlations.

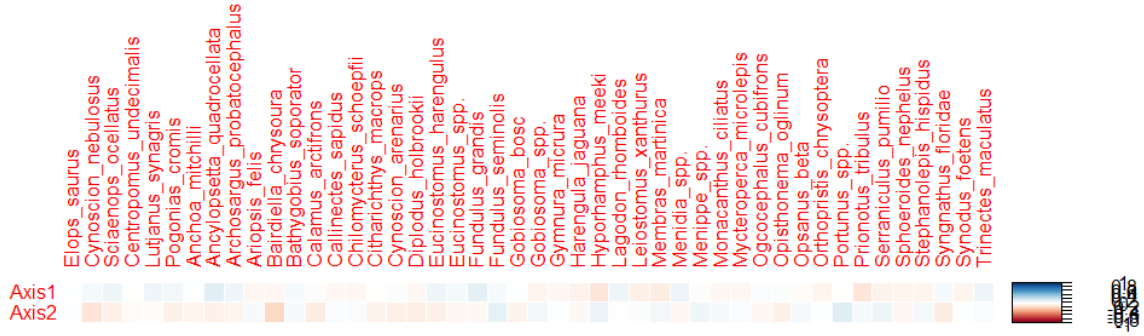



Figure 4.24: Correlations using Kendall's tau of the PCA axes of site scores of dolphin behaviors to fish relative abundance from seines (kriged across the study site using ArcGIS). There are no significant correlations.

Figure 4.25: Correlations using Kendall's tau of the PCA axes of site scores of dolphin behaviors to fish relative abundance from trawls (kriged across the study site using ArcGIS). There are no significant correlations.

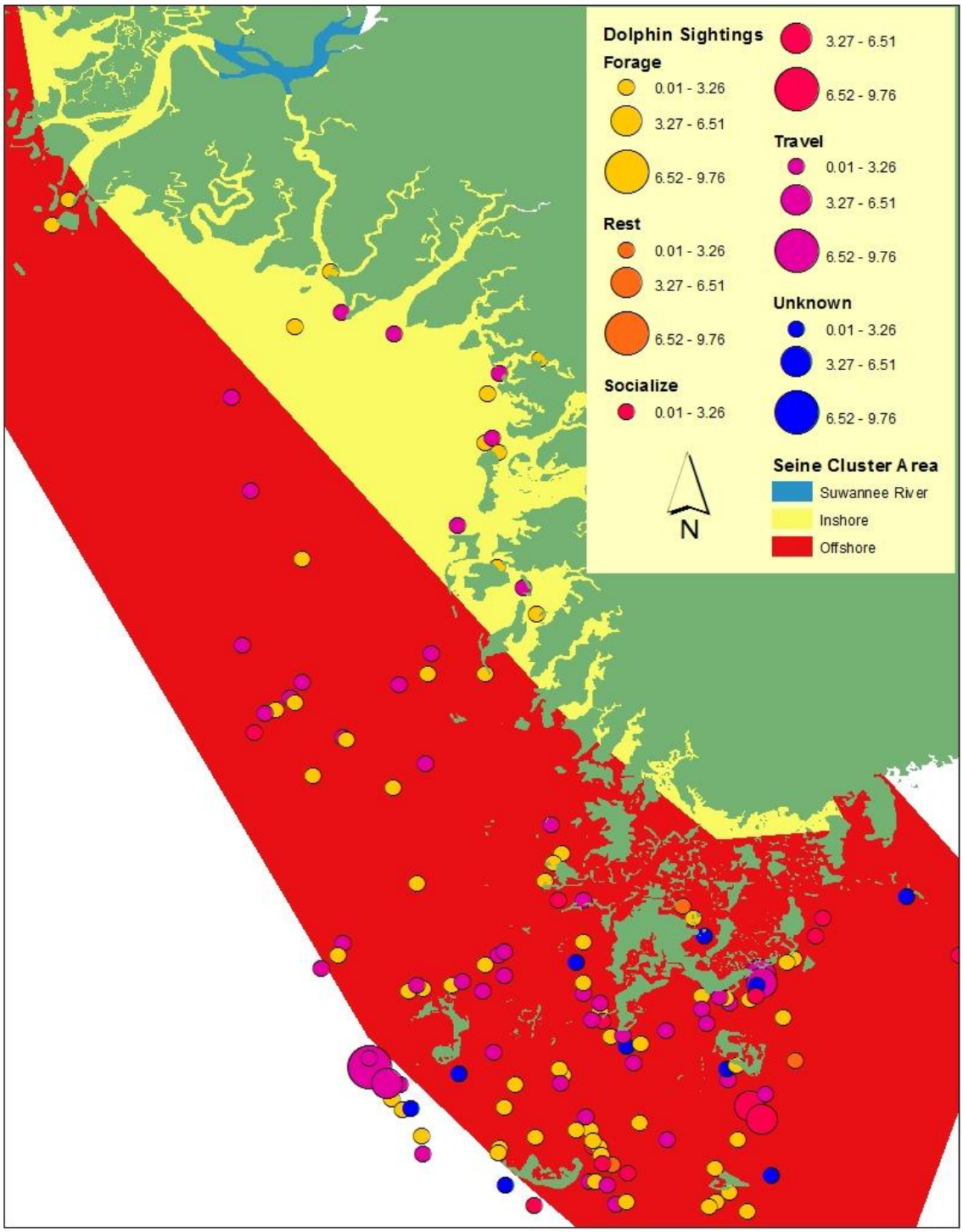



Figure 4.26: Seine cluster areas, created by using the Minimum Convex Polygon method in ArcGIS. Dolphin sightings, sized by SPUE and color-coded to behavior, are overlaid on the polygons.

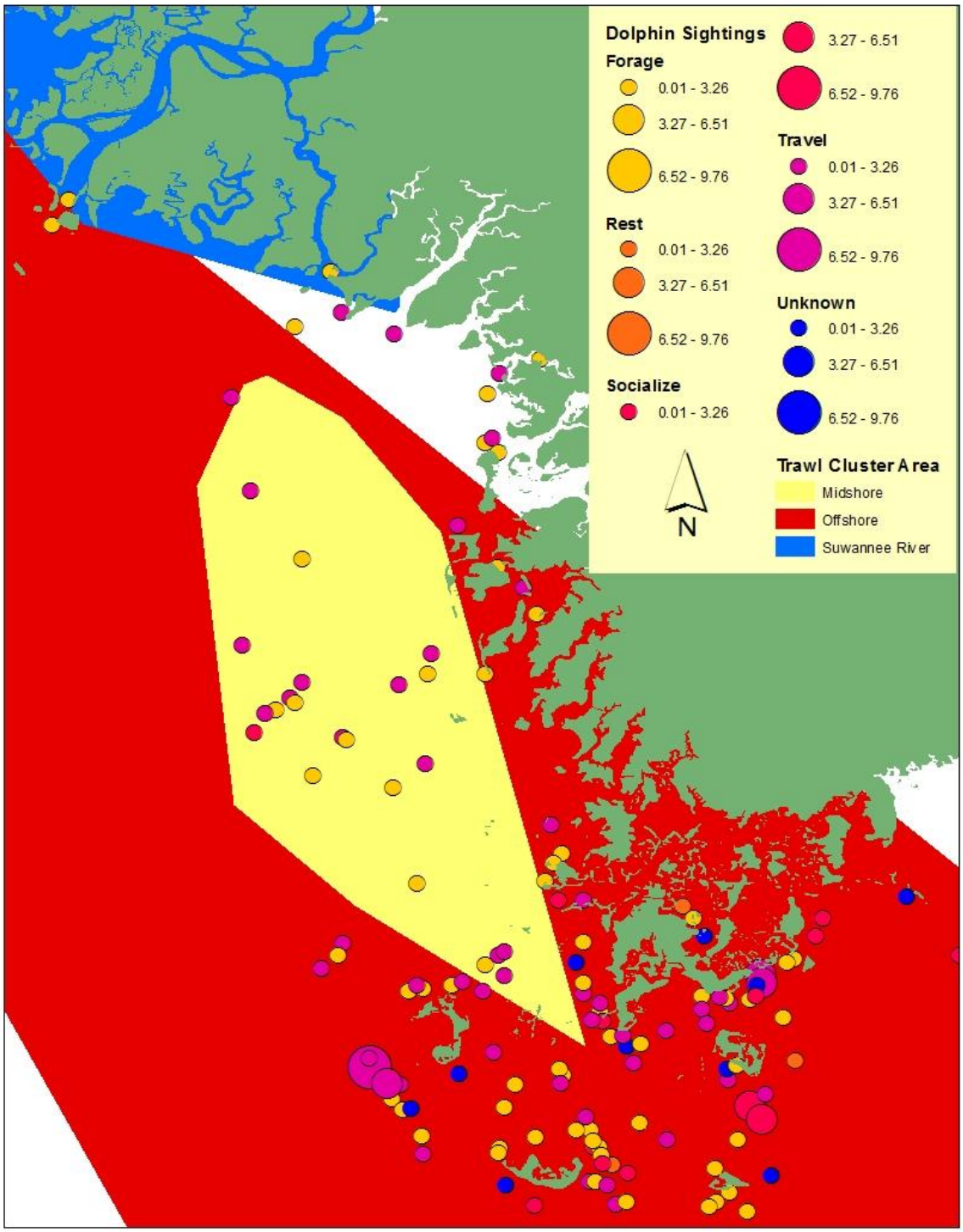



Figure 4.27: Trawl cluster areas, created by using the Minimum Convex Polygon method in ArcGIS. Dolphin sightings, sized by SPUE and color-coded to behavior, are overlaid on the polygons.

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CHAPTER 5:

CONCLUSIONS

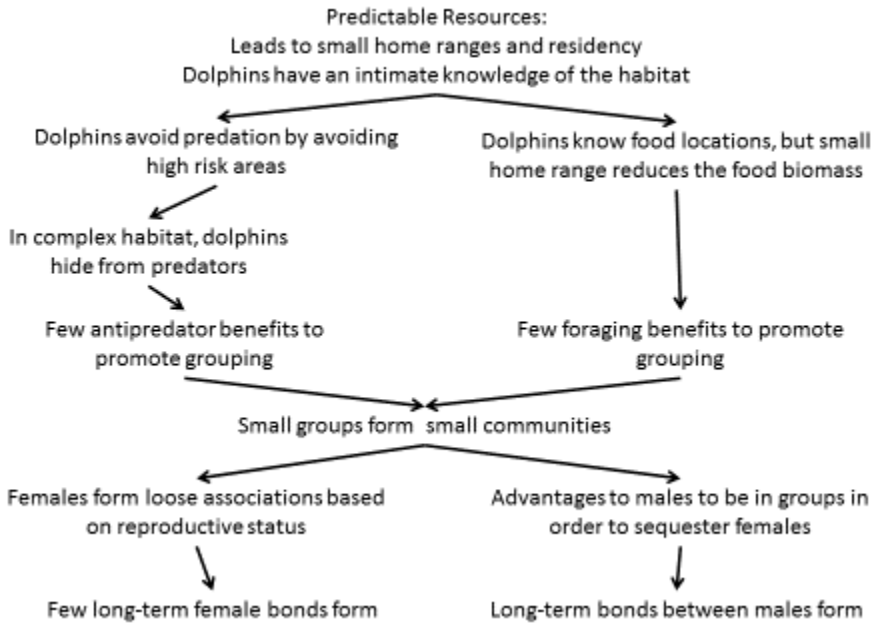


Figure 5.1 Predictions of the Gowans et al. 2007 scheme of dolphin grouping for inshore delphinid societies.

The purpose of this dissertation was to examine the influence of environmental variability on the distribution of prey and the influence of predator-prey interactions on the distributions of predators. Additionally I examined how sociological differences (behavior type and the changing of a foraging behavior specific to Cedar Key, Florida) influenced the relative roles of bottlenose dolphins within the population. I used the Gowans et al. (2007) scheme of delphinid inshore grouping to frame my questions.

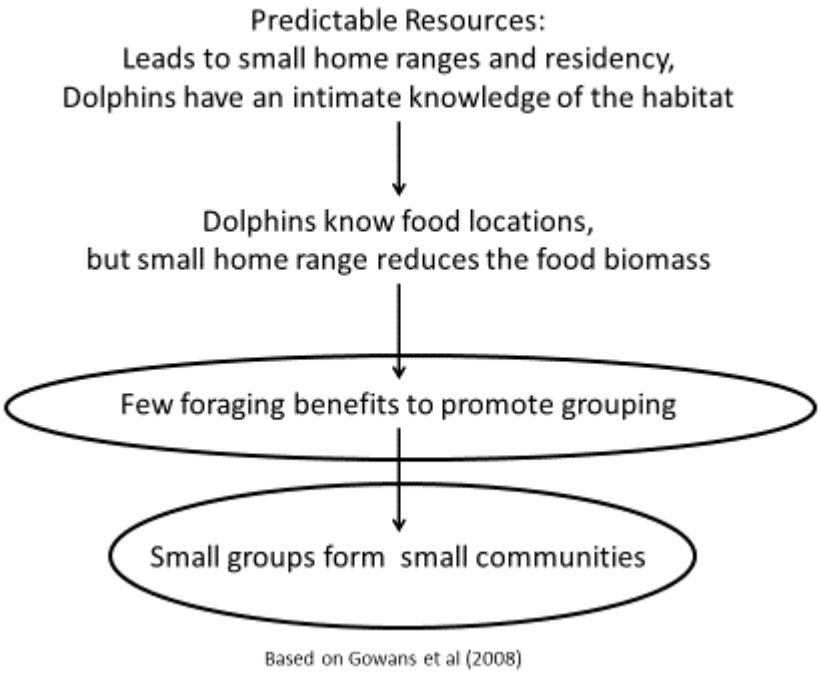


Figure 5.2: The assumptions of the scheme investigated with Network analysis.

The Gowans et al. (2007) scheme assumes that small groups form small communities; I was interested in how these small groups are composed. The scheme assumes that foraging groups are small and rare as there are few foraging benefits to promote grouping.

Networks help to clarify the associative complexities of animal groups by providing insight into behavioral dynamics at the population level through analysis of overarching network properties. Gero et al. (2005) hypothesized that the plasticity of association in a fission-fusion population, combined with the ability to relocate without substantial energy expenditure (Williams 1999), may allow individuals to maximize social benefits in each behavioral state by shifting associations. Network analysis is especially good at highlighting the differences in these population features in different

behavioral states (Lusseau and Newman 2004). Therefore, a network analysis of the population is likely to produce different results if sorted by behavior.

Using network analysis, I did find that foraging occurs in small groups or alone. There were preferential associations between individuals in Overall, Socialize, and Travel networks, but not in the Forage network.

However, the Gowans et al. (2007) scheme predicts small groups in small communities, and this is not the case for all of the behaviors studied. The Socialize network has the least number of nodes and a relatively large number of edges, and the edges have relatively large weights (HWI values) associated with them. There were fewer dolphins seen socializing, but when they were seen, they socialized with many others that were socializing, and frequently. The Gowans et al. (2007) scheme predicts that associations will not be significant, and this is not the case here.

The Forage network is the opposite of the Socialize network. Among the three activity networks, it has the largest number of nodes (more dolphins were seen foraging), relatively small number of edges (dolphins were not seen foraging with others very often), and the edges have small weights associated with them (when they were seen foraging with others, it was not consistent with whom they foraged).

The Travel network is intermediate between the Socialize and Forage networks. This indicates that while dolphins do have preferential associations while traveling, they do not travel in as large groups as they do when socialize or in as small groups as they do while foraging.

This study shows that networks representing different behavioral states (Social, Forage, and Travel) in a population of *T. truncatus* exhibit different structural

characteristics. Overall, individuals did not maintain their relative positions with the networks when sorted by behavioral states. In light of this, it is important to take into account behavior when constructing networks, as the details of different interactions between individuals that are behavior dependent can get muddled in a network that disregards behavioral state. The whole network does not show a true picture of the interactions.

Given these results, the assumptions of the Gowans et al (2007) scheme that follow this (females form loose associations and males form long term bonds) should be investigated. It is possible that this could be the case in Cedar Key if the groups are segregated by sex, but as of now only about 20% of the dolphins have been sex identified, so there is not enough data to test this.

*Chapter 3: How do group composition changes in a specialized feeding behavior affect the efficiency of the members of the group?*

The Gowans et al. (2007) scheme predicts that there are few foraging benefits to promote grouping. However, there are still examples of group foraging behavior seen in Cedar Key, Florida. I examined this driver-barrier foraging behavior over several field seasons. As the years progressed, the number of participating dolphins decreased, which allowed a unique opportunity to study the role of the barrier dolphin in this behavior, as well as how the driver dolphin does in different group sizes. This study has shown that a driver dolphin does have greater catch success than the barrier dolphins regardless of group size. This is different than what was initially predicted (Gazda et al. 2005). There is also evidence that barrier dolphins may have a role in increasing foraging efficiency by decreasing the number of incomplete bouts. Both the driver and barrier dolphins do better

in larger groups when incomplete bouts are factored in. Additionally, there is evidence of cooperation between the barriers themselves: barriers did better when there were more of them.

