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Feeding Ecology of Skates and Rays in Delaware and Narragansett Bays

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FEEDING ECOLOGY OF SKATES AND RAYS IN DELAWARE AND NARRAGANSETT BAYS: AN ANALYSIS OF RESOURCE USAGE

BY

JOHN ANDREW SZCZEPANSKI, JR.

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DOCTOR OF PHILOSOPHY DISSERTATION

OF

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ABSTRACT

Skates and rays are an integral part of the trophic structure of many estuarine ecosystems. However, there are many aspects of the fisheries biology of these species that require further exploration. For example, few comparisons have been done of the feeding habits of sympatric species that potentially overlap in resource usage, diets over time, or food preferences between fish populations from different regions. Most of what is known of batoid elasmobranch (skate and ray) diets on the Western Atlantic coast is a compilation of data from the entire continental shelf with no distinction of diets for populations within different estuaries that vary in abiotic characteristics and trophic structure. My research objectives were to: (1) quantitatively characterize the diets of the major batoid elasmobranchs (skates and rays) in Delaware Bay and in Narragansett Bay, (2) describe seasonal variation in diet, if any, (3) examine diet overlap and food resource partitioning among species within each ecosystem, and (4) compare diets of selected species between the geographic locations (specifically populations of Little, Winter, and Clearnose skates; *Leucoraja erinacea*, *L. ocellata,* and *Raja eglanteria,* respectively,). Through gut content analysis, calculation of trophic level and overlap indices, and multivariate statistical techniques such as non-metric multidimensional scaling and ANOSIM, diets of 3 different batoids were characterized; 2 from Delaware Bay and 1 from Narragansett Bay. The diets of the bullnose ray *Myliobatis freminvillii*, the Clearnose skate *Raja eglanteria*, and the little skate *Leucoraja erinacea* were also evaluated for ontogenetic, spatial, and temporal differences within their respective species. *Myliobatis freminvillii* was considered a moderate gastropod specialist with shifts in diet over ontogeny. *Raja eglanteria* was characterized as a generalist with preferences for benthic crustaceans, exhibiting ontogentic differences between juveniles and adults, and strong dietary differences between sexes. *Leucoraja erinacea* was determined to be a broad-scale generalist preferring amphipods and sand shrimp and was shown to feed based on prey availability since there were temporal and spatial differences in diet that corresponded to variations in prey abundance. These data were used to contribute to estuary-specific community analyses of batoid trophic relationships in Delaware and Narragansett Bays and a comparison of the trophic dynamics between those two communities. The skate species of Narragasett Bay exhibited significantly

different diets, but did not show ontogenetic differences when compared together. The skates and rays of Delaware Bay showed differences in diet by species and by size within species. It is proposed that a higher level of partitioning exists in Delaware Bay since there are more batoid species to compete for resources, but this would only be the case if resources were limiting and data were not collected that could confirm this. Since all the organisms studied were benthic secondary consumers based on available data, the diets of the batoids in each estuary were found not to be significantly different. Any observed differences were not due to the specific prey species that were found in the diet but to the proportions of the various prey that were consumed.

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First of all, I am indebted to Dr. David Bengtson for his confidence in my abilities and willingness to support my scholarly endeavors when others did not. I am truly grateful for his guidance as my major advisor and feedback as a fellow scientist. I would also like to thank the rest of the members of my committee for their advice and expertise: Dr. Cliff Katz, Dr. Ted Durbin, Dr. Jeremy Collie, and Dr. Brad Seibel. A major portion of my research, the sample collection, would not have been possible without the help of the RI Department of Environmental Management and the DE Department of Natural Resource and Environmental Control. Specifically, I am grateful to the crews of the R/V Chaffee and the R/V First State; Scott Olszewski, Captain Richard Mello, Dan Costa, Ken Benson, and Stewart Michels, Captain Mike Garvilla, Mike Greco, Jordan Zimmerman, Nate Rust, Garry Glanden, respectively. My sample processing and cataloguing were facilitated by Peter Schooling, a Coastal Fellow who chose to work with me, Christina Lemnotis and Juliana DeLuca; they have certainly earned my sincerest respect and gratitude for helping me undertake a good portion of the "dirty work." As my academic sibling, Dr. Barry Volson also deserves to be acknowledged. Barry kept me laughing and thinking, and reassuring me that if he could do it [earn a doctoral degree], so could I.

There are many other people I need to thank at the University of Rhode Island. I am very grateful for the constant support and advice given to me by Dr. Marian Goldsmith as I advanced through my course of study and research. I also would like to thank various faculty members, particularly Dr. Bob Bullock and Niels Hobbs for aiding in sample identification, and Dr. Brad Wetherbee for providing thoughtful comments and

discussions of my work and ideas. I certainly need to thank my fellow graduate students; specifically, Dr. Jason Ramsay, Dr. Lloyd Trueblood, Al Nyack, and Leann Elder helped provide insightful discussions, Christine Newton assisted my understanding of statistical processes and putting my data into a meaningful ecological context, Brian Smith and Erin Bohaboy (of the Collie Lab at GSO) for technical advice and help with species identification, and Stuart Bishop and Karl Cygler for sharing skates that they caught while fishing.

Travelling was a substantial part of my research project and many aspects of my trips enriched my graduate experience. I need to thank Joe Bizzarro, Matt Ajemian, and the members of the NMFS Apex Predator Group for advice on statistics, techniques, and research etiquette; these people enriched my conference experiences with the American Elasmobranch Society.

Finally, my family needs to be thanked for their constant support and love. My brother, George Szczepanski, is certainly at the top of the list. George is my best friend and consistently acted as a sounding board, provided intellectual conversation, gave me a floor of his house to live in while I visited Delaware for sample collecting trips, and reminded me that I had the ability to persevere when the light at the end of the tunnel seemed so far away. Liz Cantoni and Brian Knarr also need gratitude for their hospitality during my travels to DE. My father Dr. John Szczepanski assisted in sample collection and my mother and sister, Dorina and Ginene, respectively, always were there to give me encouragement and love. I could not have done this without them. Lastly, I need to thank my wife Stephanie for all of her love, patience, support, compassion, and motivation. She listened to my frustrations and kept me going when it got challenging, all while putting in

countless hours of time and effort into her own degree at which she excelled. I am very proud of her and glad we could experience our academics together.

I need to acknowledge my funding sources which including the URI Research Office, the Biology Department, and the College of Environment and Life Sciences. These departments contributed to funds for research equipment and for travel to conferences. The Graduate Student Associate and the Graduate Assistants United also provided funding for me to present my research at the annual Joint Meetings of Icthyologists and Herpetologists, and for this I am grateful.

PREFACE

Elasmobranch fishes often serve as top predators in marine ecosystems. They are, however, particularly vulnerable to fishing pressure due to slow growth and late maturity life history traits. Understanding trophic relationships is imperative in predicting and managing the effects of population fluctuations. Recent scientific research has focused on the feeding habits of large, higher trophic level shark species, and batoid elasmobranchs have not gained as much attention. Some studies have been done on batoid feeding ecology, but more up-to-date and comprehensive studies are still needed. The goal of this study was to evaluate the feeding habits of the bull nose ray, *Myliobatis freminvillii*, clear nose skate, *Raja eglanteria*, and little skate, *Leucoraja erinacea*, and examine them in the context of whole batoid communities, specifically in Narragansett Bay and Delaware Bay, while also accounting for the trophic relationships with other skates and rays in those habitats.

This dissertation was written using manuscript format. The first manuscript addresses ontogenetic, spatial, and temporal differences in diets of the bull nose ray, *Myliobatis freminvillii*. This manuscript will be submitted to the journal *Environmental Biology of Fishes*. The second manuscript concentrates on the same factors in clear nose skates, *Raja eglanteria* and will be submitted to the *Marine Ecology Progress Series*. The third manuscript evaluates the diets of the little skate, *Leucoraja erinacea*, also for ontogenetic, spatial, and temporal differences, and will be submitted to the *Fishery Bulletin*. Finally, the last manuscript assesses the role of batoids in Narragansett Bay and Delaware Bay and compares the whole community trophic dynamics of the two estuaries. This manuscript will also be submitted to the journal *Environmental Biology of Fishes*.

TABLE OF CONTENTS

ABSTRACT .... **ii**

ACKNOWLEDGMENTS .... **iv**

PREFACE .... **vii**

TABLE OF CONTENTS .... **viii**

LIST OF TABLES .... **x**

LIST OF FIGURES .... **xiii**

MANUSCRIPT 1. Quantitative food habits of the bullnose ray, *Myliobatis freminvillii*, in Delaware Bay **1**

- ABSTRACT 2
- INTRODUCTION 4
- METHODS 8
- RESULTS 14
- DISCUSSION 20
- REFERENCES 28

MANUSCRIPT 2. Quantitative food habits of the clearnose skate, *Raja eglanteria,* in Delaware Bay **47**

- ABSTRACT 48
- INTRODUCTION 49
- METHODS 52
- RESULTS 57
- DISCUSSION 63
- REFERENCES 73

MANUSCRIPT 3. Quantitative food habits of the little skate, *Leucoraja erinacea*, in Narragansett Bay **93**
ABSTRACT 94
INTRODUCTION 95
METHODS 99
RESULTS 105
DISCUSSION 111
REFERENCES 120
MANUSCRIPT 4. Batoid elasmobranch community trophic relationships within and across Narragansett and Delaware Bays: An analysis of resource partitioning **141**
ABSTRACT 142
INTRODUCTION 143
METHODS 145
RESULTS 149
DISCUSSION 156
REFERENCES 164
CONCLUSION 182
APPENDICES 184
BIBLIOGRAPHY 189

LIST OF TABLES

MANUSCRIPT 1 PAGE

Table 1. Detailed breakdown of *Myliobatis freminvillii* collecting efforts from June-September 2009 and 2010 in Delaware Bay 34

Table 2. Overall diet composition of 133 bullnose ray, *Myliobatis freminvillii*, from Delaware Bay collected from June-September 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI 35

Table 3. Overall diet composition of 85 YOY bullnose ray, *Myliobatis freminvillii*, from Delaware Bay collected from June-September 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI 36

Table 4. Diet compostion for 3 different size classes of bullnose ray, *Myliobatis freminvillii*, collected June-September 2009 and 2010. RMPQs and PSIRI expressed as percentages for larger prey categories...........................37