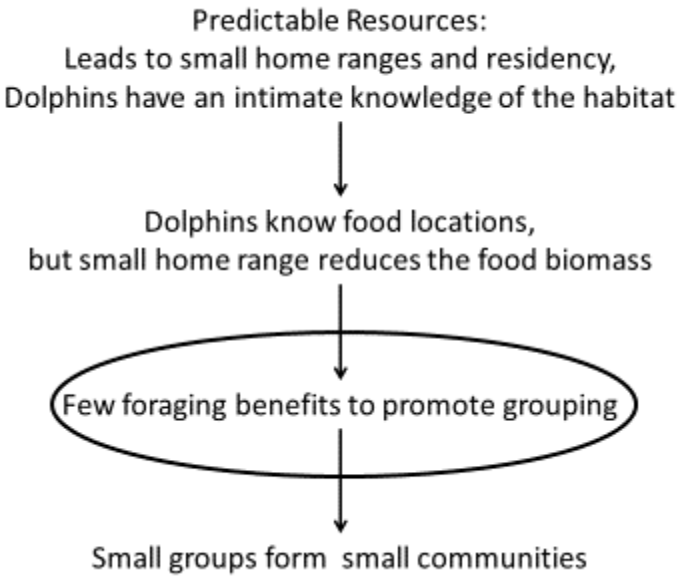


Figure 5.3: The assumptions of the scheme investigated by studying the driver barrier feeding behavior.

While the Gowans et al. (2007) scheme predicts there are few benefits to promote group foraging, clearly this is not the case in this particular behavior. The Gowans et al. (2007) scheme predicts that dolphins should spread themselves out and that they cannot defend resources, so there should be scramble-type competition evidenced by no change or a decrease in success rate because they are competing for a limited resource. This is rejected here. As Creel and Creel (1995) note, rejecting the notion of communal hunting/foraging influences on sociality is premature if costs of prey capture are not included. The Gowans et al. (2007) scheme does not account for this at all.

Because the barrier dolphins disappeared from the study site, it is difficult to determine if they were specialists at being barriers, and focal follows of barrier dolphins to clarify this are needed. It is doubtful that this behavior fits a producer-scrounger model (due to the increased catch success of the barrier dolphins when there were more present), and a division of labor with role specialization still remains the best explanation for it. However, given the correlation between group size and year, and the sample size of only one group, it is still not entirely clear what the relative importance of the barrier dolphins are in this behavior.

Determining whether barrier dolphins relate to foraging efficiency in groups (and what an appropriate measure of efficiency is) is critical to understanding the role of barriers within this behavior, as well as the impact of their removal from the system. Studies on a larger number of groups that vary in the number of barrier dolphins and where time effects can be removed are needed to clarify these issues.

*Chapter 4: Are fish density and species composition correlated to habitat variables? Are these variables, including prey availability, correlated to dolphin spatial structure?*

The Gowans et al. (2007) scheme assumes that resources are predictable: not patchy in time or space (food and/or predators). This is the basis of the schematic. In bottlenose dolphin foraging research, it is often assumed that habitat use is related to prey availability (S. Dawson, personal communication, Torres 2007, Redfern et al. 2006), though this is rarely directly tested. To examine this assumption, predator and prey data need to be on the same temporal and spatial scale, requiring intensive studies of both levels, which is often outside the capabilities of a single research project.

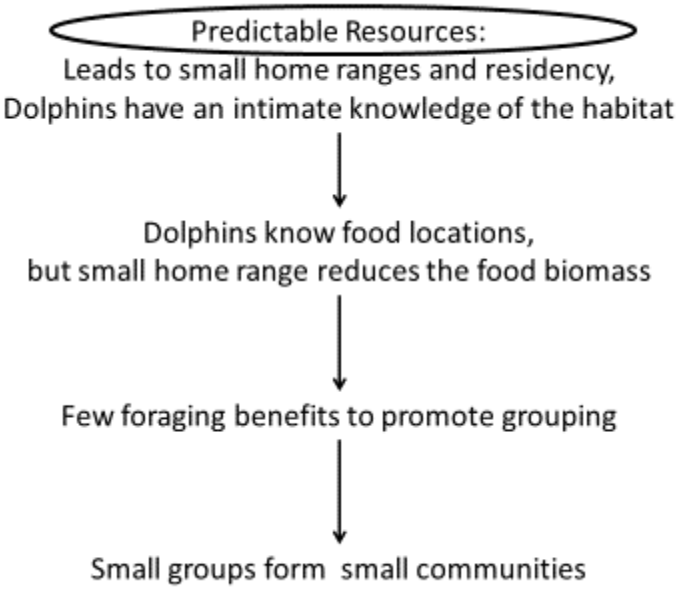


Figure 5.4: The assumptions of the scheme investigated by examining fish spatial patterns.

From my collaborative work with the Florida Fish and Wildlife Commission's Fisheries-Independent Monitoring (FIM) program, I was able to integrate data on habitat, prey, and predator, all taken at the same spatial and temporal scale. Using the FIM data, I evaluated the spatial structure of potential prey and correlated this to habitat and other habitat variables. I then evaluated dolphin behavior SPUE spatial structure and variance and correlated this to kriged fish abundance and habitat variables.

*Fish Summary:*

Chapter 4 examined whether there was a correlation of relative abundance of fish species to biotic and abiotic variables. The abiotic variables and fish abundance data were collected as part of the FWC FIM program. Biotic variables (habitat composition) was collected for each sampling grid using ArcGIS. MULTISPATI, a powerful tool that incorporates spatial analysis into Principle Components Analysis (PCA) was used.

Previous applications of this analysis have been limited to landscape and soil ecology. It has not been used for vertebrate analyses.

The results do show that there is spatial structure in fish relative abundance, and there are correlations between fish species and habitat variables. Since the Gowans et al. (2007) scheme states that resources are predictable (not patchy), one prediction of this would be that there would be spatial structure and correlations to the habitat.

*Dolphin Summary:*

MULTISPATI was used to examine spatial structure with the dolphin data. Spatial structure was only significant when both field seasons were combined. It is clear that there are differences in a classic PCA test versus MULTISPATI when the field seasons are combined. While variance is reduced in a MULTISPATI analysis, spatial autocorrelation increased. This also is demonstrated in the figures relating to contributions to the axes: while Forage was the dominant contributor to the first PCA axes, it is Socialize in MULTISPATI. Therefore, Forage can be seen as the primary contributor to the variance in SPUE in the data, whereas Socialize is the primary contributor to global positive spatial autocorrelation. However, Forage has a large influence on local spatial structure, so dolphins are foraging intensely in one area but not in others.

*Dolphin/Fish Summary:*

Dolphin distributions rarely include direct data on prey distribution because prey sampling is more difficult than sampling abiotic variables. In reality, these abiotic variables are usually used as proxies for prey distribution (S. Dawson, personal communication, Redfern et al. 2006). Abiotic variables may be correlated with the

distribution of dolphins; however, these metrics often have little direct influence on the actual selection of habitats by dolphins (Torres 2007). Therefore, as top marine predators, dolphins are removed from the direct influence of the environmental variability that is commonly used to characterize their habitat (Torres 2007). The dolphin spatial and PCA data was examined in relationship to the fish data for correlations in dolphin habitat use with the fish abundance, diversity, and habitat variables. No correlations were found.

Torres (2007) found that the predictive capacity of dolphin habitat use did not increase by including prey species and concluded that it was likely due to the too small scale of the fish collection (50 $m^2$ grids). Expanding the relative abundance of fish and dolphin SPUE to a coarser spatial scale (larger than 0.2 $nm^2$ grids) may show spatial patterns. One option is to use the zones I used to create the transect lines. They were created to accommodate the directionality of the shoreline but do have different general features.

The Gowans et al (2007) hypothesis is based on the premise that there are no schooling fish. The local spatial structure indicates that dolphins may actually be foraging on these types of species, which may not be well-represented in the catch data. Some of the fish species dolphins are known to consume are not caught in the seines or trawls, or they do not have significant spatial structure. Mullet species (*Mugil* spps) and Jack (*Caranx hippos*) are tightly schooling fish species that have been consumed by dolphins. Schooling fish can reduce the effect of the abundance estimates in the study area, as they are in high abundance contributions when caught, but also can give false negatives if they are not set on by the gear. Guinet et al. (2001) found a negative relationship between the occurrence of forage fish and the number of individual fish sampled per species, despite

the fact they sampled in the same area and during the same time of night as fur seals. They suggest that one reason for this is because the catchability of fish species was biased, therefore the sample population was not truly representative of their relative abundance.

Correlating dolphin behavior with the polygons created by the cluster areas also had similar results to the MULTISPATI and PCA analyses. There are areas where dolphins gather for socializing, traveling, and resting, and they seem to be in the areas surrounding the islands, whereas Forage happens throughout the study site.

## CONCLUSIONS

The results of this dissertation do not entirely support the predictions of the Gowans et al. (2007) scheme: Foraging groups are small and lack preferential associations, but Socialize groups are large and have preferential associations, which is not what is predicted. The driver-barrier behavior provides a benefit for barrier dolphins, as there is a positive relationship between group size and average catch success. It was predicted that there were few benefits to forming foraging groups, but this is not supported here. There was significant spatial structure in fish relative abundance, which means that potential food sources are not spread evenly throughout the study site but are predictable. Fish and biotic variables are not correlated to dolphin spatial structure, though this is likely a case of spatial and temporal scales not being appropriate and fish catch methods not able to capture what is happening at the study site.

A portion of the Gowans et al. (2007) scheme (Figure 5.5, circled) relates explanations for grouping to predator pressures. In this part, it is predicted that complex

habitats enable dolphins to hide from predators and that small groups will form small communities. According to local fishermen, bull sharks (*Carcharhinus leucas*, the most likely predator of dolphins in the Gulf of Mexico; Wells 1991) are abundant in Cedar Key but no work on quantifying their densities, sizes, or spatial patterns has been initiated. Bull sharks have been known to attack prey larger than themselves (Heithaus 2001), so knowing how big they are in Cedar Key would help quantify the likelihood that they are a source of predation pressure. Few dolphins in Cedar Key have exhibited shark attack scars, but a low proportion of scars does not necessarily indicate a low predation rate (Heithaus 2001).

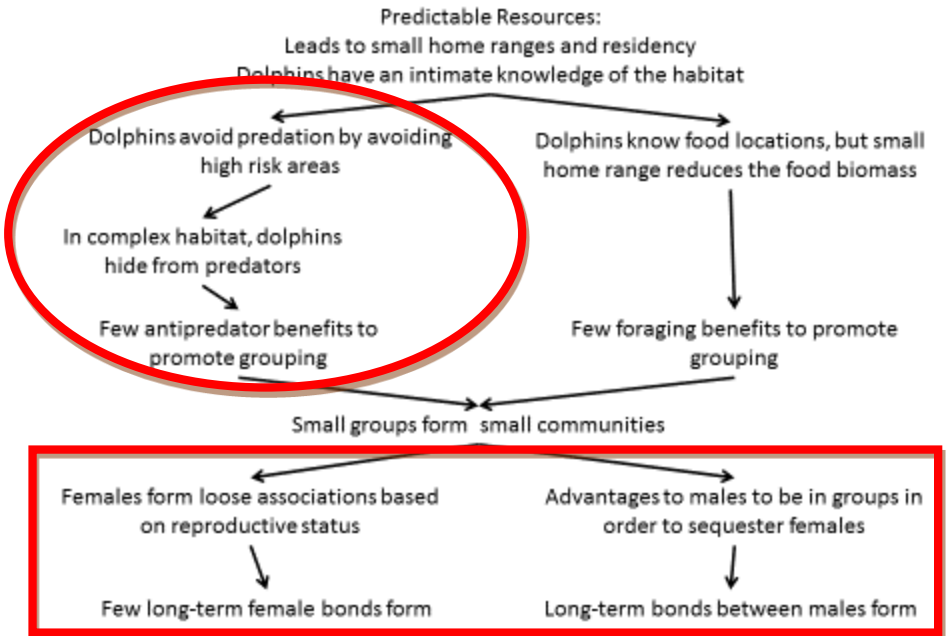


Figure 5.5: Future items to study on the Gowans et al. (2007) scheme.

Additionally, there are other predictions from the Gowans et al. (2007) scheme that are based on differences between the sexes (Figure 5.5, boxed). These can be tested using network analysis, but at this point only about 20% of the population has been positively identified as male or female.

While the Gowans et al. (2007) scheme is a useful starting point for researching populations of inshore bottlenose dolphins, it is clear that it cannot fully and accurately describe all populations. Bottlenose dolphins are long-lived and have complex social strategies that incorporate many different parameters (reproductive contests, feeding behaviors, etc.), and priorities may change with age. They cannot fit a simple scheme.

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APPENDIX A: NETWORKS GRAPHS

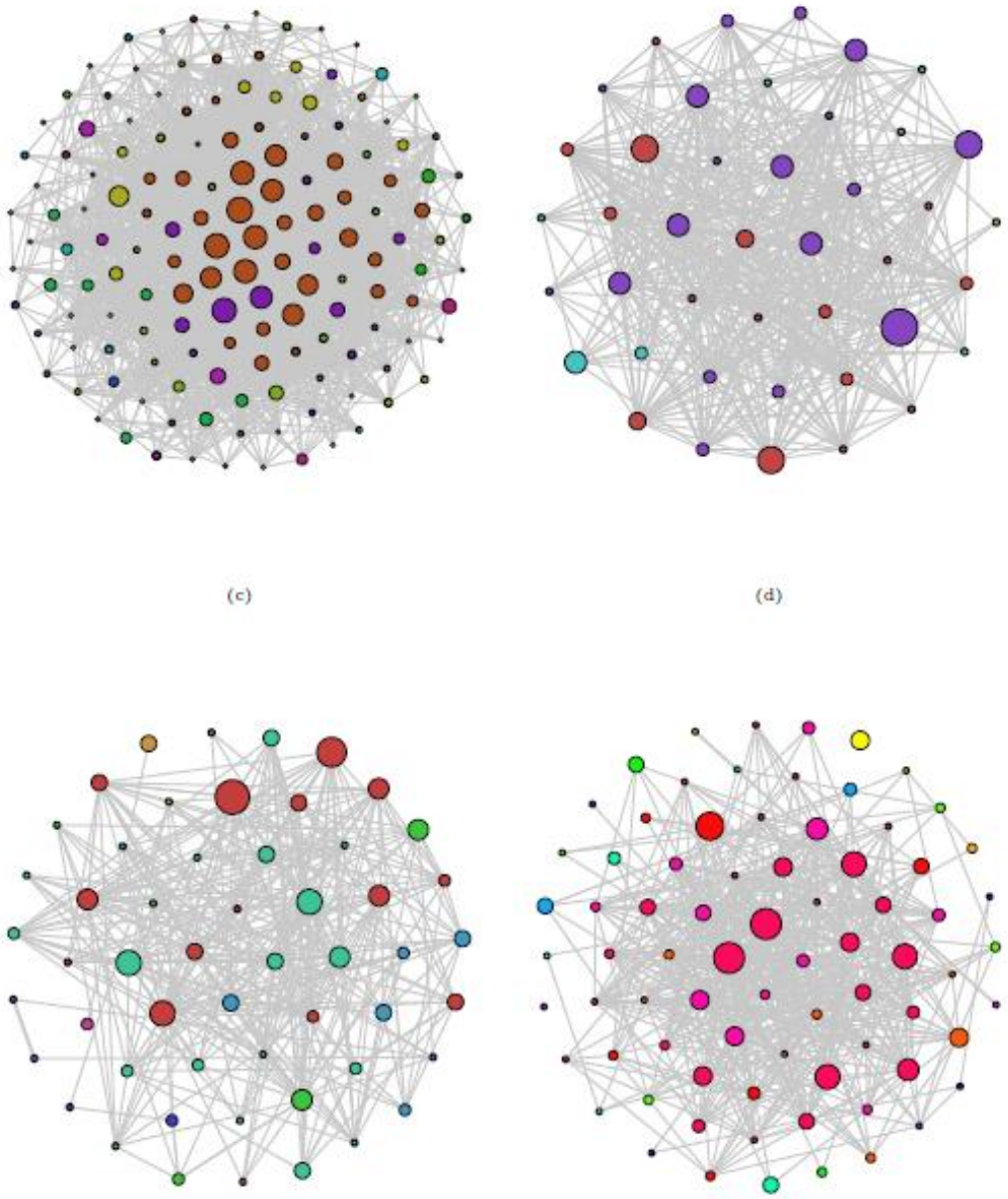



Figure A.1: Four networks were built: an overall network N (top left) that does not take behavior into account and the three networks NS (top right), NT (bottom left), and NF (bottom right) corresponding to the socializing, traveling, and foraging behaviors.

APPENDIX B: TABLES AND FIGURES RELATED TO CHAPTER FOUR

TABLES

| Scientific Name | Common Name | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|
| | | Marine | Freshwater | Brackish | |
| *Anchoa mitchilli* | Bay anchovy | Y | Y | Y | |
| *Ancylopsetta quadrocellata* | Ocellated flounder | Y | | | |
| *Archosargus probatocephalus* | Sheepshead | Y | | Y | N |
| *Ariopsis felis* | Hardhead catfish | Y | | Y | |
| *Bairdiella chrysoura* | Silver perch | Y | Y | Y | |
| *Bathygobius soporator* | Frillfin goby | Y | Y | Y | |
| *Calamus arctifrons* | Grass porgy | Y | | | |
| *Callinectes sapidus* | Blue crab | Y | | | |
| *Chilomycterus schoepfii* | Striped burrfish | Y | | | |
| *Citharichthys macrops* | Spotted whiff | Y | | | |
| *Cynoscion arenarius* | Sand weakfish | Y | | Y | P |
| *Diplodus holbrookii* | Spottail seabream | Y | | Y | |
| *Eucinostomus harengulus* | Tidewater mojarra | Y | | Y | |
| *Eucinostomus spp.* | Mojarra spps. | Y | | Y | |
| *Fundulus grandis* | Gulf killifish | | Y | Y | |
| *Fundulus seminolis* | Seminole killifish | | Y | Y | |
| *Gambusia holbrooki* | Eastern mosquitofish | | Y | Y | |
| *Gobiosoma bosc* | Naked goby | Y | | Y | |
| *Gobiosoma spp.* | Goby spps | Y | | Y | |
| *Gymnura micrura* | Smooth butterfly ray | Y | | Y | |
| *Harengula jaguana* | Scaled herring | Y | | Y | N |
| *Hyporhamphus meeki* | American halfbeak | Y | Y | Y | |
| *Labidesthes sicculus* | Brook silverside | | Y | | |
| *Lagodon rhomboides* | Pinfish | Y | Y | Y | N |
| *Leiostomus xanthurus* | Spot croaker | Y | | Y | N |
| *Lepomis auritus* | Redbreast sunfish | | Y | | |
| *Lepomis macrochirus* | Bluegill sunfish | | Y | | |
| *Lepomis microlophus* | Redear sunfish | | Y | | |

| Scientific Name | Common Name | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|
| | | Marine | Freshwater | Brackish | |
| *Lepomis punctatus* | Spotted sunfish | | Y | | |
| *Lepomis spp.* | Sunfish spps. | | Y | | |
| *Lucania parva* | Rainwater killifish | Y | Y | Y | |
| *Membras martinica* | Rough silverside | Y | | | |
| *Menidia spp.* | Silverside spps. | Y | Y | Y | |
| *Menippe spp.* | Stone crab spps. | Y | | | |
| *Micropterus salmoides* | Largemouth black bass | | Y | | |
| *Monacanthus ciliatus* | Fringed filefish | Y | | | |
| *Mycteroperca microlepis* | Gag grouper | Y | | Y | N |
| *Ogcocephalus cubifrons* | Batfish | Y | | | |
| *Opisthonema oglinum* | Atlantic thread herring | Y | | | N |
| *Opsanus beta* | Gulf toadfish | Y | | | P |
| *Orthopristis chrysoptera* | Pigfish | Y | | Y | N |
| *Pomoxis nigromaculatus* | Black crappie | | Y | | |
| *Portunus spp.* | Blue crab spps. | Y | | | |
| *Prionotus tribulus* | Bighead searobin | Y | | | N |
| *Serraniculus pumilio* | Pygmy sea bass | Y | | | |
| *Sphoeroides nephelus* | Southern puffer | Y | | Y | |
| *Stephanolepis hispidus* | Planehead filefish | Y | | | |
| *Syngnathus floridae* | Dusky pipefish | Y | | | |
| *Synodus foetens* | Inshore lizardfish | Y | | Y | N |
| *Trinectes maculatus* | Hogchoker | Y | Y | Y | |

Table B.1: Table of fish species that have significant spatial structure in the two field seasons combined for seines. Habitat information (what type of water they inhabit) is from www.fishbase.org. In the column ”Seen in Dolphin diet?” from Berens-McCabe et al. (2010), P indicates positive selection and N indicates negative selection for the species based on research in Sarasota Bay, Florida. Blank spaces indicate no information is available as to whether bottlenose dolphins consume these species.

| Scientific Name | Common Name | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|
| | | Marine | Freshwater | Brackish | |
| *Acanthostracion quadricornis* | Scrawled cowfish | Y | | | |
| *Aluterus schoepfii* | Orange filefish | Y | | | |
| *Ameiurus catus* | White catfish | | Y | | |
| *Anchoa hepsetus* | Broad-striped anchovy | Y | | Y | |
| *Anchoa mitchilli* | Bay anchovy | Y | Y | Y | |
| *Archosargus probatocephalus* | Sheepshead | Y | | | N |
| *Bairdiella chrysoura* | Silver perch | Y | Y | Y | |
| *Callinectes sapidus* | Blue crab | Y | | | |
| *Centropristis striata* | Black seabass | Y | | | |
| *Chaetodipterus faber* | Atlantic spadefish | Y | | Y | |
| *Chilomycterus schoepfii* | Striped burrfish | Y | | | |
| *Citharichthys macrops* | Spotted whiff | Y | | | |
| *Cynoscion arenarius* | Sand weakfish | Y | | Y | P |
| *Dasyatis sabina* | Atlantic stingray | Y | Y | Y | |
| *Etropus crossotus* | Fringed flounder | Y | | Y | |
| *Eucinostomus harengulus* | Tidewater mojarra | Y | | | |
| *Farfantepenaeus duorarum* | Marine shrimp | Y | | Y | |
| *Haemulon plumieri* | White grunt | Y | | | |
| *Hippocampus erectus* | Lined seahorse | Y | | | |
| *Hypleurochilus caudovittatus* | Zebratail blenny | Y | | Y | |
| *Ictalurus punctatus* | Channel catfish | | Y | | |
| *Lagodon rhomboides* | Pinfish | Y | Y | Y | N |
| *Menippe spp.* | Stone crab spp. | Y | | | |
| *Menticirrhus americanus* | Southern kingcroaker | Y | | Y | N |
| *Ogcocephalus cubifrons* | Batfish | Y | | | |
| *Oligoplites saurus* | Leatherjacket | Y | | Y | |
| *Orthopristis chrysoptera* | Pigfish | Y | | Y | N |
| *Prionotus scitulus* | Leopard searobin | Y | | | N |
| *Prionotus tribulus* | Bighead searobin | Y | | Y | N |
| *Scorpaena brasiliensis* | Barbfish | Y | | | |

| Scientific Name | Common Name | Water Habitat | | | Seen in Dolphin Diets? |
|---|---|---|---|---|---|
| | | Marine | Freshwater | Brackish | |
| *Symphurus plagiusa* | Blackcheek tonguefish | Y | | Y | |
| *Syngnathus floridae* | Dusky pipefish | Y | | | |
| *Synodus foetens* | Inshore lizardfish | Y | | Y | N |
| *Trinectes maculatus* | Hogchoker | Y | Y | Y | |

Table B.2: Table of fish species that have significant spatial structure in the two field seasons combined for trawls. Habitat information (what type of water they inhabit) is from www.fishbase.org. In the column ”Seen in Dolphin diet?” from Berens-McCabe et al. (2010), P indicates positive selection, and N indicates negative selection for the species based on research in Sarasota Bay, Florida. Blank spaces indicate no information is available as to whether bottlenose dolphins consume these species.

FIGURES

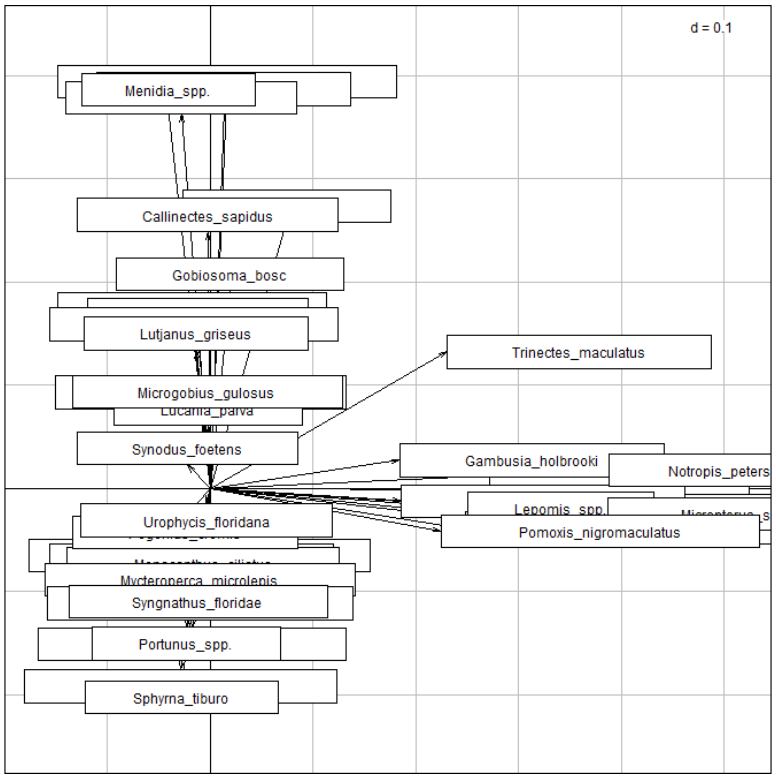
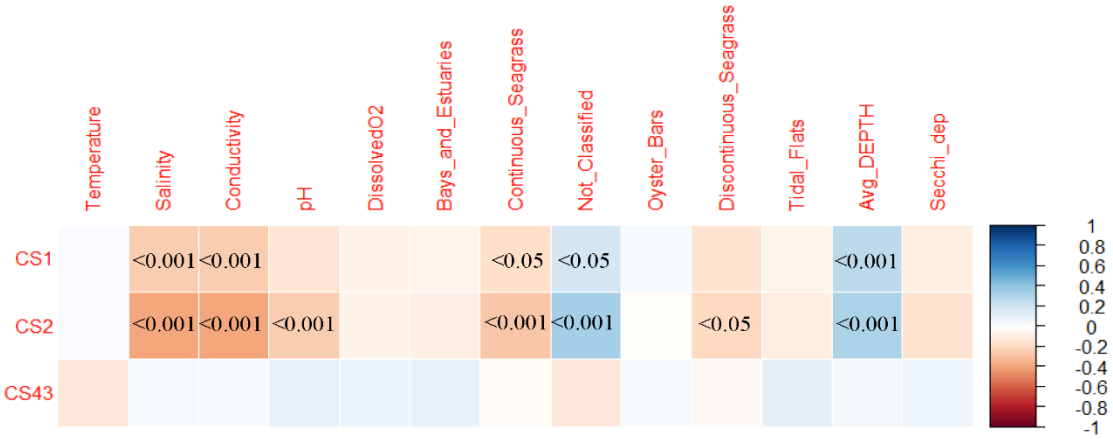



Figure B.1: Coefficients of variables projected on the first two axes of MULTISPATI for the Field Season 2008.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-Salinity | -0.3697 | -0.2502 | -0.12257 | 0.000716 |
| CS2- Salinity | -0.50206 | -0.3966 | -0.27952 | 1.72E-08 |
| CS1-Conductivity | -0.37115 | -0.25179 | -0.12423 | 0.000716 |
| CS2-Conductivity | -0.50294 | -0.3976 | -0.28062 | 1.72E-08 |
| CS2-pH | -0.37481 | -0.25576 | -0.12841 | 0.000649 |
| CS1-Continuous Seagrass | -0.29714 | -0.17221 | -0.04147 | 0.032998 |
| CS2-Continuous Seagrass | -0.38823 | -0.27038 | -0.14383 | 0.000348 |
| CS1-Not Classified | 0.056408 | 0.186695 | 0.310729 | 0.018655 |
| CS2-Not Classified | 0.212215 | 0.33454 | 0.446543 | 4.32E-06 |
| CS2-Discontinuous Seagrass | -0.32801 | -0.2052 | -0.07557 | 0.008268 |
| CS1-Average Depth | 0.140394 | 0.267129 | 0.385251 | 0.000361 |
| CS2-Average Depth | 0.192516 | 0.316175 | 0.429948 | 1.48E-05 |

Figure B.2: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for the field season 2008.

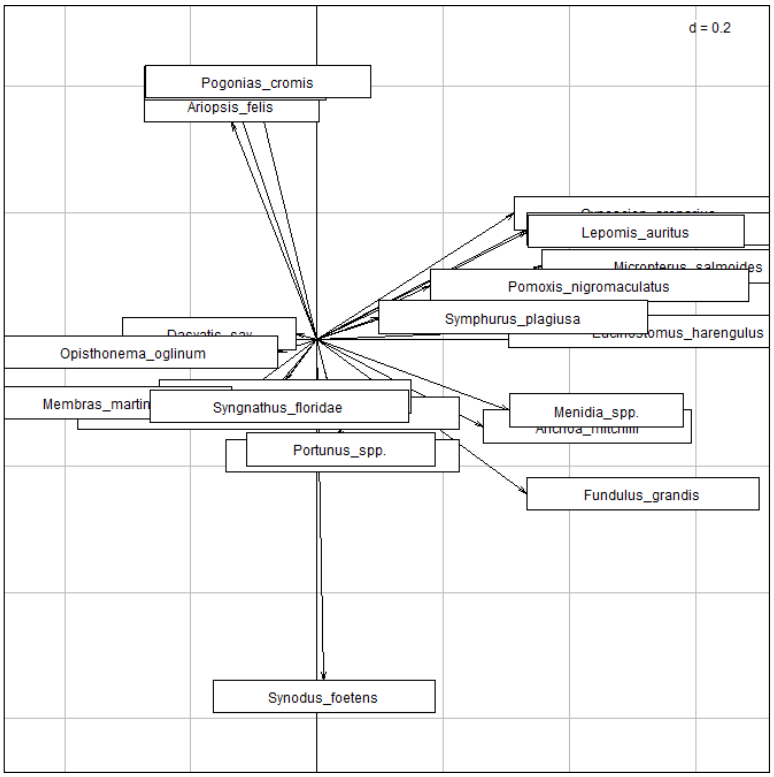
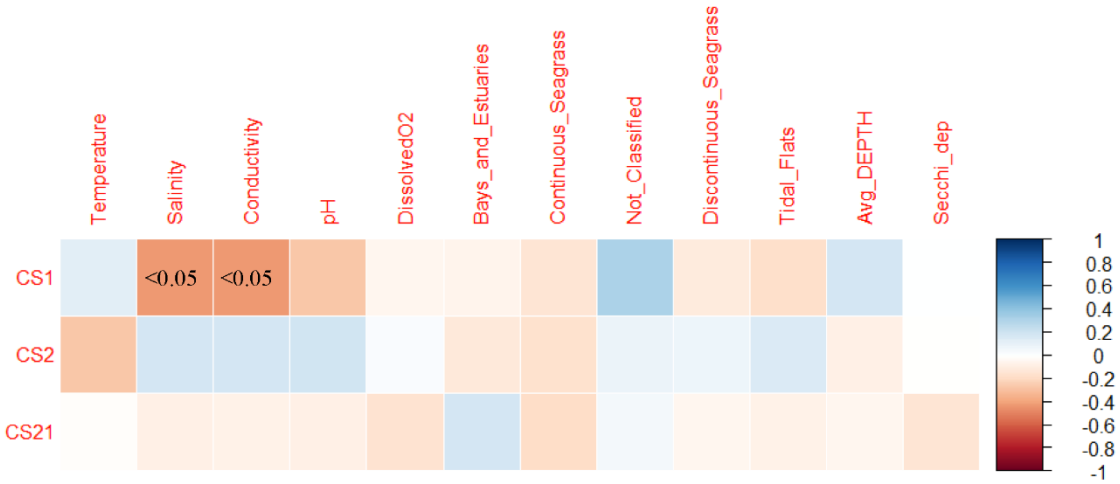



Figure B.3: Coefficients of variables projected on the first two axes of MULTISPATI for August 2008.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-Salinity | -0.64096 | -0.43886 | -0.17986 | 0.029784 |
| CS1-Conductivity | -0.6402 | -0.43782 | -0.17861 | 0.029784 |

Figure B.4: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for August 2008.