Table 5. SIMPER Test results for discriminating species of overall diet between sets of size groups. Species that contribute most to the dissimilarity between the paired size groups are denoted by an asterisk; SD is Standard Deviation...38

MANUSCRIPT 2 PAGE

Table 1. Prey categories used to calculate trophic levels of clearnose skate, *Raja eglanteria* in Delaware Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007)...79

Table 2. Detailed breakdown of *Raja eglanteria* collecting efforts from April-December 2009 and 2010 in Delaware Bay 80

Table 3. Overall diet composition of 74 clearnose skate, *Raja eglanteria*, from Delaware Bay collected from April-December 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI 81

Table 4. Diet composition for 3 different size classes of clearnose skate, *Raja eglanteria*, collected April-December 2009 and 2010. RMPQs and PSIRI expressed as percentages for larger prey categories 82

Table 5. SIMPER Test results for discriminating species of overall diet that contribute to the significant differences between sexes for RMPQ's %N, %W, and %FO. Species that contribute most to the dissimilarity between sexes are denoted by an asterisk; SD is Standard Deviation. 83

Table 6. SIMPER Test results for discriminating species that contribute to the significant monthly differences in overall diet between YOY and ADU, and site differences between JUV and ADU; both tests based on %N data. Species that contribute most to the dissimilarity between sexes are denoted by an asterisk; SD is Standard Deviation.. 84

MANUSCRIPT 3 PAGE

Table 1. Prey categories used to calculate trophic levels of little skate, *Leucoraja erinacea* in Narragansett Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007) 126

Table 2. Detailed breakdown of *Leucoraja erinacea* collecting efforts from April-December 2009 and 2010 in Narragansett Bay 127

Table 3. Overall diet composition of 389 little skate, *Leucoraja erinacea*, from Narragansett Bay collected from March-December 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI 128

Table 4. Diet composition for 3 different size classes of little skate, *Leucoraja erinacea*, collected March-December 2009 and 2010 from Narragansett Bay; RMPQs and PSIRI expressed as percentages for larger prey categories 131

MANUSCRIPT 4 PAGE

Table 1. Prey categories used to calculate trophic levels of little skate, *Leucoraja erinacea* in Narragansett Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007) 171

Table 2. The %PSIRI of prey types in the diet of batoids collected from Narragansett Bay, RI between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), and *Raja eglanteria* (Re); each separated by available size class...................... 172

Table 3. Dietary overlap indices for batoid elasmobranch species in Narragansett Bay collected March 2009- December 2010. Values range from 0 to 1, with 0 indicating absolutely no overlap and 1 meaning total overlap. ... 173

Table 4. The %PSIRI of prey types in the diets of batoids collected from Delaware Bay between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Dasyatis say* (Ds), *Gymnura altavela* (Ga), *Myliobatis freminvillii* (Mf), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), *Raja eglanteria* (Re), and *Rhinoptera bonasus* (Rb); each separated by available size class. 174

Table 5. Dietary overlap indices for batoid elasmobranch species in Narragansett Bay collected March 2009- December 2010. Values range from 0 to 1, with 0 indicating absolutely no overlap and 1 meaning total overlap. ... 175

Table 6. The %PSIRI of prey types in the diets of batoids collected from Narragansett (RI) and Delaware (DE) Bays between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Dasyatis say* (Ds), *Gymnura altavela* (Ga), *Myliobatis freminvillii* (Mf), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), *Raja eglanteria* (Re), and *Rhinoptera bonasus* (Rb); species separated by bay. 176

LIST OF FIGURES

MANUSCRIPT 1 PAGE

Figure 1. Stations sampled in Delaware Bay during the 2009-2010 DNREC otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red circle indicates the stations where *M. freminvillii* were caught. Average depths in meters for those stations are as follows: 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors. 39

Figure 2. Frequency of *M. freminvillii* caught in Delaware Bay by DNREC monthly finfish trawl surveys in 2009 and 2010. Graphs profile catch by a) month of the year, only June-September, and b) trawl station 40

Figure 3. Cumulative Prey Curves for bullnose ray, *Myliobatis freminvillii*, sampled from June-September 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of ray stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from rays ≥40 cm DW, c) stomachs from female rays 41-80 cm DW and male rays 41-60 cm DW, and d) stomachs from female rays >80 cm DW and male rays >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05, therefore, sufficient sample size 41

Figure 4. Cumulative Prey Curves for bullnose ray, *Myliobatis freminvillii*, sampled from June-September 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of ray stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from rays ≥40 cm DW, c) stomachs from female rays 41-80 cm DW and male rays 41-60 cm DW, and d) stomachs from female rays >80 cm DW and male rays >60 cm. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size...42

Figure 5. Feeding Strategy diagram of all *M. freminvillii* collected June-September 2009 and 2010 from Delaware Bay (n=133). Each point represents a separate prey species from Table 2, Blue diamonds represent gastropod prey, red squares represent bivalve prey, green triangles represent crustacean prey, and the X represents the unidentified prey item, Unknown 001................43

Figure 6: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.)...44

Figure 7: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.) 45

Figure 8: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %FO highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.) 46

MANUSCRIPT 2 PAGE

Figure 1. Stations sampled in Delaware Bay during the 2009-2010 DNREC otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red circle indicates the stations where *R. eglanteria* were caught. Average depth in meters for those stations is as follows: 41=8.1 m, 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors. 85

Figure 2. Frequency of *R. eglanteria* caught in Delaware Bay by DNREC monthly finfish trawl surveys in 2009-2010. Graphs profile catch by a) month of the year, March-December, and b) trawl station 86

Figure 3. Cumulative Prey Curves for clearnose skate, *Raja eglanteria*, sampled from April-December 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates ≥35 cm DW, c) stomachs from 35-60 cm DW, and d) stomachs from skates >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size 87

Figure 4. Cumulative Prey Curves for clearnose skate, *Raja eglanteria*, sampled from April-Deceember 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates ≥35 cm DW, c) stomachs from 35-60 cm DW, and d) stomachs from skates >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size 88

Figure 5. Feeding Strategy diagram of all *R. eglanteria* collected April-December 2009 and 2010 from Delaware Bay (n=74). Each point represents a separate prey species from Table 2, symbols represent different prey categories used in statistical analyses 89

Figure 6: Non-metric multidimensional scaling plots of stomach content from *R. eglanteria* collected April -December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.)......... 90

Figure 7: Non-metric multidimensional scaling plots of stomach content from *R.egalnteria* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.)......... 91

Figure 8: Non-metric multidimensional scaling plots of stomach content from *R. eglanteria* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %FO highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.)......... 92

MANUSCRIPT 3 PAGE

Figure 1. Stations sampled in Narragansett Bay during the 2009-2010 RIDEM otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red star indicates the station where *Leucoraja erinacea* were caught by rod and reel (#99). Approximate depth range in meters for each station is as follows: 1 = 6-9 m, 2 = 9-21 m, 13 = 9-21 m, 25 = 9-21 m, 26 = 3-6 m, 89 = 6-9 m, 132 = 12-15 m, 138 = 9-18 m, 158 = 21-34 m, 161 = 6-9 m, 194 = 6-12 m, 197 = 9-15 m, and 205 = 27-37 m.. 132

Figure 2. : Frequency of *Leucoraja erinacea* caught in Narragansett Bay by rod and reel and by DEM monthly finfish trawl surveys in 2009-2010. Graphs profile catch by a) month of the year, March-December, and b) trawl station.. 133

Figure 3. Cumulative Prey Curves for little skate, *Leucoraja erinacea*, sampled from April-December 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates >30 cm DW, c) stomachs from 30-45 cm DW, and d) stomachs from skates >45 cm DW. The

numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size 134

Figure 4. Cumulative Prey Curves for little skate, *Leucoraja erinacea*, sampled from April-December 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates >30 cm DW, c) stomachs from 30-45 cm DW, and d) stomachs from skates >45 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size 135

Figure 5. Feeding Strategy diagram of all *Leucoraja erinacea* collected April-December 2009 and 2010 from Narragansett Bay (n=389). Each point represents a separate prey species from Table 3; symbols represent different prey categories used in statistical analyses 136

Figure 6: Non-metric multidimensional scaling plots of stomach content from *L.erinacea* collected April -December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.). To more closely examine the relationship of the dense cluster of points in the nMDS in each plot (denoted by the dashed box), an nMDS subset was configured and superimposed 137

Figure 7: Non-metric multidimensional scaling plots of stomach content from *L.erinacea* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.) 138

Figure 8: Non-metric multidimensional scaling plots of stomach content from *L. erinacea* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %FO highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.) 139

Figure 9. Proportional diet composition for different sizes of *Leucoraja erinacea* at different trawl sites relative to benthic prey abundance. Estuarine habitats map adapted from French *et al.* (1992). Pie charts are centered over the corresponding station, unless otherwise noted with an arrow 140

MANUSCRIPT 4 PAGE

Figure 1. Stations sampled in Narragansett Bay during the 2009-2010 RIDEM otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red star indicates the station sampled by rod and reel (#99). Approximate depth range in meters for each station is as follows: 1 = 6-9 m, 2 = 9-21 m, 13 = 9-21 m, 25 = 9-21 m, 26 = 3-6 m, 89 = 6-9 m, 132 = 12-15 m, 138 = 9-18 m, 158 = 21-34 m, 161 = 6-9 m, 194 = 6-12 m, 197 = 9-15 m, and 205 = 27-37 m 177

Figure 2. Stations sampled in Delaware Bay during the 2009-2010 DNREC 30' otter trawl monthly finfish survey. Numbers indicate assigned station numbers. Average depth in meters for those stations is as follows: 41=8.1 m, 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors 178

Figure 3: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Narragansett Bay, RI. Prey groups (see Szczepanski ms 3 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. To more closely examine the relationship of the dense cluster of points in the nMDS of %W (denoted by the dashed box), an nMDS subset was configured and superimposed. Symbols represent species abbreviations and numbers represent size classes (1=YOY, 2=JUV, and 3=ADU)..................................... 179

Figure 4: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Delaware Bay, DE. Prey groups (see Szczepanski ms1 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. Symbols represent species abbreviations and numbers represent size classes (1=YOY, 2=JUV, and 3=ADU)... 180