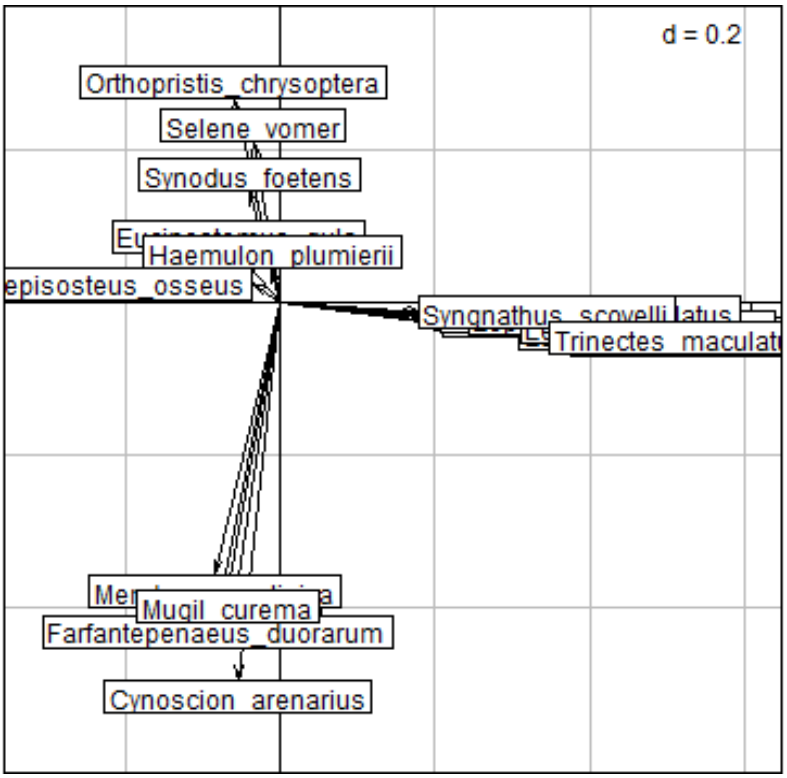
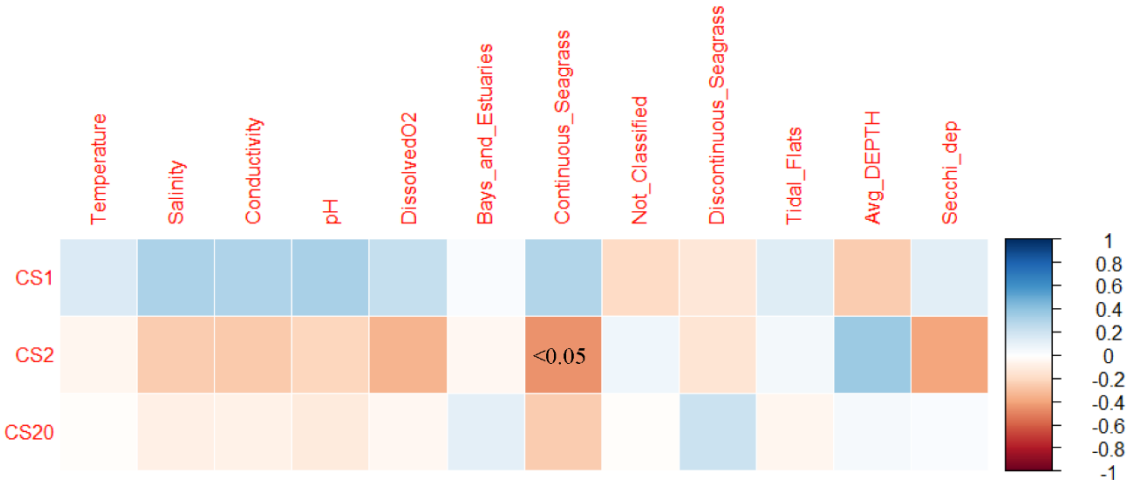



Figure B.5: Coefficients of variables projected on the first two axes of MULTISPATI for September 2008.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS2-Continuous Seagrass | -0.65053 | -0.45202 | -0.1957 | 0.040037 |

Figure B.6: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for September 2008.

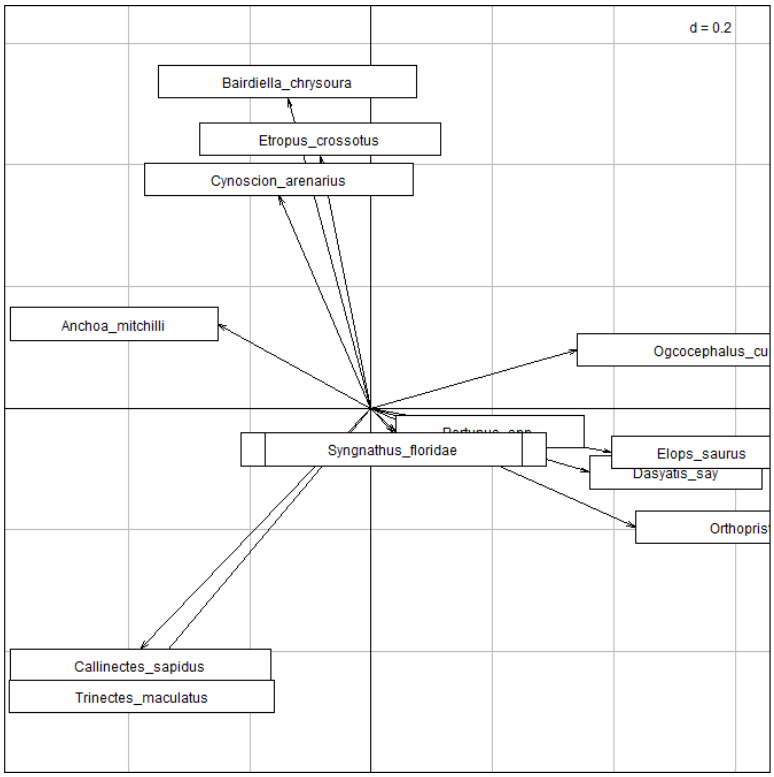
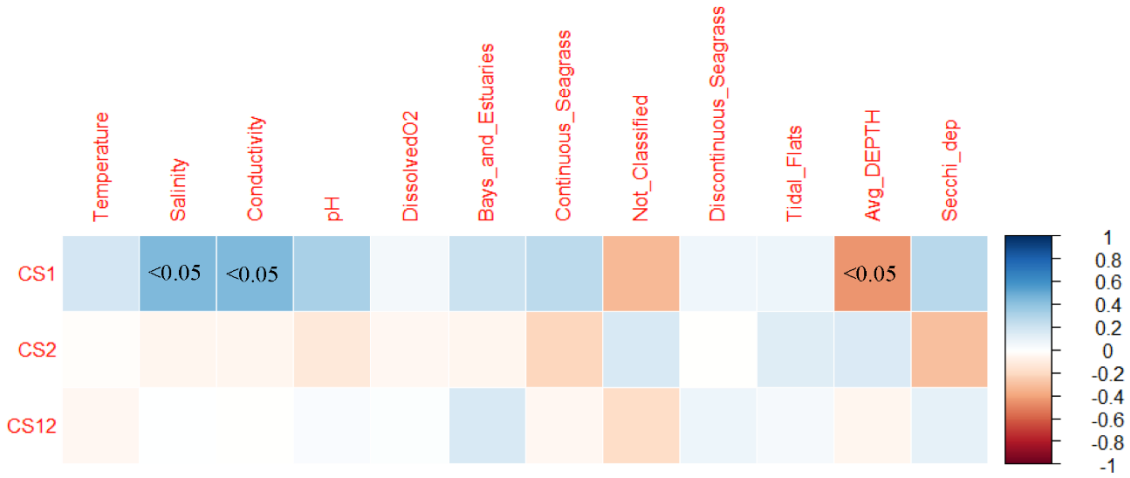



Figure B.7: Coefficients of variables projected on the first two axes of MULTISPATI for for October 2008.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-Salinity | 0.173707 | 0.447509 | 0.657091 | 0.030907 |
| CS1-Conductivity | 0.175281 | 0.448807 | 0.658012 | 0.030907 |
| CS1-Average Depth | -0.65415 | -0.44337 | -0.1687 | 0.030907 |

Figure B.8: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for October 2008.

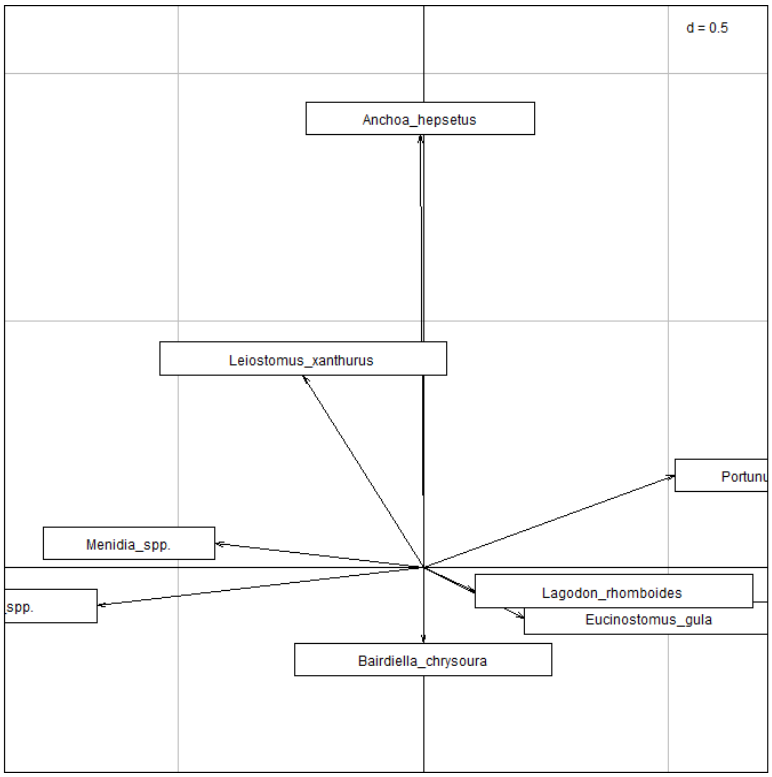
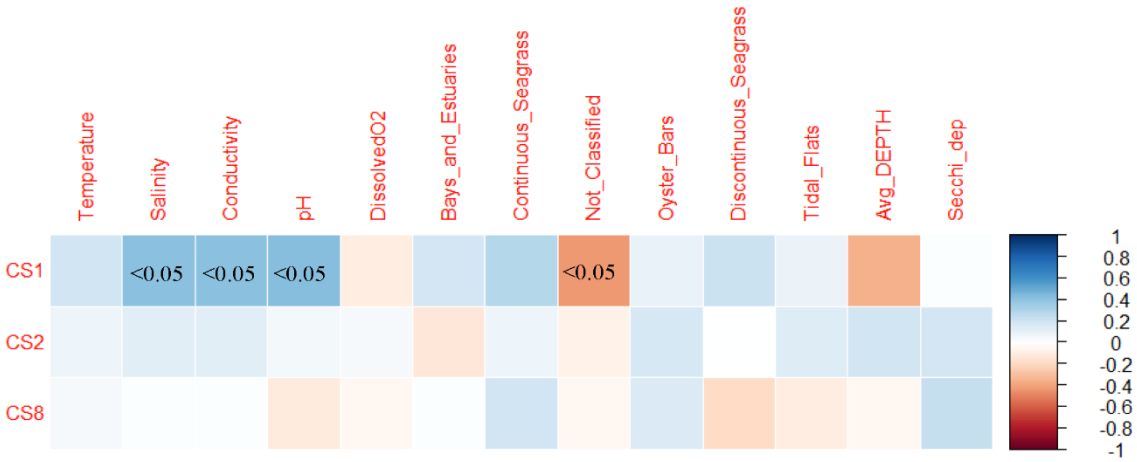



Figure B.9: Coefficients of variables projected on the first two axes of MULTISPATI for November 2008.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-Salinity | 0.13512 | 0.415339 | 0.634039 | 0.04927 |
| CS1-Conductivity | 0.136122 | 0.416184 | 0.634649 | 0.04927 |
| CS1-pH | 0.140975 | 0.420266 | 0.637594 | 0.04927 |
| CS1-Not Classified | -0.64911 | -0.43631 | -0.16017 | 0.04927 |

Figure B.10: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for November 2008.

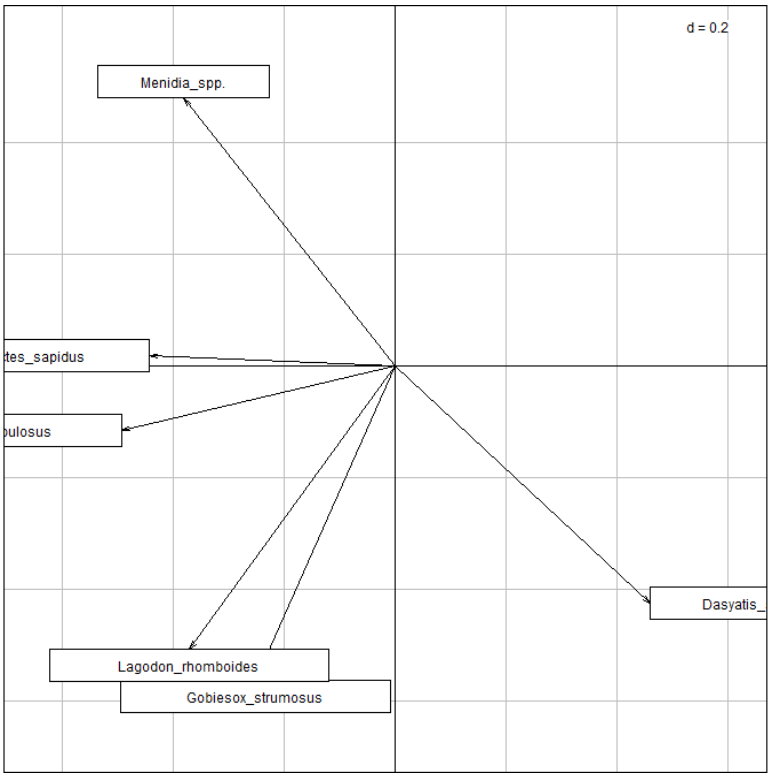



Figure B.11: Coefficients of variables projected on the first two axes of MULTISPATI for December 2008.

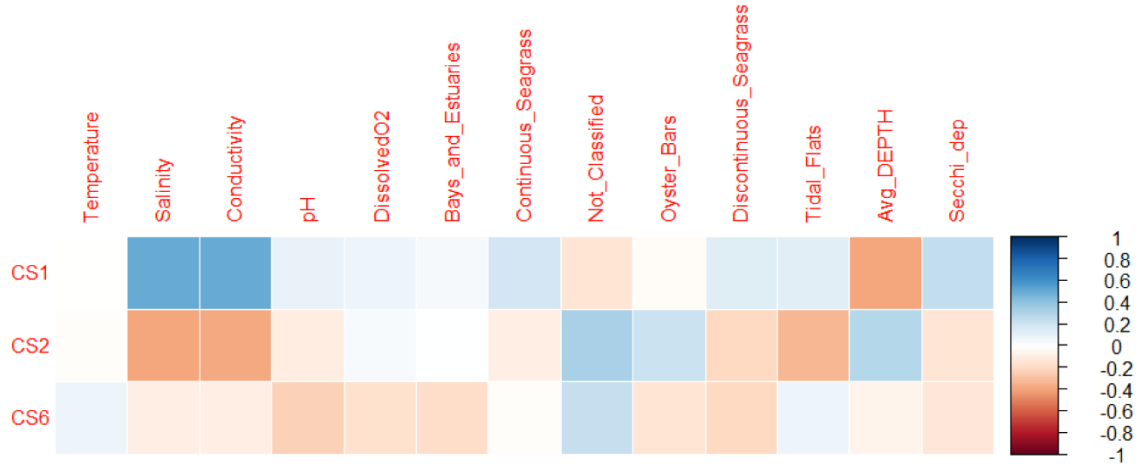



Figure B.12: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for December 2008. There are no significant correlations.

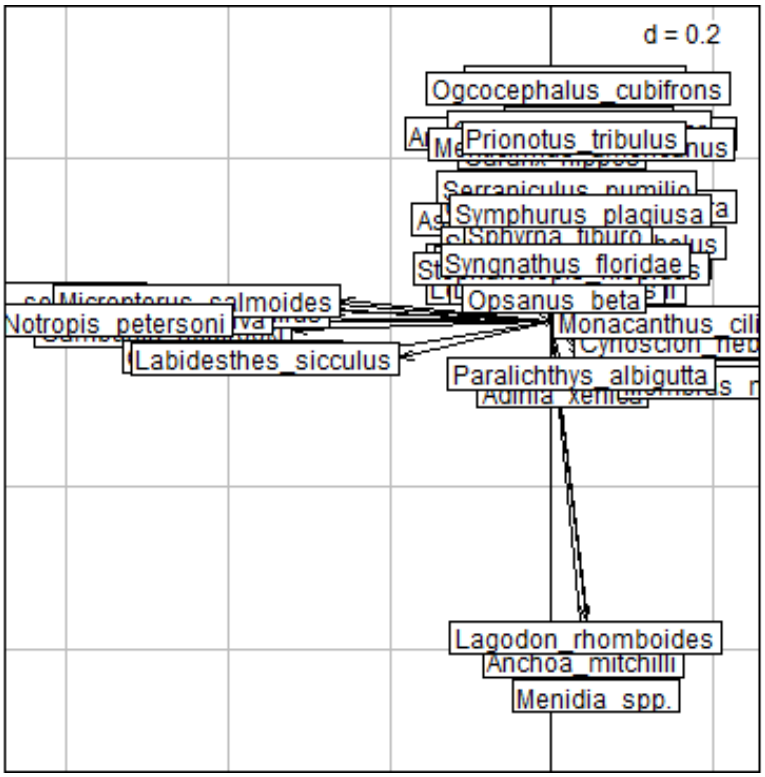
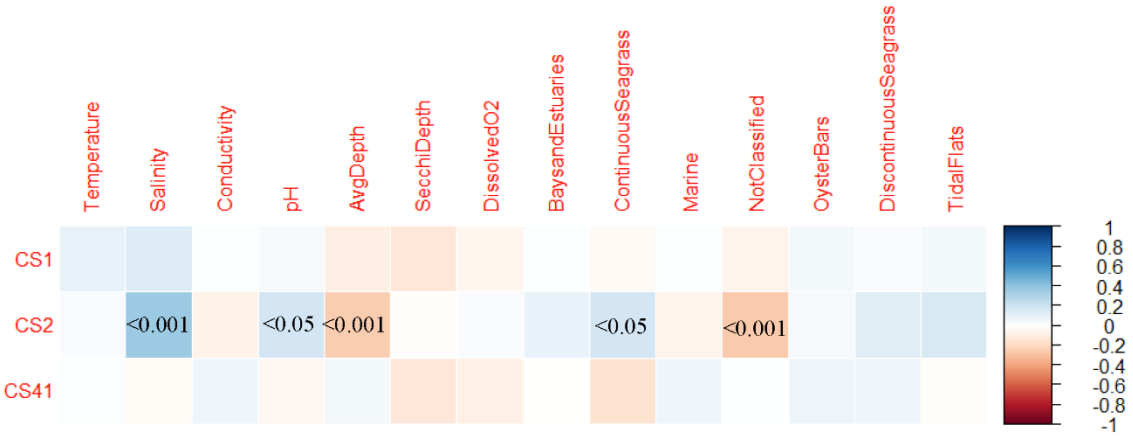



Figure B.13: Coefficients of variables projected on the first two axes of MULTISPATI for Contributions of species to the first and second MULTISPATI axes for the Field Season, 2010.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS2-Salinity | 0.252878 | 0.368911 | 0.474483 | 2.30E-07 |
| CS2-pH | 0.056814 | 0.183452 | 0.304281 | 0.047294 |
| CS2-Average Depth | -0.37069 | -0.25481 | -0.13111 | 0.001091 |
| CS2-Continuous Seagrass | 0.05334 | 0.180083 | 0.301116 | 0.047294 |
| CS2-Not Classified | -0.3825 | -0.26763 | -0.14461 | 0.000677 |

Figure B.14: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for the Field Season 2010.

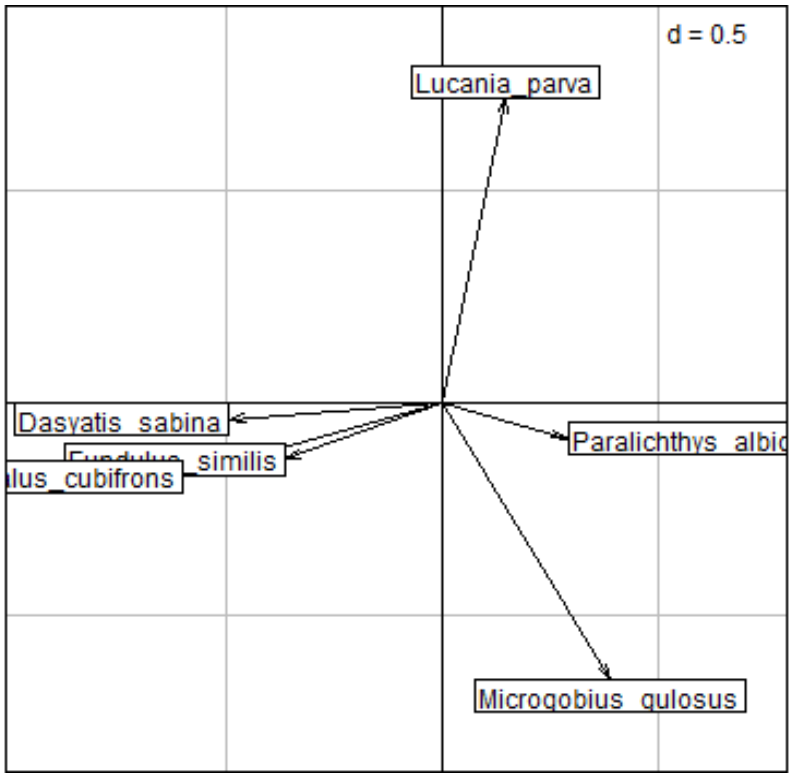



Figure B.15: Coefficients of variables projected on the first two axes of MULTISPATI for April 2010.

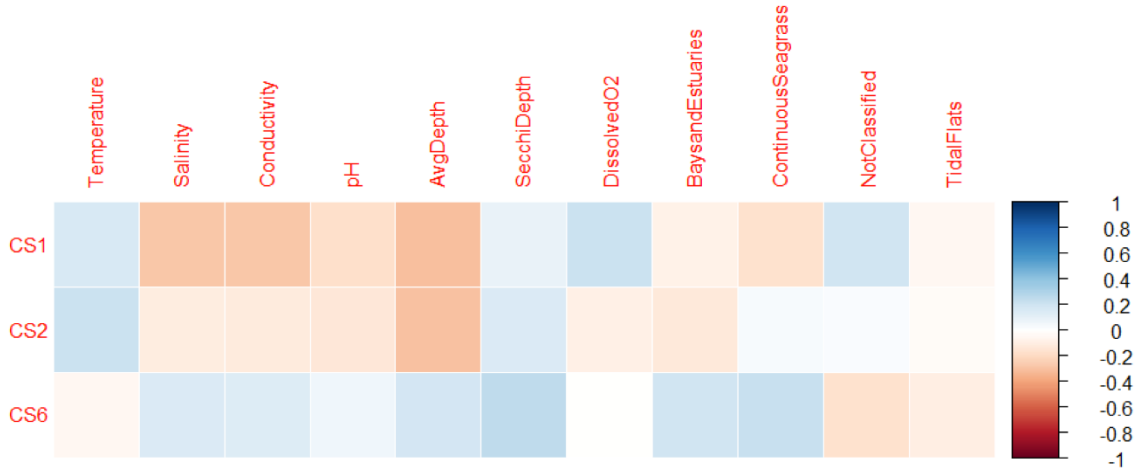



Figure B.16: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for April 2010. There are no significant correlations.

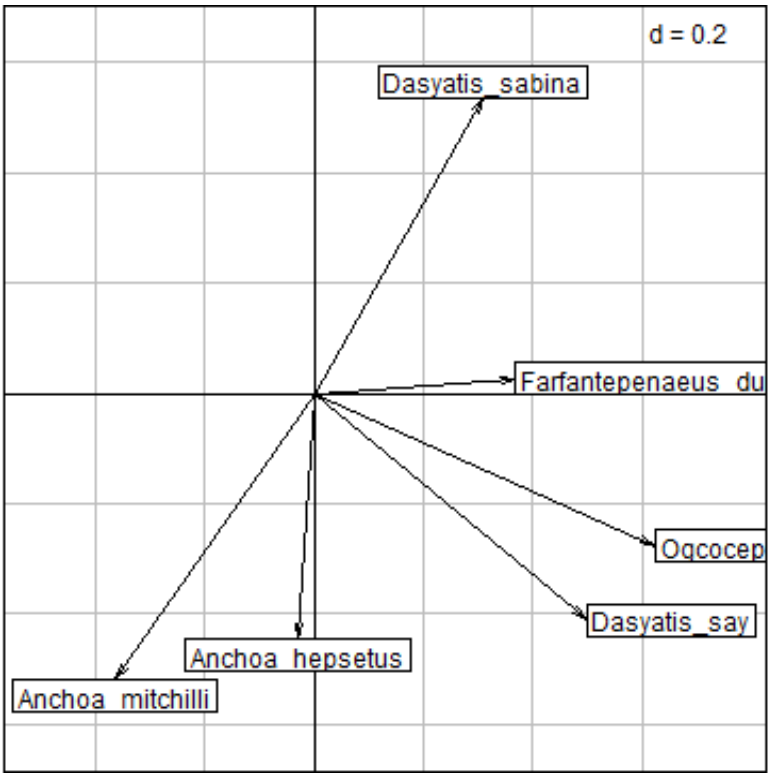



Figure B.17: Coefficients of variables projected on the first two axes of MULTISPATI for May 2010.

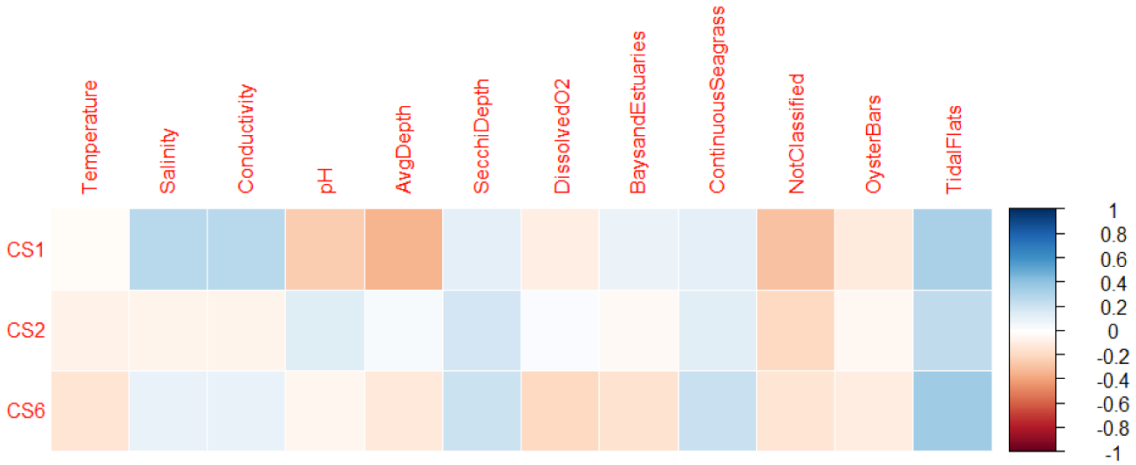



Figure B.18: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for May 2010. There are no significant correlations.

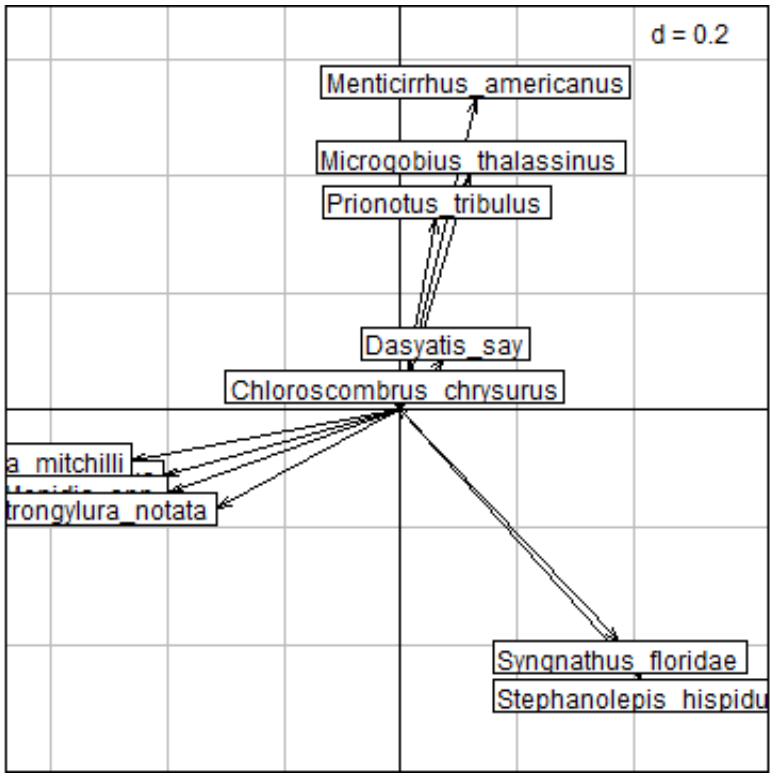
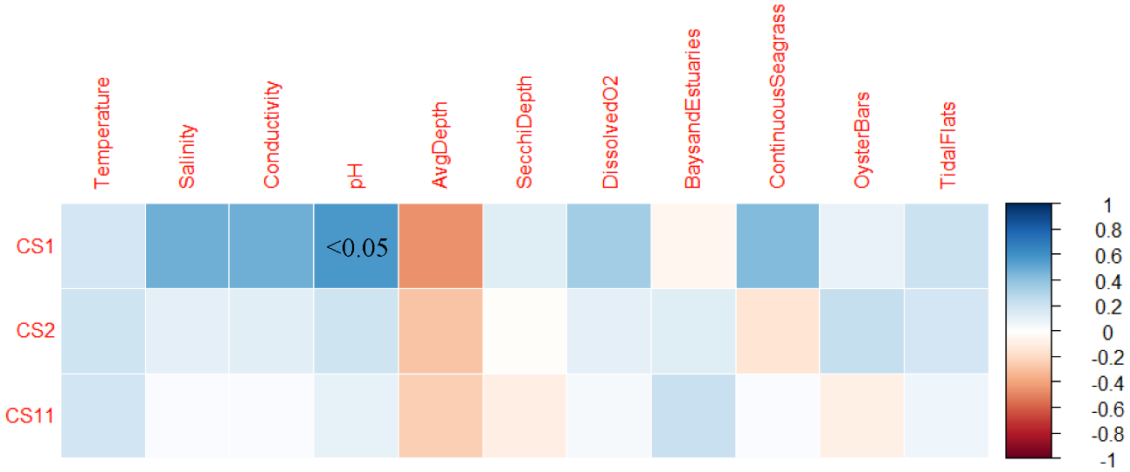



Figure B.19: Coefficients of variables projected on the first two axes of MULTISPATI for June 2010.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-pH | 0.269995 | 0.574393 | 0.774409 | 0.029767 |

Figure B.20: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for June 2010.

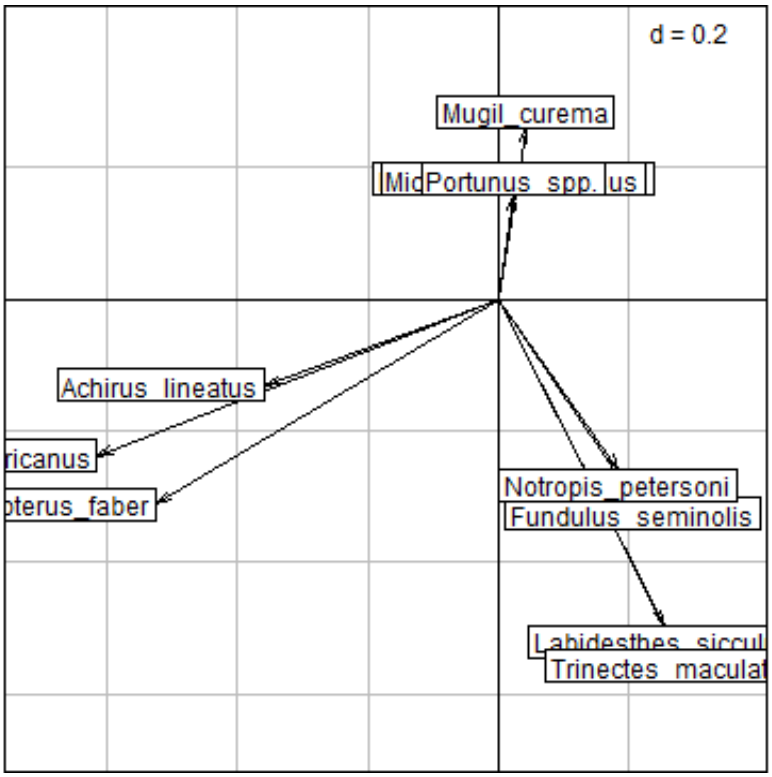



Figure B.21: Coefficients of variables projected on the first two axes of MULTISPATI for July 2010.