Figure 5. Figure 5: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Narragansett Bay (RI) and Delaware Bay (DE). Prey groups (see Szczepanski ms.1 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. To more closely examine the relationship of the dense cluster of points in the nMDS of %W (denoted by the dashed box), an nMDS subset was configured and superimposed. Symbols represent species abbreviations and labels denote geoghraphic location 181

MANUSCRIPT 1

Quantitative food habits of the bullnose ray, *Myliobatis freminvillii*, in Delaware Bay

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ABSTRACT

Feeding habits of many batoid elasmobranchs (skates and rays) have been recorded, but diets, prey selection, and resource partitioning within specific populations are not fully understood. Few descriptions exist of the diet of a batoid species throughout its entire life history. Through gut content analysis, my research examined the feeding habits of the bullnose ray, *Myliobatis freminvillii*, to understand the diet and trophic role of this species in the estuarine ecosystem at various life stages. I was able to collect a higher abundance of neonate and juvenile rays than expected allowing for a more comprehensive diet characterization than in past studies. 160 specimens (78 male and 82 female) were collected over the course of two years through fisheries-independent trawl surveys. Gastropods were the most abundant prey followed closely by crustaceans and then bivalves. *Pagurus longicapris* was found to be the most important prey item in all indices along with *Euspira heros*, *Busycon* sp. and *Ilynassa trivitata* in descending order. There were small but significant ontogenetic differences in proportional weight of prey in the diets, mostly between the small and medium rays in which the focus of consumption shifted from pagurid crustaceans to bivalves. There were no significant sexual or temporal differences in diet exhibited by these batoids, overall or among size groups. There were significant differences in diet among collection sites indicating potential prey selection by availability. In addition to the feeding data, the increasing proportional abundance of smaller (and therefore younger) size classes through the summer months provides some evidence indicating that Delaware Bay may serve as a nursery area for the bullnose ray. Though recently proposed criteria characterizing shark nursery areas cannot fully be fulfilled by my data alone, the calculated abundance trends along with the

diet data shown can provide new information for future efforts in conservation, ecosystem-based fisheries management and modeling.

INTRODUCTION

Many of the world's fish populations, including elasmobranchs, have experienced heavy fishing pressure for decades. Sharks and rays are particularly vulnerable to over-exploitation because of their K-selected life-history (characterized by slow growth, late attainment of sexual maturity, long life spans, low fecundity, and a close relationship between the number of young produced and the size of the breeding biomass) and may take decades to recover from population declines (Stevens *et al.*, 2000, Ellis *et al.*, 2005a,b). In the past decade, concerns have been raised about the status of shark and ray assemblages due to the vulnerability of the elasmobranchs and the unsustainable nature of the commercial and sport fisheries (Pauly *et al.*, 1998a; Baum *et al.*, 2003; Myers *et al.*, 2007; Dulvy *et al.*, 2008). Myers *et al.* (2007) suggested that the decline of larger pelagic sharks (many of which are thought to prey on smaller elasmobranchs) has relieved pressure on the mesopredators like dogfish, skates, and rays. Consequently, weakened apex trophic level predation by these "great sharks" on their smaller elasmobranch prey might cascade to even lower trophic levels (Peterson *et al.*, 2001; Farhrenthold, 2004; Myers *et al.*, 2007). This means that there would be less predation pressure on mesopredators leading to an increase in their abundance and, consequently, a greater need for food (Myers *et al.*, 2007), which may or may not be available. However Myers *et al.* (2007) did not provide direct evidence for the interactions (such as specific dietary information), just corresponding changes in population abundance implying the connections. Therefore, these claims of negative impacts may be exaggerated.

The concerns of over-exploitation of marine fisheries have spurred a movement towards increased use of multi-species and ecosystem-based models in fisheries management (Garrison, 2000; Link & Almeida, 2000; Link, 2010; Link *et al.,* 2012). These particular models require considerable information about predation rates. Improved understanding of the ecological mechanisms underlying these factors is essential to effective stock assessment and management (Garrison, 2000, Fogarty *et al.,* 2012; Fu *et al.,* 2012; Link *et al.,* 2012; Pranovi *et al.,* 2012), particularly as the focus turns more towards ecosystem-based fisheries management (EBFM) and less on single-species, broad-scale efforts that do not account for spatial specifics (Gamble *et al.,* 2012; Lucey *et al.*, 2012). Data obtained in my study can be used in the future by ecosystem modelers using trophic web models, such as Ecopath.

The bullnose ray, *Myliobatis freminvillii,* is a benthic elasmobranch species commonly found in coastal waters of the Western Atlantic ranging from New York to Central Brazil, occasionally straying north to Cape Cod (Bigelow & Schroeder, 1953; personal observations). This ray is known to make seasonal migrations toward coastlines during summer months to feed and mate (Bigelow and Schroeder, 1953; Michels and Greco, 2008, 2011; personal observations). Large benthic predators like *M. freminvillii* can heavily impact invertebrate populations and play an integral role in structuring benthic communities as they excavate the bottom for food (Karl & Obrebski, 1976; Smith & Merriner, 1985; Peterson, *et al.*, 2001), often fluidizing sediment to expose prey items and then consuming or swimming along the bottom and biting mollusk siphons and feet that remain above the sediment. Concerns have arisen about durophagous rays negatively impacting marine aquaculture, like the Eastern oyster (*Crassostera virginica*) or the Bay scallop (*Argopecten irradians concentricus)* despite a lack of evidence. It has been anecdotally reported that cownose rays have disrupted oyster restoration efforts by consuming a majority of the seed organisms used in the program (Fahrenthold, 2004). In the same area however, a subsequent quantitative study showed that reef depth was a major factor in the success of similar oyster restoration efforts (Schulte *et al.* 2009). Though this information seems contradictory, it emphasizes that more factors may have a profound effect on prey populations than just predation by elasmobranchs and that the trophic cascades proposed by Myers *et al.* (2007) may not have as much negative impact as suggested.

The feeding ecology of batoid elasmobranchs needs further examination, particularly for bullnose rays. Dietary information and feeding strategy for some species of batoid elasmobranchs have been documented, though the data are sparse. The available data are also somewhat spatially and temporally specific (Bigelow & Schroeder, 1953; Bearden, 1959; Bowman *et al.,* 2000; McElroy *et al.,* 2006). In the 1950's, scientists documented the diets of certain sting rays in the Delaware Bay (Bearden, 1959; Hess, 1959) but remarked that these habits tended to vary with locality (Bigelow & Schroeder, 1953; Bearden, 1959). Smith and Merriner (1985) found that the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay fed primarily on soft shell clams, *Mya arenaria*. Other reports show that the cownose rays in the Chesapeake have been preying heavily on bay scallops, *Argopecten irradians concentricus* (Peterson *et al.*, 2001) and stocks of oysters, *Crassostrea virginica* (Fahrenthold, 2004). A study of *R. bonasus* diets in the northern Gulf of Mexico and Mobile Bay, Alabama, further demonstrated spatial variability in the feeding habits of batoid species (Ajemian & Powers, 2011); findings included diets with high proportions of veneroid and tellinid clams.

Delaware Bay is the second largest estuary on the eastern coast of the United

States and, along with other mid-Atlantic estuaries, provides important nursery and feeding habitat for a number of elasmobranch species (Rountree & Able, 1996; Merson & Pratt, 2001; McCandless *et al.*, 2007; McElroy, 2009). Finfish surveys have shown *Myliobatis freminvillii* to be a predominant elasmobranch species in Delaware Bay during summer months (Michels & Greco, 2008), indicating that this species may also use this estuary as nursery and foraging grounds. Thus, Delaware Bay provides a unique opportunity to evaluate the ecological role of multiple life-history stages within one habitat.

This research aims to increase the knowledge of batoid feeding habits in estuarine enviroment in order to ascertain if increasing mesopredators numbers could actually have a negative impact benthic invertebrate communities. The principal objective of the current study was to characterize the diet of *Myliobatis freminvillii* in the Delaware Bay, as a species and for each life history stage. Another specific goal of this study was to identify how the feeding habits may change ontogenetically, temporally, and spatially within the Bay; testing the null hypotheses that there is no difference in stomach contents among individuals of different sizes, during different months of the year, or at different sampling locations. Differences in diets between males and females were also investigated by testing the null hypothesis of no difference in diet between individuals of different sexes. This research was used to evaluate the ecological role of the bullnose ray and was included in a larger examination characterizing trophic interactions among batoid elasmobranch populations within Delaware Bay and how the dynamics may differ from those of other batoid communities, specifically in Narragansett Bay.

METHODS

Study Site and Specimen Collection

This study was carried out in the Delaware Bay estuary. Delaware Bay is characterized as having a mud, sand, and mixed-sediment bottom with extensive shallow flats and shoals interspersed with deeper sloughs (Kraft, 1988). The bay has little stratification, is well mixed, and has a considerable freshwater input from the Delaware River to the north. Delaware Bay has nutrient-rich waters but high turbidity results in moderate levels of phytoplankton productivity (Pennock & Sharp, 1986) and little benthic plant growth. The bay is surrounded by salt marshes with winding rivers and creeks with narrow beaches.

Specimens of *Myliobatis freminvillii* were collected aboard fishery-independent monthly bottom trawl surveys conducted by the Delaware Department of Natural Resource and Environmental Control (DNREC) in March-December of 2009 and 2010. The nine haul stations were randomly stratified between depths of 7-20 m and located throughout the western half of Delaware Bay (Figure 1), though most specimens were collected closer to the mouth of the bay and during the summer months (Figure 2). Across sites, bottom salinities ranged from 15-28‰ and bottom temperatures of 5.2-26.7º C.

Data collected from each specimen on the boat included: disc width (DW, cm), total length (TL, cm), and sex. Stomachs were excised from the cardiac sphincter to the pyloric sphincter, the contents removed, and then stored on ice until they could be analyzed in the lab.

Stomach Content Analysis

Stomach contents were identified, separated accordingly, counted, and weighed. Prey items were identified to the lowest taxonomic level possible using field guides and taxonomic keys (Smith, 1964; Gosner, 1971 and 1978; Rehder, 1981; Pollock, 1996), and consultation with biologists at the University of Rhode Island (URI), Woods Hole Oceanographic Institute (WHOI), and Virginia Institute of Marine Science (VIMS). Any highly digested items that could not be identified (with the exception of the items known as "Unknown 001"), parasites, and sediments were counted and noted, but not included in statistical testing. The number of each prey item in a stomach sample was estimated using the most conservative count when detached components were present. Items were then weighed (to the nearest 0.01 g) after excess moisture was blotted off.