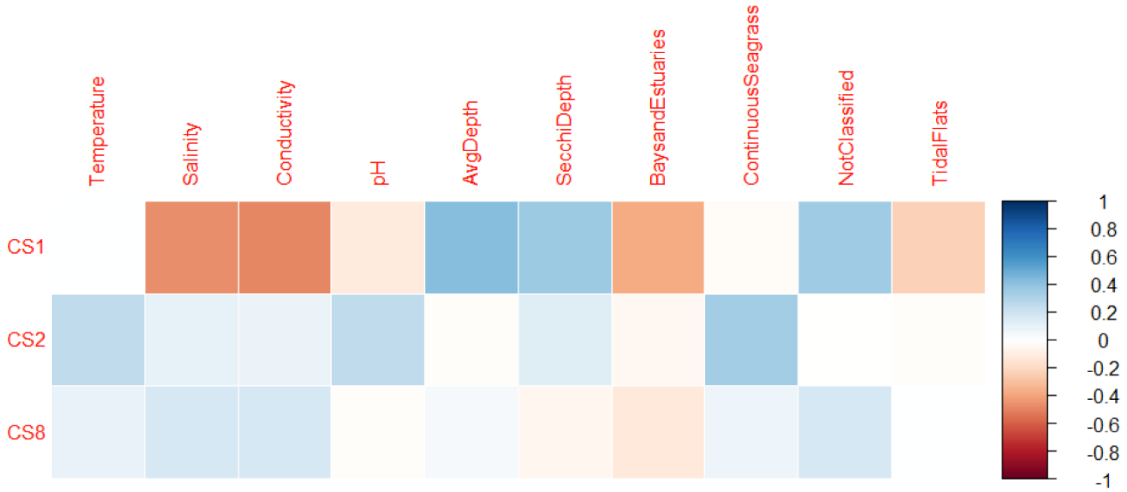



Figure B.22: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for July 2010. There are no significant correlations.

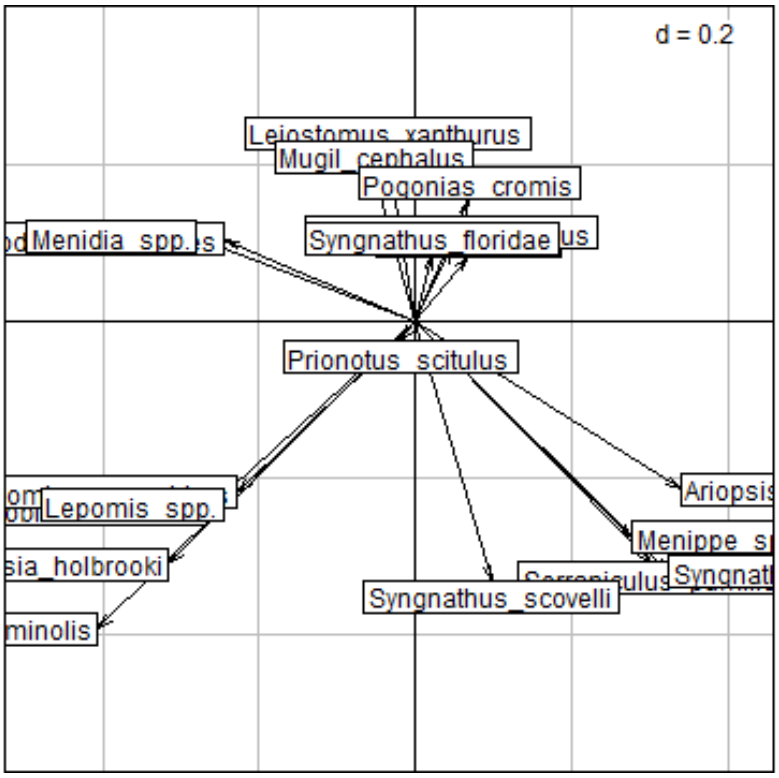
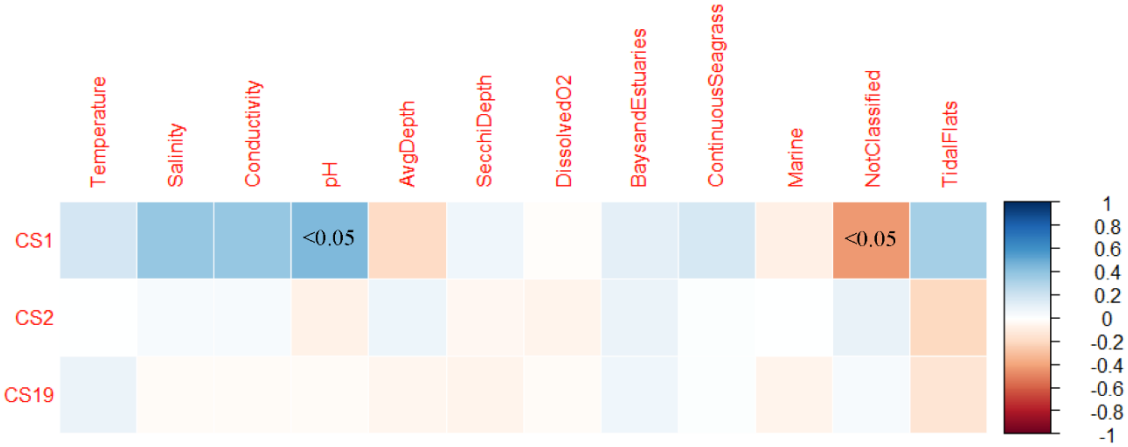
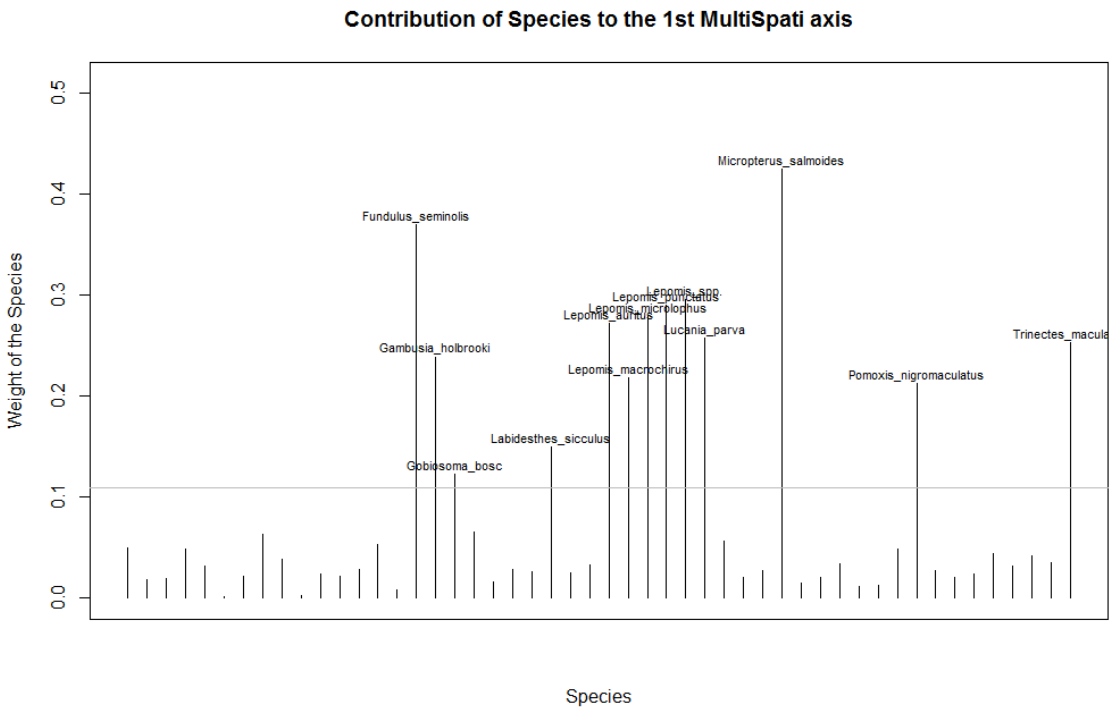


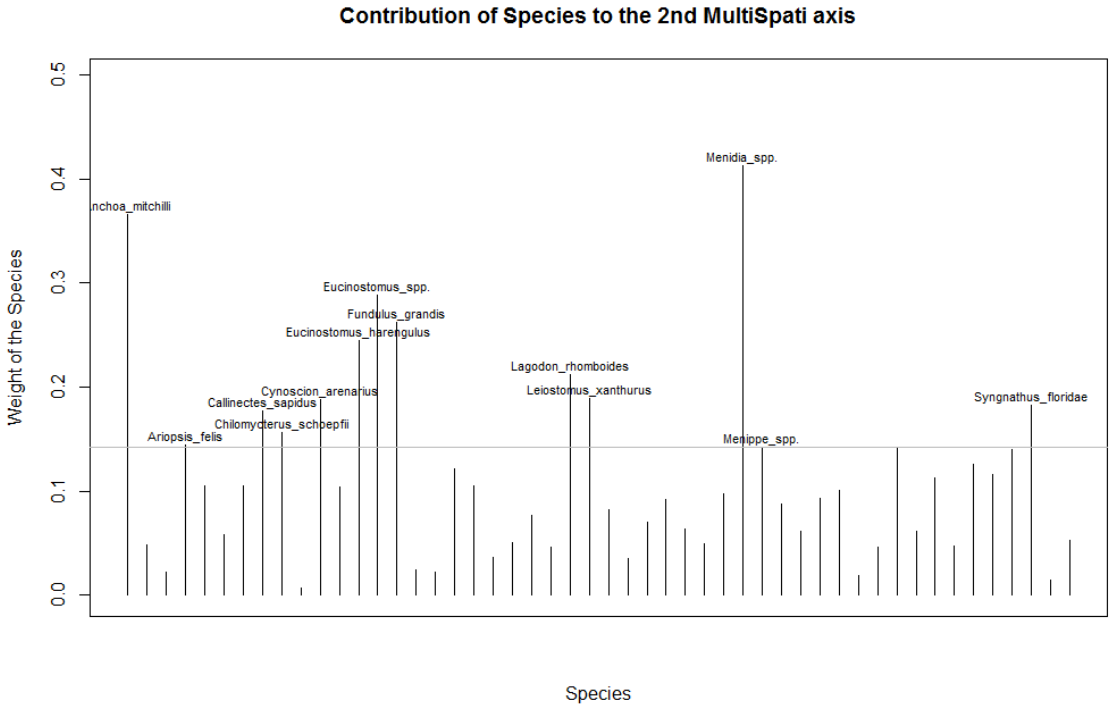

Figure B.23: Coefficients of variables projected on the first two axes of MULTISPATI for August 2010.




| | Lower C.I. | r | Upper C.I. | *p*-value |
|---|---|---|---|---|
| CS1-pH | 0.192992 | 0.44978 | 0.648905 | 0.03435 |
| CS1-Not Classified | -0.63636 | -0.43257 | -0.17234 | 0.03435 |

Figure B.24: Plot of correlations and table of significant correlations using Kendall's tau for the first two axes of the MULTISPATI site scores to environmental variables for seines for August 2010.


Contribution of Species to the 1st MultiSpati axis
Weight of the Species
0.0
0.1
0.2
0.3
0.4
0.5
Micropterus_salmoides
Fundulus_seminolis
Lepomis_spp.
Lepomis_punctatus
Lepomis_macrolophus
Lepomis_auritus
Lucania_parva
Trinectes_macula
Gambusia_holbrooki
Lepomis_macrochirus
Pomoxis_nigromaculatus
Labidesthes_sicculus
Gobiosoma_bosc
Species


Contribution of Species to the 2nd MultiSpati axis
Weight of the Species
0.0
0.1
0.2
0.3
0.4
0.5
Menidia_spp.
nchoa_mitchilli
Eucinostomus_spp.
Fundulus_grandis
Eucinostomus_harengulus
Lagodon_rhomboides
Leiostomus_xanthurus
Cynoscion_arenarius
Callinectes_sapidus
Chilomycterus_schoepfii
Ariopsis_felis
Syngnathus_floridae
Menippe_spp.
Species

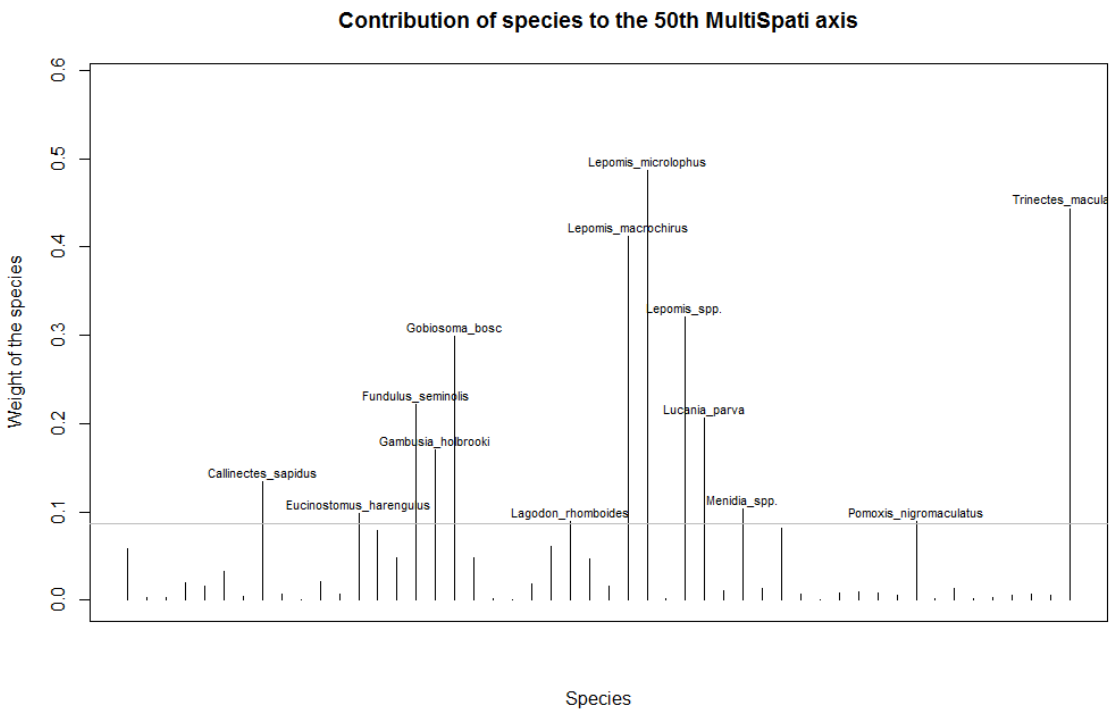
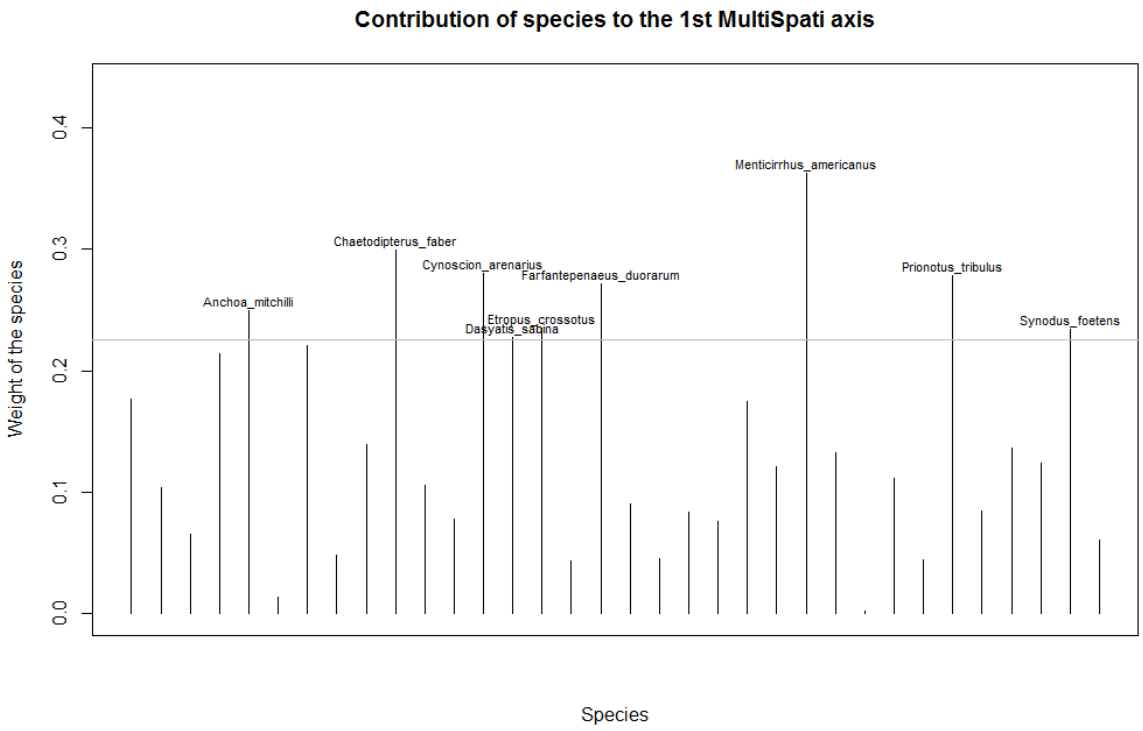
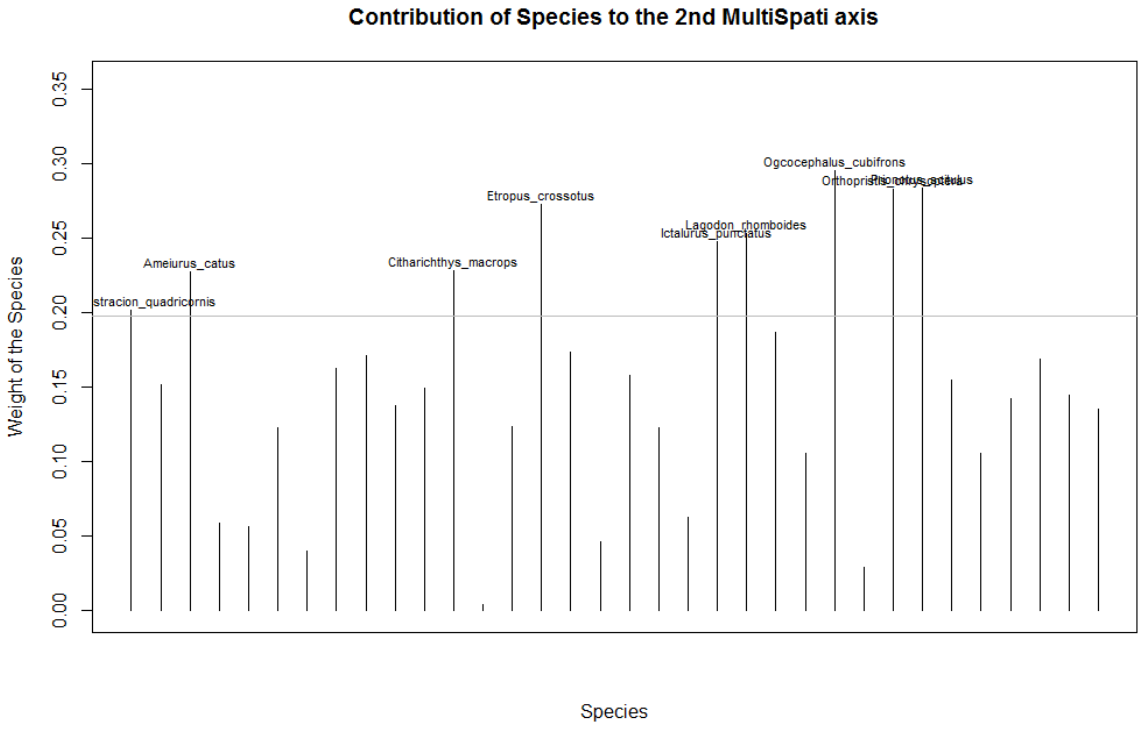



Figure B.25: Contributions of species to the first, second, and last MULTISPATI axes for both field seasons combined for seine collections. The species in the third quantile (upper third of the total species) that contribute to the total loading are named. This gives information on the most representative species that contribute to the analysis.


Contribution of species to the 1st MultiSpati axis
Weight of the species
0.0
0.1
0.2
0.3
0.4
Anchoa_mitchilli
Chaetodipterus_faber
Cynoscion_arenarius
Farfantepenaeus_duorarum
Etropus_crossotus
Dasyatis_sabina
Menticirrhus_americanus
Prionotus_tribulus
Synodus_foetens
Species


Contribution of Species to the 2nd MultiSpati axis
Weight of the Species
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
stracion_quadricornis
Ameiurus_catus
Citharichthys_macrops
Etropus_crossotus
Ictalurus_punctatus
Lagodon_rhomboides
Ogcocephalus_cubifrons
Species

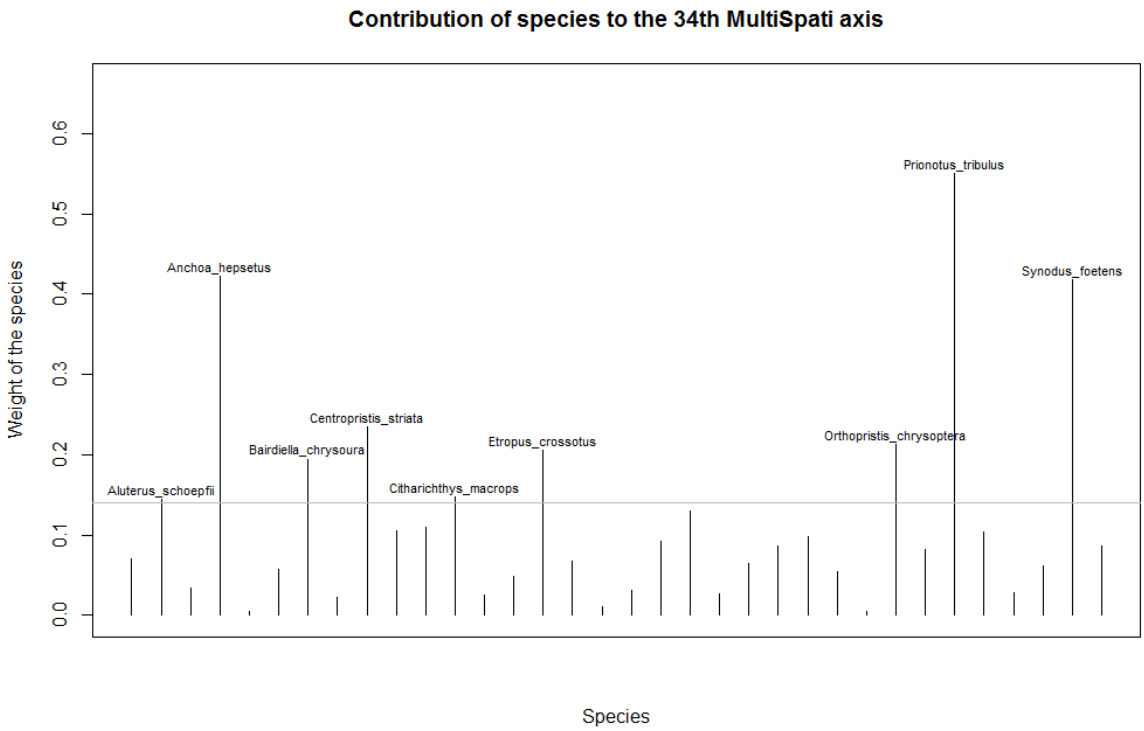
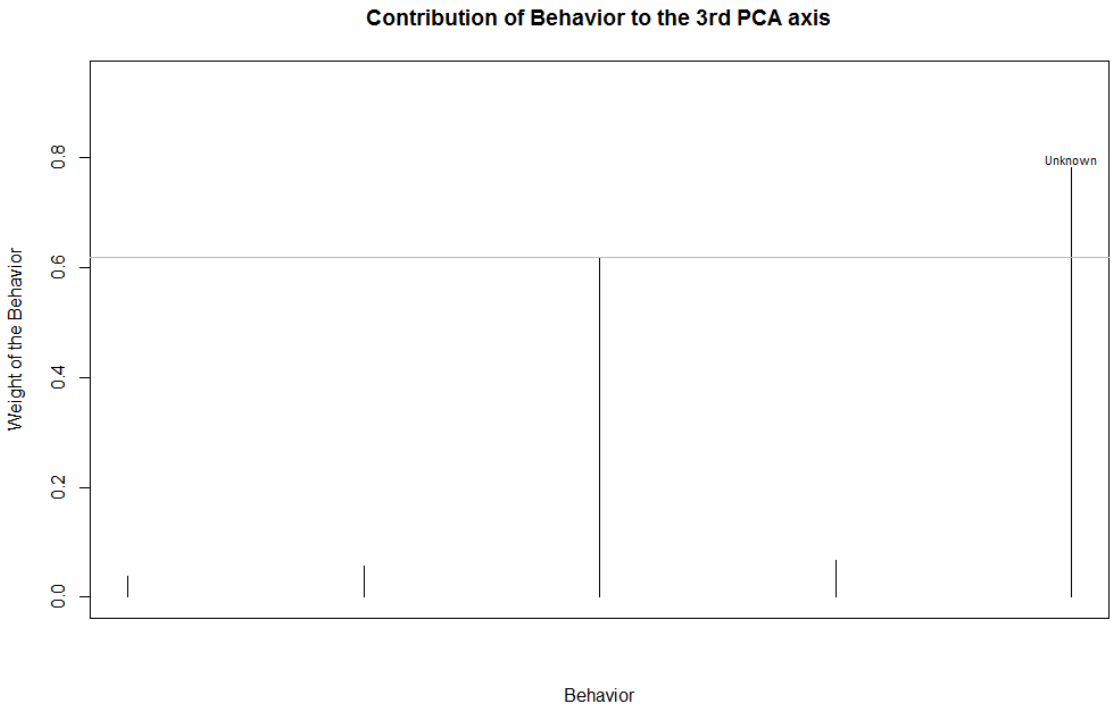
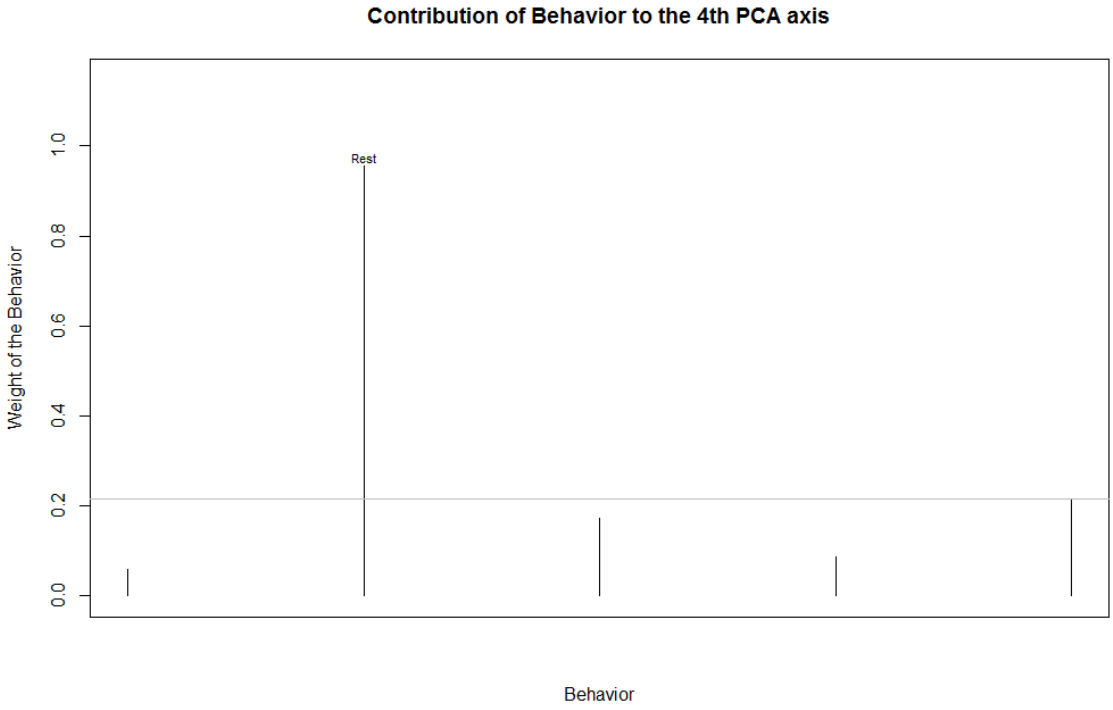



Figure B.26: Contributions of species to the first, second, and last MULTISPATI axes for both field seasons combined for trawl collections. The species in the third quantile (upper third of the total species) that contribute to the total loading are named. This gives information on the most representative species that contribute to the analysis.


Contribution of Behavior to the 3rd PCA axis
Unknown
Weight of the Behavior
0.0
0.2
0.4
0.6
0.8
Behavior


Contribution of Behavior to the 4th PCA axis
Rest
Weight of the Behavior
0.0
0.2
0.4
0.6
0.8
1.0
Behavior

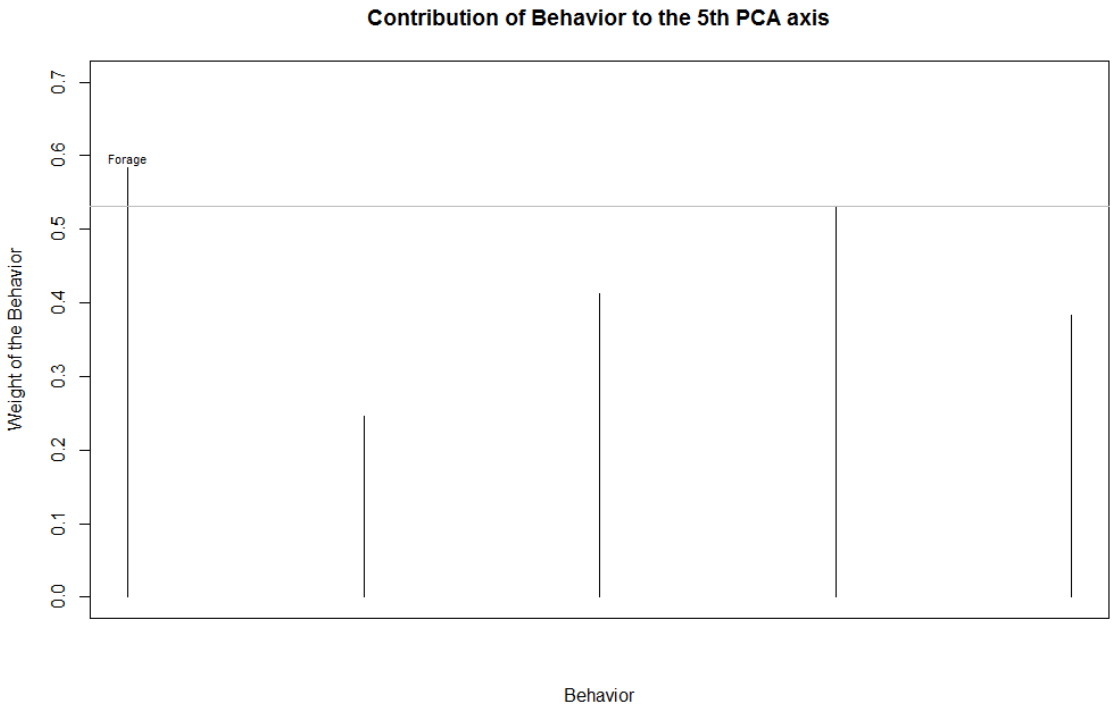
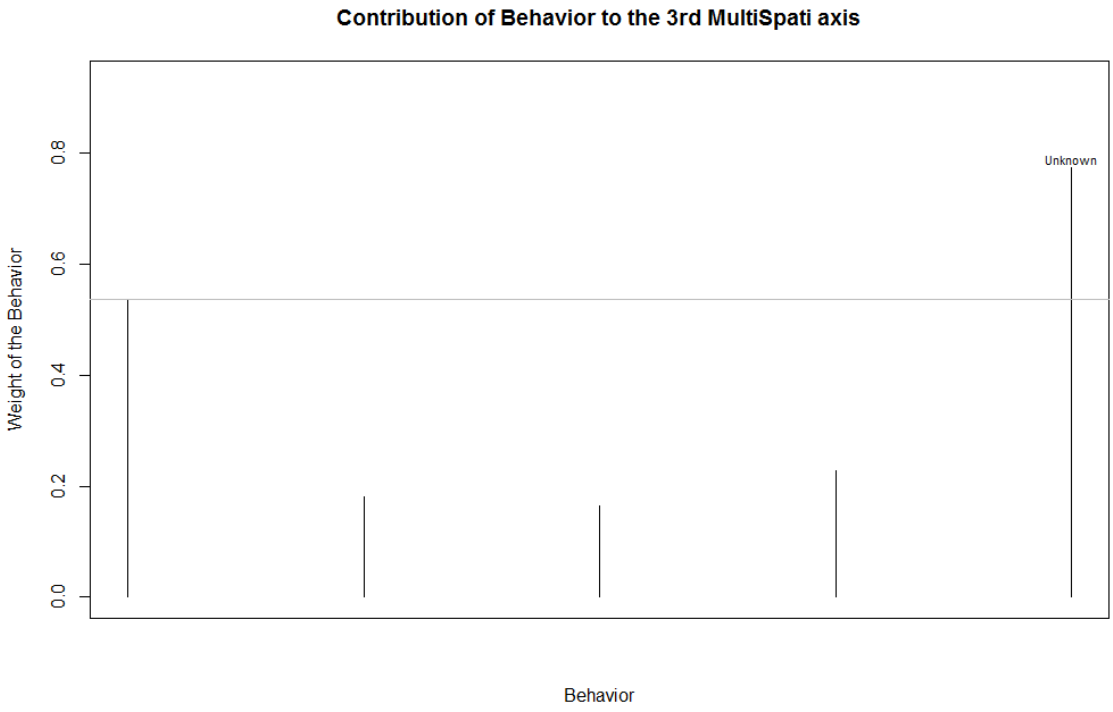
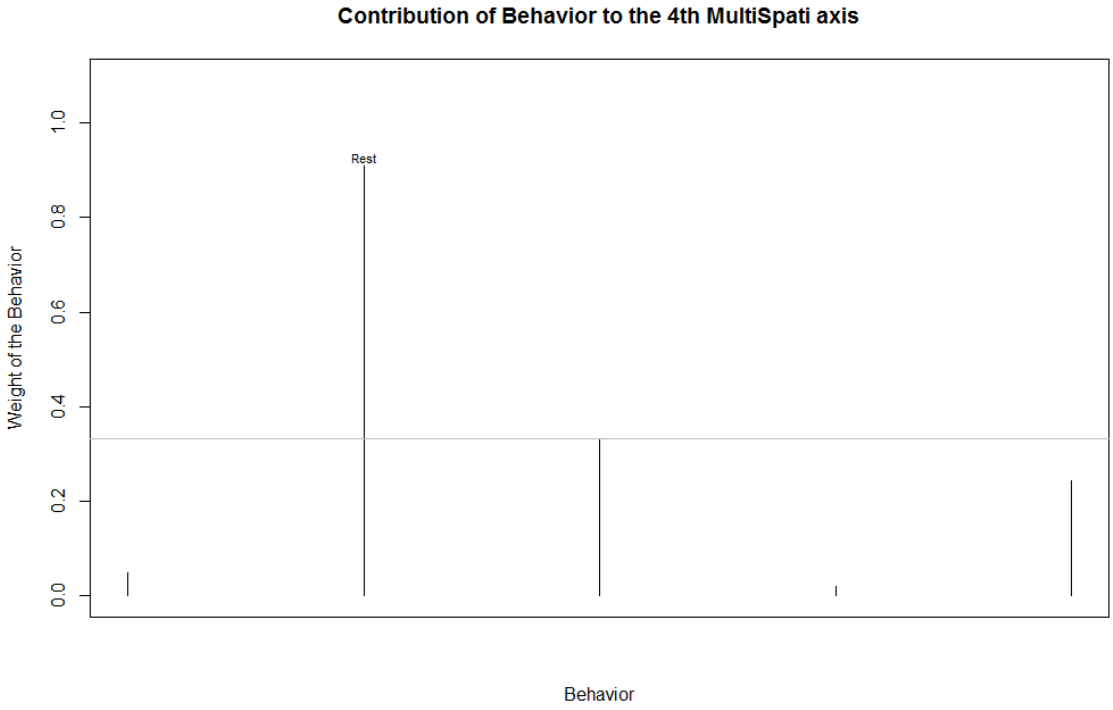