Sample Size Sufficiency

To evaluate whether the sample size was large enough to sufficiently describe the ray's diet, cumulative prey curves (Ferry & Cailliet, 1996) were computed using EstimateS (Version 8.2.0, R.K. Colwell, http://purl.oclc.org/estimates). In this power analysis, the number of possible novel prey items is plotted against an increasing number of stomachs analyzed. The order of the samples was randomized 999 times, with empty stomachs excluded and the mean and standard deviation calculated for each sample size. As the curve reaches an asymptote, the sample size is considered to be sufficient. Visual examination of the curve for an asymptote (Ferry & Cailliet, 1996) is not reliable. To determine if the curve has reached an asymptote, the slope of the linear regression (b) of the final four curve endpoints was used as an objective criterion where $b \leq 0.05$ signified an acceptable plateau of the prey curve for diet characterization (Bizzarro *et al.,* 2009; Brown *et al.*, 2011)..

Statistical Analysis

Diet Characterization

The contribution of each prey taxon to diet composition was estimated with three relative measures of prey quantity (RMPQ) described by Hyslop (1980). These measures include number (N), wet weight (W), and frequency of occurrence (FO) (Hyslop, 1980). All singular indices were expressed as percentages. Percent by number (%N) was calculated as the total number of individuals from a prey category divided by the total number of all prey items from all categories and percent by weight (%W) was calculated as the total wet weight of all items from a prey category divided by the total wet weight of all prey items from all categories. Percent frequency of occurrence (%FO) was calculated as the total number of stomachs that contained prey from a given category divided by the total number of stomachs that contained any prey.

Prey-specific abundances by number (%PN) and by weight (%PW) were calculated to identify each prey item's relative importance independent of the other prey found (Amundsen *et al.,* 1996). These measures are defined as the percent of abundance (number or weight) of a prey item averaged over only the stomach samples in which it occurs. Prey-specific abundances are important not only as descriptive indices but also in the construction of a graphical model of specialization and a compound index, both described below.

Since relative importance of prey can vary depending on which index is used, composite indices were also used. These were more comprehensive as they incorporated number, weight, and frequency all together. Index of Relative Importance (IRI) was calculated for each prey category by multiplying the sum of %N and %W by %FO (Pinkas *et al.,* 1971; Cortés, 1997; Koen Alonso *et al.*, 2001) to maintain comparability with published work; this was expressed as a percentage of the total IRI for all prey species. Prey-Specific Index of Relative Importance, %PSIRI (Brown *et al.*, 2011), was also used as it is more precise than IRI, which can be biased by %FO and over-emphasizes common species (Hansson, 1998) often exceeding 100% (Bizzarro *et al.,* 2007). This measure was calculated by multiplying the sum of %PN and %PW by %FO and dividing by 2 since %PSIRI sums to 200% otherwise. %PSIRI accurately portrays the roles of each individual prey species independent of the other species, is additive with respect to taxonomic levels, and accounts for %FO redundancies of %IRI (Brown *et al.,* 2011).

Trophic level and dietary specializations were examined to make inferences about the species' potential for dealing with environmental changes in resource availability. Trophic level (*TRL*) was calculated with Cortés' Trophic Level Index (1999). Prey species were combined into higher taxonomic or functional groupings (e.g.- Paguridae or bivalve, etc.) to aid in calculation of trophic level; %W was used in the calculation of *TRL* as the proportion of prey in the diet. Trophic levels of prey items were determined using calculated values from Pauly & Chistensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert & Bizzarro (2007). Dietary breadth was calculated using Levins' standardized index (Krebs, 1989):

$$B=\left(\frac{1}{n-1}\right)\left(\frac{1}{\sum p_{ij}^{2}}\right)-1$$

where, B = Levins standardized index for predator i; p_{ij} = proportion of diet of predator i that is made up of prey j; and n = number of prey categories. This index ranges from 0 to 1, low values indicating diets dominated by few prey items (specialist predators) and higher values indicating generalist diets (Krebs, 1989; Fanelli *et al.,* 2009). In order to avoid problems derived by different states of prey digestion the index was calculated with %PSIRI. Dietary specialization was portrayed graphically by plotting %PN against %FO (Amundsen, 1996).

Significance Tests for Variation

Samples were defined as the averaged stomach content proportions for all individuals of a specific size group and sex at each station each month. Size groups reflected life history stages (Bearden, 1959): young-of-the-year (YOY) comprised individuals < 40 cm DW, juveniles (JUV) included rays from 41-80 cm DW for females and 41-60 cm DW for males, and adults (ADU) were fish > 80 cm DW for females and >60 cm DW for males. Ontogenetic diet overlap was initially examined using the Schoener dietary overlap index (S_{do}) and simplified Morisita index (C_h) (Clarke & Warwick, 2001; McElroy *et al.,* 2006; Bizzarro *et al.*, 2007; Mabragaña & Giberto 2007). Diet was tested for differences first among just size classes and then with the following independent variables: sex, sampling months, and sites. Significance testing involved only the 3 RMPQ's (N, W, FO) separately since each indicates different things about the diet and is also susceptible to different types of bias. Prey species were combined into larger groupings as described above for statistical analysis since many groups of uncommon prey were represented by few instances and unnecessarily skewed the results; these groupings aided in the interpretation of the ecological importance of the results.

Non-metric multidimensional scaling (nMDS) ordination plots were constructed using PRIMER v6.1.13 (Clarke & Warwick, 2001) to look for relative similarities in overall diet for each RMPQ. The amount of possible distortion in a plot was measured by stress; lower stress values (<0.1) correspond to good ordination with little chance of misinterpretation and comparison to higher-dimensional ordinations and plots will not add any useful information (Clarke & Warwick, 2001). Differences in diet among size groups, sexes, months and stations were tested for each RMPS by using permutation tests called analysis of similarities (ANOSIM). ANOSIM creates a pair-wise similarity matrix between all data points then examines similarity between groups by examining the ratio of between-group to within-group similarities (Smith *et al.*, 1990). Bray-Curtis similarity index was applied to dependent variables of prey number (N) and wet weight (W) after they had each been standardized by stomach; Jacard similarity index was used for the dependent variable of prey frequency (FO) as it is more appropriate for presence-absence data (Clarke & Warwick, 2001). Data were permutated 999 times for a distribution to determine the p-value of ANOSIM's R statistic (R = 0 is identical, R = -1 or 1 is most divergent). The null hypothesis was rejected if R did not fall within the 95% CI of global R values. Similarity of percent contribution (SIMPER) analysis was used to identify the significantly important dietary categories that contributed to statistical differences in ANOSIM when differences were present.

RESULTS

A total of 160 individuals was collected (78 females, 82 males) between March 2009 and December 2010 (Table 1); all individuals were caught between June and September of both years (Figure 2a). YOY was represented by 107 individuals, JUV was represented by 45 rays, and ADU was represented by 8 samples. Out of all the stomachs collected, 132 (82.5%) contained prey; 28 (17.5%) were empty. Of the 107 YOY stomachs, 85 (79.4%) were found to contain food items and 21 (20.6%) were empty. Of the 45 JUV, 39 (86.7%) contained prey items while 6 (13.3%) did not. All individuals from ADU contained prey items. Maximum number of prey categories in a single stomach was 6 (DW = 49.9) with 3 stomachs having 5 different items (DW = 58.8, 54.3, and 45.0 cm, all JUV). The average stomach content weight for all individuals with prey was 4.82 g and increased according to size class: YOY = 0.63 g, JUV = 4.26 g, and ADU = 52.08 g.

The cumulative prey curve for all rays reached an asymptote with b = 0.05 at 74 stomachs indicating the sample size collected was sufficient to characterize the diet of the species as a whole; the slope of the curve at the last 4 points was b = 0.007 (Figure 3a). The slope of each individual size class showed that the number of samples for YOY was sufficient at 72 stomachs with a final slope of b = 0.036 (Figure 3b). The slope for JUV ended as b = 0.107 (Figure 3c) and therefore did not reach sufficiency. For ADU, the curve was not close the reaching an asymptote ending at b = 2.39 (Figure 3d). To examine sample size sufficiency for statistical tests, curves were generated using the corresponding larger prey groupings (Figure 4a-d). For all stomachs together (Figure 4a), the asymptote was achieved at 19 stomach samples since there were only 7 distinct categories (Unknown 001 was omitted), with a final slope of $b \ll 0.001$. YOY and JUV both achieved an asymptote, at n = 18 and 30 respectively (Figure 4b and 4c). ADU did not reach an asymptote with $b = 0.25$ (Figure 4d).

The overall diet of *Myliobatis freminvillii* was characterized by 16 unique prey items identified to species, 2 more identified to genus, and 1 completely unidentified but distinct (not highly digested beyond recognition) (Table 2). The diet consisted mostly of mollusks and crustaceans. Gastropods occurred in 54% of stomachs and contributed to the diet most (34.2% N, 39.65% W). Crustaceans were the most frequent at 60% and contributed 28.3% by number and 26.19% by weight to the diet. Bivalves were found in 29% of the stomachs as 17.1% of the numerical abundance and 18.81% of the wet weight. %IRI for each of these classes was 41.40%, 33.98%, and 10.76%, respectively.

Pagurus longicarpus, occurring in 51% of stomachs, was the most abundant species overall by number and by weight (23.8 %N, 23.70 %W), followed by a still unknown item (Unknown 001, 20.5 %N, 15.34 %W), which was found in 37% of the samples. Also very prevalent in the diet were *Euspira heros* (13.8 %N, 18.75 %W), *Busycon* sp. (12.1 %N, 13.51 %W), *Ensis directus* (9.5 %N, 10.45 %W), and *Illyanassa trivitata* (7.3 %N, 6.41 %W). With respect to IRI, *P. longicarpus* had the highest value (41.14%); Unknown 001 (22.7%), *E. heros* (17.68%), *Busycon* sp. (8.63%), and *E. directus* (5.68%) also had considerable contributions to diet. Other organisms did contribute to the diet as well, though in much smaller proportions. Less important gastropods included *Crepidula fornicata* and *Nucella lapillus*. Bivalves in low abundance included *Anadara ovalis*, *Mytilus edulis, Yoldia* sp., *Tagelus divisus*, and some unidentified specimens (Order Veneroida and some identified as bivalve only by the presence of a shell hinge). Other crustaceans found in the diet included *Crangon septemspinosa*, *Spirontocaris lilljeborgii*, *Pagurus acadianus*, *Pagurus pollicaris*, *Callinectes sapidus*, *Carcinus maenus*, and *Ovalipes ocellatus.*

Of all the relative measures of importance, %PSIRI accounts for individual preferences along with species-wide prey abundances. Gastropods contributed 36.93% by PSIRI, while crustaceans and bivalves had PSIRI values of 27.24% and 17.93%, respectively. *Pagurus longicarpus* contributed 23.73% to PSIRI, Unknown 001 contributed 17.90%, *Euspira heros* contributed 16.27%, *Busycon* sp. contributed 12.82%, and *Ensis directus* contributed 9.97%.

In the overall diet for YOY, crustaceans and gastropods occurred most frequently at 79%FO and 64%FO, respectively (Table 3). Crustaceans in general contributed to the diet 35.2% by numerical abundance and 36.79% by weight. Gastropods were almost as important in the diet contributing 32.0 %N and 35.66 %W. Bivalves were only found in 19% of these samples and contributed to the diet 9.8 %N and 10.73 %W. The IRI for the orders were 36.0%, 33.81%, and 9.42% for crustaceans, gastropods, and bivalves, respectively.

Pagurus longicarpus was the most frequently occurring species in the YOY diet (68.24 %FO) and contributed substantially by number and weight (33.3 %N and 34.53 %W) (Table 3). Unknown 001 was found in 46% of samples and was the second most abundant item by number and weight (23.1 %N and 16.82 %W). Other important prey items included *Busycon* sp. (12.6 %N, 13.52 %W), *Ilynassa trivitatta* (11.1 %N, 9.83 %W), *Euspira heros* (6.7 %N, 10.78 %W), and *Ensis directus* (5.6 %N, 6.30 %W). Considering RMPQs together, *P. longicarpus* had the most substantial contribution to the diet of *Myliobatis freminvillii* with 59.19 %IRI, followed by Unknown 001 at 23.40 %IRI. *Busycon* sp. and *E. heros* were the only other items that had more than 5 %IRI (5.51% and 5.5%, respectively); *I. trivitatta* contributed to the diet by 4.72 %IRI with all other species having considerably lower %IRI values. *Mytilus edulis*, *Spirontocaris lilljeborgii*, *Pagurus pollicaris*, *Carcinus maenus*, and *Ovalipes ocellatus* were absent from these stomachs.

Comparison of the diets of the different size classes indicated that gastropods and pagurid crustaceans were most important to YOY whereas bivalves and gastropods were most important to JUV; ADU seemed to feed solely on gastropods, with some pagurids as a smaller supplement (Table 4). There was a distinct increase in bivalve consumption between YOY and JUV, then a drop off in ADU. Epibenthic and miscellaneous crustaceans were both eaten infrequently by YOY and consumption decreased to zero in the ADU. Gastropod consumption was substantial for YOY and JUV, yet consumption doubled in ADU. Prey items from the family Paguridae were consumed in highest proportions by YOY. This consumption decreased by approximately 40-50% in JUV and ADU. Portunid crabs were found in the diet but not consumed in any notable proportions in any size class. Unknown 001 seemed to be an important item to YOY but importance did decrease slightly in JUV and then to none in ADU.

Overall dietary breadth of the bullnose ray was calculated as $B = 0.37$; YOY and JUV respectively had dietary breadths of $B = 0.41$ and $B = 0.44$ while ADU had a dietary breadth of $B = 0.30$.

The graph of %PN and %FO showed most prey items along the y-axis with only a few in the middle with similarly intermediate values (Figure 5). The overall Trophic

Level (*TRL*) was calculated to be 3.23, with YOY having *TRL* = 3.29 while TRL_{JUV} = 3.13 and TRL_{ADU} = 3.14. This is evidenced by the higher proportion of mollusks eaten by the larger sizes of rays and more varied diets of the smallest rays.

To investigate any ontogenetic differences, Schoener's dietary overlap index (S_{do}) and simplified Morisita index (C_h) were calculated. The highest degree of overlap was between YOY and JUV (S_{do} = 0.72, C_h = 0.79) and the least overlap was between JUV and ADU (S_{do} = 0.48, C_h = 0.70). The overlap between YOY and ADU was similar to that of JUV and ADU (S_{do} = 0.55, C_h = 0.70). Though there is a considerable amount of overlap in these diets, there may be significant differences in which prey items of the diet do not overlap.

Examination of the nMDS plots based on %N for each factor (size, sex, month, and station) for all stomach samples illustrated that the large number of samples introduced high degrees of variability and therefore patterns that are not readily discernible (Figure 6). There do seem to be three similar groupings of different size classes but with a high degree of overlap, and the diet of males is more variable than that of females (Figure 6a, stress = 0.11). There was also some grouping by site and by month, but again there was a high degree of overlap (Figure 6b, stress = 0.11). ANOSIM tests run on each of the factors resulted in high degrees of overlap for all factors (R_{size} = 0.09, R_{sex} = -0.01, R_{month} = 0.08, and $R_{station}$ = 0.2) and only one with significant difference: collecting station ($p \ll 0.01$). The tests on the factors of size and month were close to significant, each p = 0.06; ANOSIM on sex as a factor was not nearly significant (p = 0.49).

Similarity plots of samples based on %W exhibited more distinct groupings

(Figure 7, stress = 0.12). YOY samples were tightly clustered, with JUV and ADU samples each grouped but with greater variability. Both of the latter groups overlapped slightly and opposite sexes seemed to overlap considerably (Figure 7a). September was the only month that showed a clear cluster, though other months clustered somewhat but were widely dispersed and overlapping; station 52 grouped separately from station 62 and 72 samples (Figure 7b). Statistical testing resulted again in a high degree of overlap for all factors ($R_{size} = 0.11$, $R_{sex} = 0.02$, $R_{month} = 0.08$, and $R_{station} = 0.15$) with significant differences among different sizes ($p = 0.04$) and stations ($p = 0.01$). Sampling month differences approached significant ($p = 0.07$) and there was no difference in diets of each sex ($p = 0.26$). SIMPER tests run on size as a factor for %W show *Pagurus longicarpus* and *Euspira heros* to be the distinguishing prey items (Table 5).

Diets plotted based on %FO indicated some possible groupings but a considerable amount of overlap (Figure 8, stress = 0.09). YOY samples clustered close together, while JUV and ADU samples formed broader groupings that overlapped each other; JUV also overlapped YOY somewhat as well (Figure 8a; $R_{size} = 0.09$, $R_{sex} = -0.02$). Samples from different months were highly overlapping while samples from stations 52 and 72 clustered separately, both being overlapped by samples from station 62 (Figure 8b; $R_{month} = 0.06$, $R_{station} = 0.16$). ANOSIM tests resulted in station differences being significant ($p \ll 0.01$) and size differences approaching significant ($p = 0.07$) while there were no differences between diets of different sexes ($p = 0.6$) or stations ($p = 0.15$).

DISCUSSION

This study presents the first fully comprehensive and detailed diet analysis for *Myliobatis freminvillii* in Delaware Bay, with special emphasis on individuals 40 cm DW or less (YOY). Though the smallest size class of rays was the only ontogenetic group that had a sufficient sample size to characterize its particular diet to the level of prey species, comparative statistical analysis involved grouping prey items into larger categories; sample sizes based on these categories were sufficient for YOY and JUV according to cumulative prey curves. Few adult rays were caught partly as a function of the seasonal nature of the rays presence within the Bay. As reported in Table 1, almost no small rays were caught early in the season while large and medium rays were common. As the season continued, collection of large rays became less common with complete absence in catch by midsummer. Medium rays showed a similar decrease and absence a month later, while small ray presence increased into August and began to decline in September and were absent from collections by October.

Even though there were only 8 samples for ADU, the items found in these stomachs were similar to items noted by Bearden (1959) and whose measures like abundance and frequency of the prey categories were relatively consistent with those seen in Table 3. In Bearden's (1959) study, gastropods were most important (67.6%N, 87%FO), followed by Pagurid crustaceans (15.0%N, 33%FO) and bivalves (8.9%N, 17%FO). The gastropods in the 1959 study (*Polinices duplicate*) were nearly identical in biology and morphology to *Euspira heros*. Also, Bearden found *Pagurus pollicaris* as a major prey item for *M. freminvillii*; the pagurid crustaceans consumed by ADU of this study were also *P. pollicaris* (unlike the *P. longicarpus* of the smaller sizes). It is reasonable to conclude that the few samples collected here share substantial characteristics of their diet with the samples taken in 1959. Though the abundance measures are not identical, they do add a degree of confidence to comparisons in this study that include ADU.

In addition to Bearden's research (1959) aiding in the strength of comparisons made herein by supporting the limited findings in ADU diet, the current study helps to build a more complete diet profile for a highly abundant summer resident of Delaware Bay filling in previous gaps in diet data for smaller size classes. Elucidating the diet of YOY is particularly important in understanding the early life history of this species. Bearden (1959) described the diet of this species for Delaware Bay from 191 specimens, but very few of those (~15%) were less than 41 cm DW. It is reasonable to assume from the cumulative prey curves constructed in the current study that Bearden had achieved a sufficient sample size overall, but not enough to specifically describe a diet for the smallest individuals ($n<30$); according to the data collected here, there needed to be at least 72 to reach sample size sufficiency. The smallest size class of ray was found to frequently consume relatively high abundances of *Pagurus longicarpus* and various small gastropods, but did also occasionally eat other small crustaceans, gastropods, and bivalves. As mentioned, these rays have a slightly higher trophic level ($TRL = 3.29$) than the larger rays, likely due to the content of bivalves in their diet. The complete set of diet data contained herein for YOY in Delaware Bay was important to catalogue since this estuary provides a nursery and feeding habitat for many elasmobranch species, particularly sharks (Rountree & Able, 1996; Merson & Pratt, 2001; McCandless *et al.*, 2007; McElroy, 2009) and the frequency of size classes of rays inhabiting the Bay through the course of the summer seems to suggest that it is also important for these rays as well (Table 1, Figure 2a). This study helps to evaluate the ecological role of a vital life history stage that has not been done before.