Figure B.27: Contributions of the dolphin behavior SPUEs to the third, fourth, and fifth PCA axes. The behavior in the third quantile (upper third of the total behaviors) that contribute to the total loading are named. This gives information on the most representative behaviors that contribute to the analysis.


Contribution of Behavior to the 3rd MultiSpati axis
Weight of the Behavior
0.0
0.2
0.4
0.6
0.8
Unknown
Behavior


Contribution of Behavior to the 4th MultiSpati axis
Weight of the Behavior
0.0
0.2
0.4
0.6
0.8
1.0
Rest
Behavior

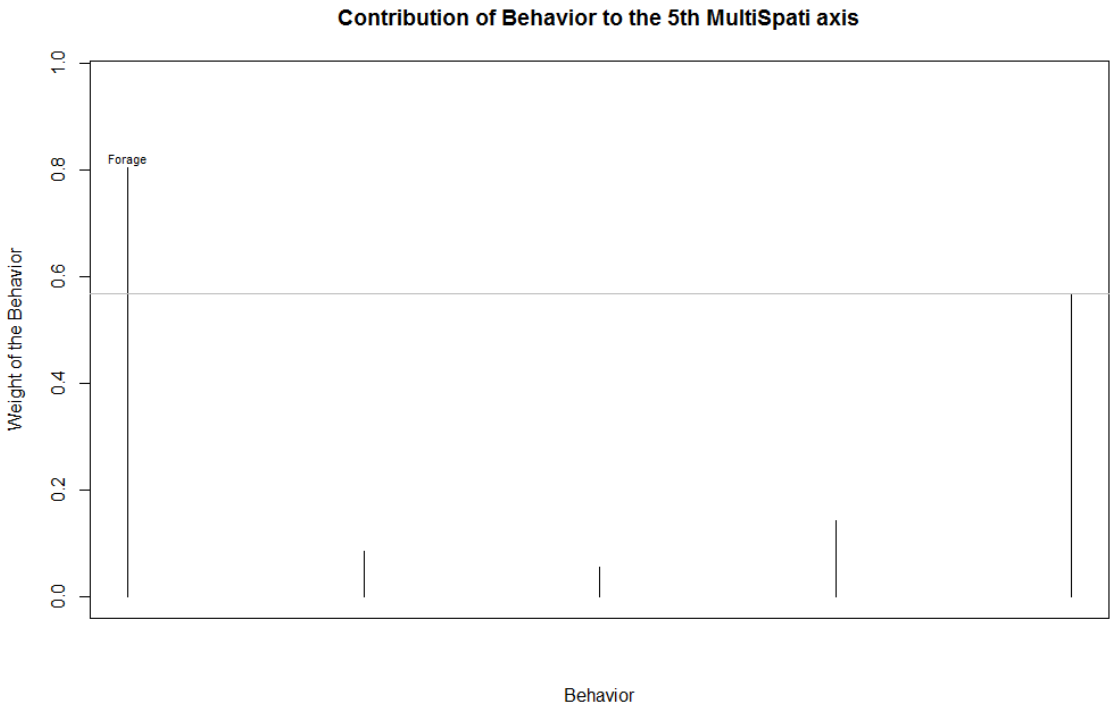



Figure B.28: Contributions of the dolphin behavior SPUEs to the third, fourth, and fifth MULTISPATI axes. The behavior in the third quantile (upper third of the total behaviors) that contribute to the total loading are named. This gives information on the most representative behaviors that contribute to the analysis.

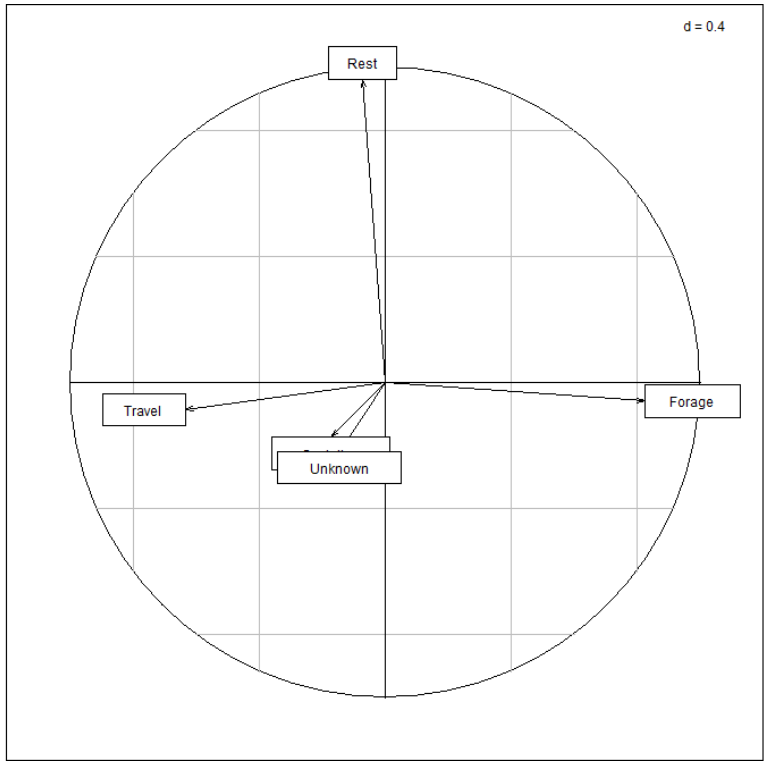



Figure B.29: PCA axis 1 (x axis) vs. 4 (y axis) for dolphin behavior SPUE.

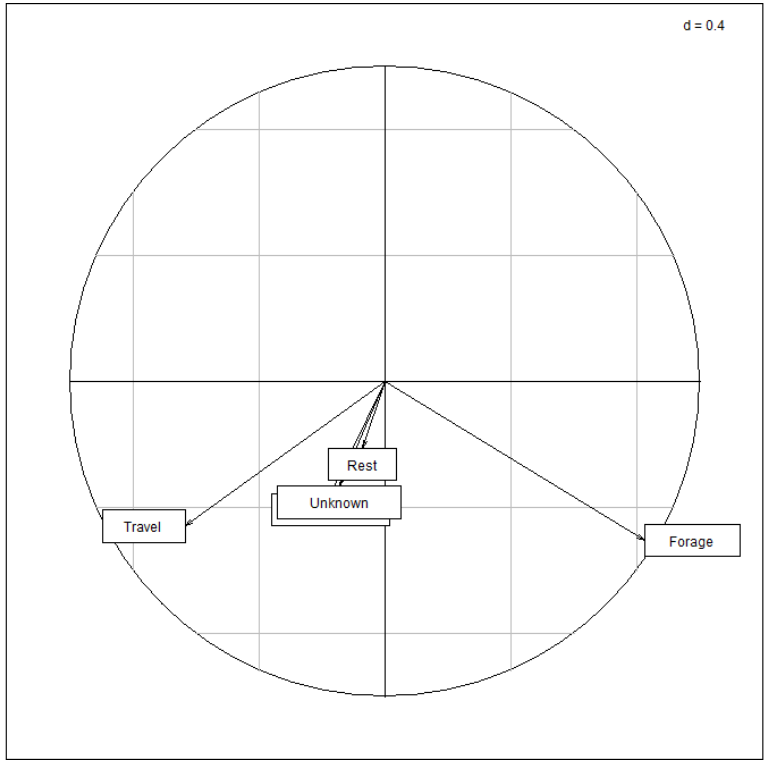



Figure B.30: PCA axis 1 (x axis) vs. 5 (y axis) for dolphin behavior SPUE.

## EDUCATION

| | | |
|---|---|---|
| | **University of Massachusetts Boston** | Boston, MA |
| 2007–present | *Ph.D. Candidate, Intercampus Marine Sciences Graduate Program* | |
| | *Expected Date of Graduation: Winter 2015* | |
| | **University of Massachusetts Dartmouth** | North Dartmouth, MA |
| 2002 | *Master of Science, Marine Biology* | |
| | **University of New Hampshire** | Durham, NH |
| 2000 | *Bachelor of Science, Marine and Freshwater Biology* | |

## PROFESSIONAL EXPERIENCE

| | | |
|---|---|---|
| | **University of Massachusetts Boston** | Boston, MA |
| | *Instructor of Record:* | |
| 2012–present | Introduction to Biology, semester II | |
| 2012 | Animal Behavior | |
| 2009–present | *Graduate Teaching Assistantship:* | |
| | Marine Mammal Biology | |
| | Population Biology | |
| | Introduction to Nutrition | |
| | Introduction to Biology Laboratories | |
| 2008 | *Graduate Research Assistantship:* | |
| | Habitat in Relation to Foraging Behaviors in Bottlenose Dolphins *(Tursiops truncatus)* off Cedar Key, Florida. | |
| | **New England Aquarium** | Boston, MA |
| 2002–2007 | *Program Supervisor: Overnights and Outreaches* | |
| 2002 | *Overnight Program Coordinator* | |
| 2000–2002 | *Program Educator* | |
| | **University of Massachusetts Dartmouth** | North Dartmouth, MA |
| 2002 | *Assistant to the Biology Laboratory Coordinator* | |
| 2001–2002 | *Graduate Research Assistantship* | |
| 2000–2002 | *Master of Science Thesis* | |
| | Title: Evidence of Role Specialization among Foraging Bottlenose Dolphins (*Tursiops truncatus*) off Cedar Key, Florida. | |
| 2000–2002 | *Graduate Teaching Assistantship* | |

**PUBLICATIONS**

Gazda S, S. Iyer, T. Killingback, R. Connor, and S. Brault. 2015. The importance of delineating networks by activity type in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida. *Royal Society Open Science*. 2: 140263. http://dx.doi.org/10.1098/rsos.140263

Gazda, S.K., R. C. Connor, R. K. Edgar, and F. Cox. 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 272: 135–140.

Gazda, S. K. 2004. Cooperative hunting among dolphins. In: *Encyclopedia of Animal Behavior*, Volume 2. ed: Bekoff, M. Greenwood Press. 508–509.

**CONFERENCE PRESENTATIONS**

2012

Mehta, A., S. Gazda, and S. Brault. *Stable isotope analysis of juvenile fish species of the coastal ecosystem of the Gulf of Mexico*. Talk presented at: The Biology/Biochemistry Honors Poster Session 2012 May 23; Boston MA.

Paynter, I., S. K. Gazda, and S. Brault. *Range overlap networks in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida.* Talk presented at: The School for Marine Sciences Research Colloquium, 2012; Boston, MA.

Soden, C., S. Gazda, and S. Brault. *Identification of PCBs in Coastal fishes from the Gulf of Mexico, off Cedar Key Florida*. Talk presented at: The Biology/Biochemistry Honors Poster Session 2012 May 23; Boston MA.

2011

Gazda, S.K., S. Iyer, T. P. Killingback, R. C. Connor, and S. Brault. *Network analysis by activity reveals community overlap and differences in centrality of individuals in Bottlenose Dolphins (Tursiops truncatus) in Cedar Key, Florida.* Poster session presented at: The 19th Biennial Conference on the Biology of Marine Mammals; 2011 Nov 28—Dec 2; Tampa Bay, FL.

Paynter, I., S. K. Gazda, R. C. Connor, and S. Brault. *Are network position and habitat use predictors of dietary specialization in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida*? Poster session presented at: The 18th Biennial Conference on the Biology of Marine Mammals; 2011 Nov 28—Dec 2; Tampa Bay, FL.

Gazda, S.K., S. B. Brault, S. Iyer, T. Killingback, and R. C. Connor. *Social Networks of bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida.* Talk presented at: The School for Marine Sciences Research Colloquium, 2011, April 8; Lowell, MA.

**CONFERENCE PRESENTATIONS**

| | |
|---|---|
| 2010 | Ciarfella, C., S. K. Gazda, S. Iyer, S Brault, and T. Killingback. *Residency patterns and social structure of bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida*. Poster session presented at: The Biology/Biochemistry Honors Poster Session, 2010 June 1; Boston, MA. |
| 2009 | Gazda, S.K., R. C. Connor, and S. Brault. *Don't hit that crab pot! Foraging behavior and distribution of bottlenose dolphins in relation to prey in Cedar Key, Florida.* Poster session presented at: The 18th Biennial Conference on the Biology of Marine Mammals; 2009 Oct 12-16; Quebec City, Canada. |
| 2003 | Gazda, S.K, R. C. Connor, and R. K. Edgar. *Evidence of role specialization among foraging bottlenose dolphins* (Tursiops truncatus) *off Cedar Key, Florida.* Talk presented at: The Society for Marine Mammalogy 15th Biennial Conference, 2003 Dec, Greensboro, NC. |
| 2002 | Gazda, S.K, R. C. Connor, and R. K. Edgar. *Evidence of role specialization among foraging bottlenose dolphins* (Tursiops truncatus) *off Cedar Key, Florida.* Talk presented at: New England Estuarine Research Society, 2002 May, Bar Harbor, |

**GRANTS AWARDED**

| | |
|---|---|
| 2012 | Herbert Lipke Memorial Endowment Fund<br>$350.00 |
| 2011 | School for Marine Sciences Seed Grant (co PI; PIs S. Brault, R. C. Connor) |
| 2010 | Nancy Goranson Endowment (PI)<br>$1,000.00 |
| 2010 | Waitt Grant, National Geographic Society (PI; co PIs S. Brault, R. Connor)<br>$14,520.00 |
| 2010 | International Fund for Animal Welfare (PI)<br>$7,000.00 |
| 2009 | Herbert Lipke Memorial Endowment Fund<br>$500.00 |
| 2008 | American Society of Mammalogists (PI)<br>$1,500.00 |
| 2008 | Explorer's Club of New York (PI)<br>$1,500.00 |
| 2008 | National Geographic Society (PI; co PI R. Connor)<br>$26,000.00 |

**PROFESSIONAL MEMBERSHIPS**

American Society of Mammalogists
Animal Behavior Society
Society for Marine Mammalogy

**SYNERGISTIC ACTIVITIES**

| | |
|---|---|
| **2007** | *Humanimal, the Animal Mind,* "The Dolphin" Mona Lisa Productions |
| **February 12, 2005** | *Quirks and Quarks*, "Dolphin Herders" CBC Radio One |
| **June 2003** | *Wildlife on One*, "Dolphins—Deep Thinkers?" BBC |

**AWARDS**

| | |
|---|---|
| **2002** | Addison-Wesley/Benjamin-Cummings/Longman Book Publisher's Award |

**CERTIFICATIONS**

| | |
|---|---|
| **1999–present** | Massachusetts Licensed Commercial Driver, Class B, air brake certified |
| **1988–present** | SCUBA Certification, Registered PADI Advanced Open Water Diver |