This study presents data that are more complete than those of others and now the most up-to-date for the Delaware Bay. Bigelow & Schroeder (1953) described the diet of specimens taken in Woods Hole, MA to include lobster, *Cancer* crabs, *Mya* clams, and *Lunatia* (now *Euspira*) snails. After Bearden's (1959) study, the only other diet research on the bullnose ray diet was done by Bowman *et al.* (2000) based on 15 specimens collected near Cape Hatteras, NC. These workers reported the diet consisting of 73.1% bivalves, 10.7% misc. mollusks and 6% crabs (both of the latter groups mostly include species that don't range into Delaware Bay), with some worms but very few other crustaceans. There is no description of the size of the individuals sampled by either Bowman *et al.* (2000) or Bigelow & Schroeder (1953).

Consistent with data from previous studies, mollusks and crustaceans were the prey consumed most by these rays, particularly gastropods and pagurid crabs. These organisms are particularly abundant in Delaware Bay (Maurer *et al.*, 1978; Michels & Greco, 2011; Raineault *et al.*, 2012). There has been some recent concern about the possible negative impact that durophagous rays could have on the benthic invertebrate community, which has mostly been suggested of a sympatric related species, *Rhinoptera bonasus* (Peterson, *et al.,* 2001; Fahrenthold, 2004). However, *M. freminvillii* did not prey on commercially important species.

Interestingly, it has been suggested that the appearance of *P. pollicaris* in the diet of the ray may be accidental as a case of mistaken identity, since hermit crabs in this region occupy gastropod shells (Bearden, 1959). The data from the current study indicate that young rays eat the smaller *P. longicarpus* while the larger rays eat the larger *P. pollicaris*. Younger rays also eat smaller species of gastropod, whose shells may be occupied by *P. longicarpus,* while larger rays eat larger snails (based on opercula size, personal observations) and whelks, whose shells may have been occupied by *P. pollicaris.* However, the relative importance of the respective pagurid species seems too high to be accidental and is therefore unlikely to be coincidental consumption. This cannot be determined with certainty without fully detailed abundance data for all benthic invertebrates in and around Delaware Bay.

An issue that arose with the analysis of stomach contents was the presence of an item that could not be identified, but was consistent in many samples. Denoted "Unknown 001", this item was found frequently in *M. freminvillii* diet and in noteworthy abundance. It was, therefore, important to determine its identity. However, it did not match parts from reference samples gathered at any of the collection sites. Many references, field guides, and biologists were then consulted but no confident identification could be made. Due to the nature of the collecting protocol, no sediment samples were able to be taken that would help indicate possible prey species. It was initially suspected to be a gastropod operculum based on its shape, texture, and size, a reasonable conclusion since much of the ray's diet was made up of other gastropods. However, no matching example could be found. The most similar looking image found was of *Rapana venosa*, an invasive whelk known to inhabit estuaries on the Mid-Atlantic Coast of the U.S. (Harding & Mann, 2003). However, an author of that article was able to determine that the samples were not from *R. venosa* and also considered the possibility that the suspected mollusk had established a presence in Delaware Bay unlikely (Harding, personal communication). The samples were not of a size consistent with that of an ostracod, as some other experts had hypothesized. Two possibilities exist regarding the identity of this particular item: the item is either 1) an obscure part of an already ingested prey item's anatomy and, therefore, would only change the relative proportions of the diet characteristics slightly or 2) a part of the ray's anatomy that is shed and consequently ingested accidentally (parts of the teeth plates, etc.). The latter concept arises from the fact that none of the other batoids in the region have this item in their diet, including some highly generalized, opportunistic feeders (*L. erinacea,* see Chapter 3 of this dissertation) indicating that it is a species-specific stomach content.

Based on the %PN and %FO of the prey items calculated in this study, *M. freminvillii* should be characterized as a moderately specialized gastropod and pagurid predator occasionally feeding on abundant bivalve crustaceans. They are considered only moderately specialized since the graphical display of specialization (Figure 5) shows some prey items in the middle of the plot space, and the rest of the prey items eaten infrequently at varying levels of prey-specific abundance. The graphic representation of feeding strategy does not show a strong specialization for any prey, in which there would be a few points concentrated in the upper right corner, with the rest in the lower left, nor does it show a generalized diet, in which the points would be spread along the lower half of the graph with the more important prey taxa being consumed by more than half of the fish (Amundsen *et al.*, 1996). This moderate specialization results in an average trophic level of 3.23 with smaller rays contributing more as part of a higher trophic level. This is likely due to a higher consumption of crustaceans while larger rays eat more filterfeeding bivalves and low trophic level gastropods. The moderate specialization and higher trophic level of smaller rays indicates that changes in prey abundance would have a greater impact on the batoid species as a whole since mollusks are sensitive to environmental changes and since fluctuations in population of smaller rays affects recruitment. This vulnerability may be countered by the fact that smaller rays consume a broader range of prey and may be more able to shift their diets accordingly, as indicated by the graphic display of feeding strategy that shows some plasticity.

Differences in diet composition between different size rays were significant for the proportional weight of the prey items, but not numerical abundance or frequency. However, these latter measures were just above the rejection threshold (each at $p = 0.06$) and would likely have been significantly different as well with a larger ADU sample size; adult diets were consistently full of large gastropod remains. This would also be consistent with findings of ontogenetic differences in diet recorded for *M. freminvillii*'s Pacific coast counterpart, *M. californica* (Gray *et al.*, 1997).

Unlike those studies conducted on the related species, *M. californica* (Gray *et al.*, 1997), this study on *M. freminvillii* did not exhibit any differences in diet between sexes, overall or within size groups. Though there seems to be a slight trend when frequency of prey items is considered, the similarities among the various size/sex combinations are too high to be separated.

Though there were no significant differences in diet among months, diets do seem change with the population size structure changes observed from June to September (Table 1). nMDS plots seem to show shifts associated with this variation in species abundance, potentially indicating competitive release of prey resources by a larger size class. The resources would be available to smaller individuals as the larger ones leave the Bay. This is not unusual for related rays (Gray *et al.*, 1997), like *M. californica.* That species shows similar changes in size structure of population during the summer months in Humboldt Bay with associated significant differences in diet within each size class across those months. Statistical differences may have been more evident with a more sufficient sample size of the larger rays. However, juvenile rays may have to modify their diets more since they are present in the bay while young-of-the-year abundance is quite low through to when it is very high and need to compete for resources first with mostly adults and then, as time progresses, with an increasing number of young-of-the-year.

Most rays were collected at the deeper sites. These sites have historically had medium to fine sediments (Maurer *et al.*, 1978). The differences in diet among sites were significant and cross referencing stomach content differences via trawl site with sediment and benthic community type from the corresponding site indicates a potential level of selection on the part of the rays; no notable abundance of moonsnail (*Polinices duplicata* or *Euspira heros*) was found at areas near the three major trawl sites (62, 71, and 72). *Pagurus* sp. and *Busycon* sp. were recorded at most of the areas, and bivalves such as *Mytilus edulis* and *Ensis directus* were reported at areas near station 71 (Raineault *et al.*, 2012). Older studies also showed that this area was dominated by assemblages of bivalves and polychaetes that prefer fine sediments (Maurer *et al.,* 1978). YOY likely consumed species of snails and crustaceans that were manageable for their size; JUV were more locally selecting the available bivalves and other invertebrates; ADU selected most for *E. heros* that were reportedly not as abundant. Though most of the prey items were not highly digested and therefore likely ingested close to where they were caught, the proximity of the more southern stations (62, 71, and 72) does not preclude the rays caught at one station from having foraged at another. However, the significant differences in diets at different stations indicate that the prey items were likely representative of the available prey at the given location. It is also possible to have some animals that exhibit individual specialization (Matich *et al.,* 2011) and habitat-specific feeding (Ajemian and Powers, 2011), but these phenomena would be difficult to determine with the proximity of some of the sampling sites used here. It seems most likely with the available data that jaw morphology dictates the differences the rays experience in feeding across sites.

The dominant factors in *Myliobatis freminvillii* feeding ecology determined by this study are foraging site and size, potentially producing a certain amount of intra-specific competition (though there are no data to directly support this). Any temporal factors that could affect diet are influenced by the organisms' sizes. Small rays had a similar yet more diverse diet compared to the larger rays, which ate larger shared prey items. Medium rays seemed to be limited by size and site. Understanding this information and the more specific details of this study helps us understand the ecological role of the bullnose ray in Delaware Bay as a species that may use it as a nursery and as part of a larger ecosystem. The characteristics of this diet are incorporated into larger community dynamics studies of other similar batoid elasmobranchs (Szczepanski, ms. 4) as well as future whole-estuarine community interactions.

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Table 1: Detailed breakdown of *Myliobatis freminvillii* collecting efforts from June-September 2009 and 2010 in Delaware Bay.

Number of Rays	**Catches at Trawl Site by Month**														
	52				**62**				**71**		**72**				**Total**
Size class	**6**	**7**	**8**	**9**	**6**	**7**	**8**	**9**	**6**	**7**	**6**	**7**	**8**	**9**	
YOY															
F		7	17	12			1	8	1				3		49
M	1	3	12	6		4	2	3					3	2	36
JUV															
F	6		1		1		3				1		1		13
M	5	6	1		7		1			3	1	1	1		26
ADU															
F	5	1				1						1			8
Total	**17**	**17**	**31**	**18**	**8**	**5**	**7**	**11**	**1**	**3**	**2**	**2**	**8**	**2**	**132**

Table 2: Overall diet composition of 133 bullnose ray, *Myliobatis freminvillii*, from Delaware Bay collected from June-September 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI.

Class	Order	Family	Species	Prey Category	% FO	% PN	% N	% PW	% W	% IRI	% PSIRI
Gastropoda					**54**	**63.6**	**34.2**	**73.72**	**39.65**	**41.40**	**36.93**
		Buccinidae	*Busycon* sp.	Gastropod	20	61.6	12.1	68.60	13.51	8.63	12.82
		Calyptraeidae	*Crepidula fornicata*	Gastropod	2	34.6	0.5	42.21	0.64	0.03	0.58
		Muricidae	*Nucella lapillus*	Gastropod	2	32.8	0.5	22.96	0.35	0.02	0.42
		Nassariidae	*Ilyanassa trivitata*	Gastropod	12	59.9	7.3	52.85	6.41	2.83	6.83
		Naticidae	*Euspira heros*	Gastropod	32	43.3	13.8	58.92	18.75	17.68	16.27
Bivalvia					**29**	**59.2**	**17.1**	**65.35**	**18.81**	**10.76**	**17.93**
	Arcoida	Arcidae	*Anadara ovalis*	Bivalve	2	6.8	0.2	13.09	0.30	0.02	0.23
	Mytiloida	Mytilidae	*Mytilus edulis*	Bivalve	5	57.9	3.1	58.25	3.09	0.56	3.08
	Nuculoida	Yoldiidae	*Yoldia sp.*	Bivalve	1	100.0	0.8	100.00	0.76	0.02	0.76
	Veneroida				20	58.7	12.0	66.89	13.68	5.76	12.85
		Pharidae	*Ensis directus*	Bivalve	17	56.9	9.5	62.71	10.45	5.68	9.97
		Solecurtidae	*Tagelus divisus*	Bivalve	2	55.6	1.3	79.29	1.80	0.12	1.53
		Unidentified Veneroid	Unidentified	Bivalve	2	83.3	1.3	94.32	1.43	0.07	1.35
	Unidentified Bivalve		Unidentified	Bivalve	3	35.1	1.1	32.58	0.99	0.11	1.02
Crustacea					**60**	**47.3**	**28.3**	**43.76**	**26.19**	**33.98**	**27.24**
	Decapoda				60	47.1	28.2	43.73	26.17	35.66	27.17
		Crangonidae	*Crangon septemspinos*	Epibenthic Crustacean	2	42.3	1.0	35.59	0.81	0.07	0.88
		Hippolytidae	*Spirontocaris lilljeborg*	Epibenthic Crustacean	1	11.1	0.1	1.99	0.02	<0.01	0.05
		Paguridae			60	43.8	26.2	41.22	24.67	31.32	25.44
			Pagurus acadianus	Paguridae	7	20.3	1.4	6.23	0.42	0.21	0.90
			Pagurus longicarpus	Paguridae	51	46.8	23.8	46.70	23.70	41.14	23.73
			Pagurus pollicaris	Paguridae	4	28.1	1.1	14.26	0.54	0.10	0.80
		Portunidae			4	14.3	0.5	17.68	0.67	0.05	0.61
			Callinectes sapidus	Portunidae	2	13.8	0.2	39.10	0.59	0.01	0.40
			Carcinus maenas	Portunidae	1	12.5	0.1	1.08	0.01	<0.01	0.05
			Ovalipes ocellatus	Portunidae	2	15.6	0.2	4.57	0.07	0.01	0.15
		Unidentified Decapod	Unidentified	Misc. Crustacean	1	50.0	0.4	0.66	0.01	<0.01	0.19
	Unidentified Crustacean		Unidentified	Misc. Crustacean	1	16.7	0.1	2.63	0.02	<0.01	0.07
Unknown			Unknown 001	Uknown 001	37	55.1	20.5	41.34	15.34	22.70	17.90

Table 3: Overall diet composition of 85 YOY bullnose ray, *Myliobatis freminvillii*, from Delaware Bay collected from June-September 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI.

Class	Order	Family	Species	Prey Category	%FO	%PN	%N	%PW	%W	%IRI	%PSIRI
Gastropoda					**64**	**50.3**	**32.0**	**56.13**	**35.66**	**36.00**	**33.81**
		Buccinidae	*Busycon sp.*	Gastropod	16	76.7	12.6	82.10	13.52	5.51	13.08
		Calyptraeidae	*Crepidula fornicata*	Gastropod	2	34.6	0.8	42.21	0.99	0.05	0.90
		Muricidae	*Nucella lapillus*	Gastropod	2	32.8	0.8	22.96	0.54	0.04	0.66
		Nassariidae	*Ilyanassa trivitata*	Gastropod	18	62.9	11.1	55.69	9.83	4.72	10.46
		Naticidae	*Euspira heros*	Gastropod	25	26.9	6.6	43.62	10.78	5.50	8.71
Bivalvia					**19**	**51.9**	**9.8**	**57.00**	**10.73**	**3.23**	**9.42**
	Arcoida	Arcidae	*Anadara ovalis*	Bivalve	4	6.8	0.2	13.09	0.46	0.03	0.35
	Nuculoida	Yoldiidae	*Yoldia sp.*	Bivalve	4	6.8	0.2	13.09	0.46	0.03	0.35
	Veneroida				11	100.0	10.6	79.19	8.38	1.72	7.89
		Pharidae	*Ensis directus*	Bivalve	8	68.5	5.6	76.51	6.30	1.26	5.97
		Solecurtidae	*Tagelus divisus*	Bivalve	1	50.0	0.6	77.14	0.91	0.02	0.75
		Unidentified Veneroid	Unidentified	Bivalve	1	100.0	1.2	100.00	1.18	0.04	1.18
	Unidentified Bivalve		Unidentified	Bivalve	4	26.8	0.9	20.00	0.71	0.07	0.83
Crustacea					**75**	**46.8**	**35.2**	**48.86**	**36.79**	**45.43**	**36.00**
	Decapoda				74	47.2	35.0	49.60	36.76	45.64	35.89
		Crangonidae	*Crangon septemspinosa*	Epibenthic Crustacean	2	56.3	1.3	52.86	1.24	0.08	1.28
		Paguridae			69	48.1	33.4	49.84	34.60	59.65	33.98
			Pagurus acadianus	Paguridae	1	6.3	0.1	5.41	0.06	<0.01	0.07
			Pagurus longicarpus	Paguridae	68	48.8	33.3	50.61	34.53	59.19	33.91
		Portunidae			2	13.8	0.3	39.10	0.92	0.04	0.62
			Callinectes sapidus	Portunidae	2	13.8	0.3	39.10	0.92	0.04	0.62
	Unidentified Crustacean		Unidentified	Misc. Crustacean	1	16.7	0.2	2.63	0.03	<0.01	0.11
Unknown			Unknown 001	Uknown 001	46	50.3	23.1	36.66	16.82	23.40	19.94

Table 4. Diet compostion for 3 different size classes of bullnose ray, *Myliobatis freminvillii*, collected June-September 2009 and 2010. RMPQs and PSIRI expressed as percentages for larger prey categories.

		Bivalve	Epibenthic Crustacean	Gastropod	Misc. Crustacean	Paguridae	Portunidae	Unknown 001
%N	YOY	9.8	1.3	32.0	0.2	33.4	0.3	23.1
	JUV	35.6	0.7	30.5	1.3	12.1	1.0	19.0
	ADU	4.2	0.0	76.0	0.0	19.0	0.8	0.0
%W	YOY	10.73	1.24	35.66	0.03	34.60	0.92	16.82
	JUV	40.24	0.04	38.05	0.02	6.09	0.26	15.28
	ADU	0.24	0.00	89.99	0.00	9.77	0.01	0.00
%FO	YOY	19	2	51	1	69	2	46
	JUV	56	5	51	3	38	5	26
	ADU	13	0	100	0	50	13	0
%PSIRI	YOY	10.25	1.28	33.81	0.11	33.98	0.62	19.94
	JUV	37.92	0.35	34.28	0.65	9.07	0.61	17.12
	ADU	2.20	0.00	83.01	0.00	14.39	0.39	0.00

Table 5: SIMPER Test results for discriminating species of overall diet between sets of size groups. Species that contribute most to the dissimilarity between the paired size groups are denoted by an asterisk; SD is Standard Deviation.

	YOY x JUV				
	Average dissimilarity = 86.78%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Pagurus longicarpus*	17.09	1.02	19.69	19.69
	Unknown 001	15.95	0.89	18.38	38.07
	Ensis directus	11.53	0.62	13.28	51.35
	Euspira heros	11.47	0.7	13.22	64.57
	Busycon sp.	9.89	0.63	11.4	75.97
	Ilynassa trivitata	5.67	0.42	6.54	82.51
	Mytilus edulis	4.76	0.35	5.49	88
	Pagurus acadianis	1.86	0.37	2.14	90.15
	JUV x ADU				
	Average dissimilarity = 83.37%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Euspira heros*	26.77	1.44	32.11	32.11
	Busycon sp.	10.8	0.75	12.96	45.07
	Ensis directus	9.91	0.56	11.89	56.96
	Unknown 001	9.48	0.55	11.37	68.33
	Pagurus pollicaris	7.5	0.74	8.99	77.32
	Mytilus edulis	6.35	0.47	7.62	84.94
	Pagurus longicarpus	3.91	0.37	4.69	89.63
	Pagurus acadianis	3.51	0.53	4.21	93.85
	YOY x ADU				
	Average dissimilarity = 92.83%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Euspira heros*	28.74	1.55	30.96	30.96
*	*Pagurus longicarpus*	16.65	0.96	17.93	48.89
*	*Busycon* sp.	11.76	0.72	12.66	61.56
*	Unknown 001	11.53	0.7	12.42	73.98
	Pagurus pollicaris	7.43	0.72	8	81.98
	Ilynassa trivitata	5.55	0.41	5.98	87.96
	Ensis directus	2.82	0.27	3.04	90.99

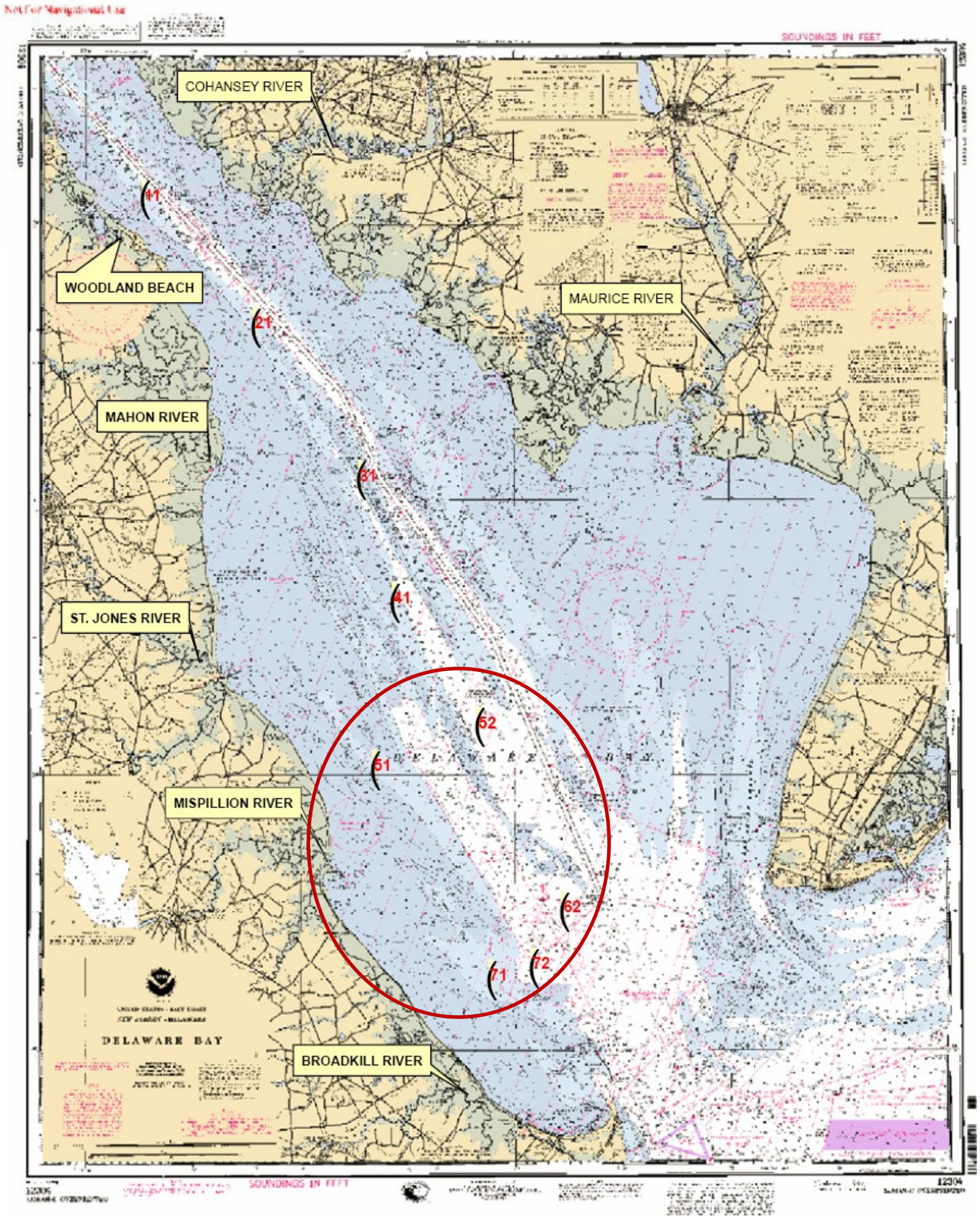

Figure 1: Stations sampled in Delaware Bay during the 2009-2010 DNREC otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red circle indicates the stations where *M. freminvillii* were caught. Average depths in meters for those stations are as follows: 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors.

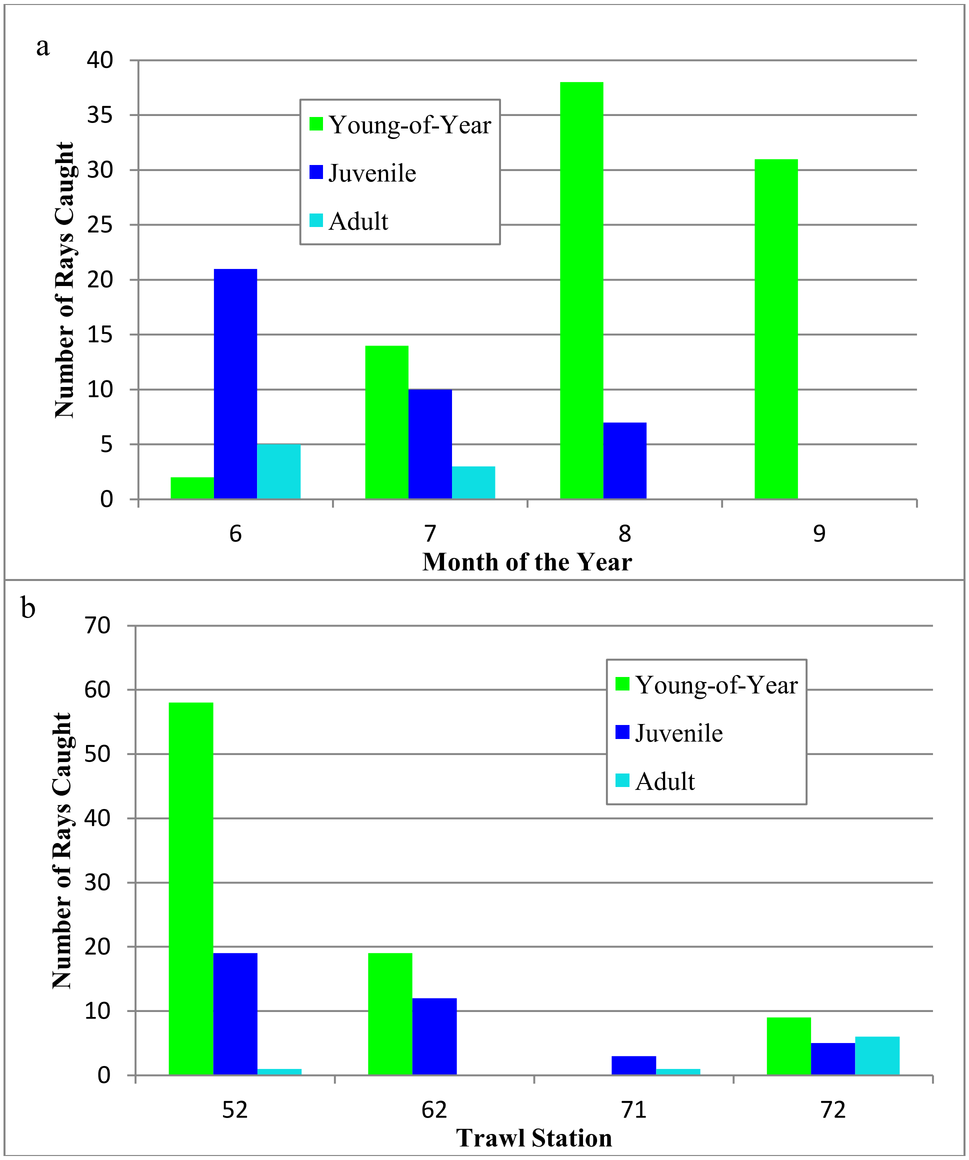

Figure 2: Frequency of *M. freminvillii* caught in Delaware Bay by DNREC monthly finfish trawl surveys in 2009 and 2010. Graphs profile catch by a) month of the year, only June-September, and b) trawl station.

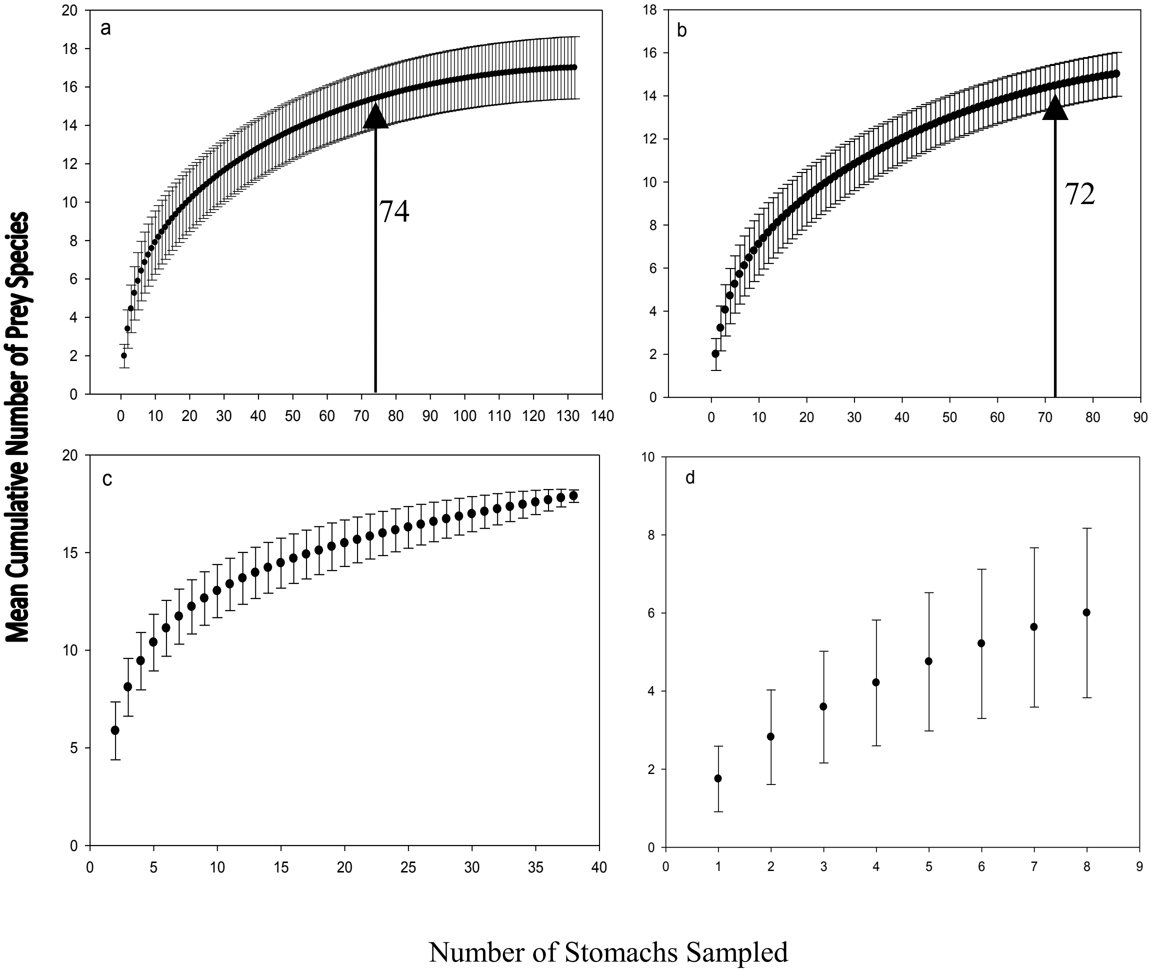

Figure 3: Cumulative Prey Curves for bullnose ray, *Myliobatis freminvillii*, sampled from June-September 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of ray stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from rays ≥40 cm DW, c) stomachs from female rays 41-80 cm DW and male rays 41-60 cm DW, and d) stomachs from female rays >80 cm DW and male rays >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

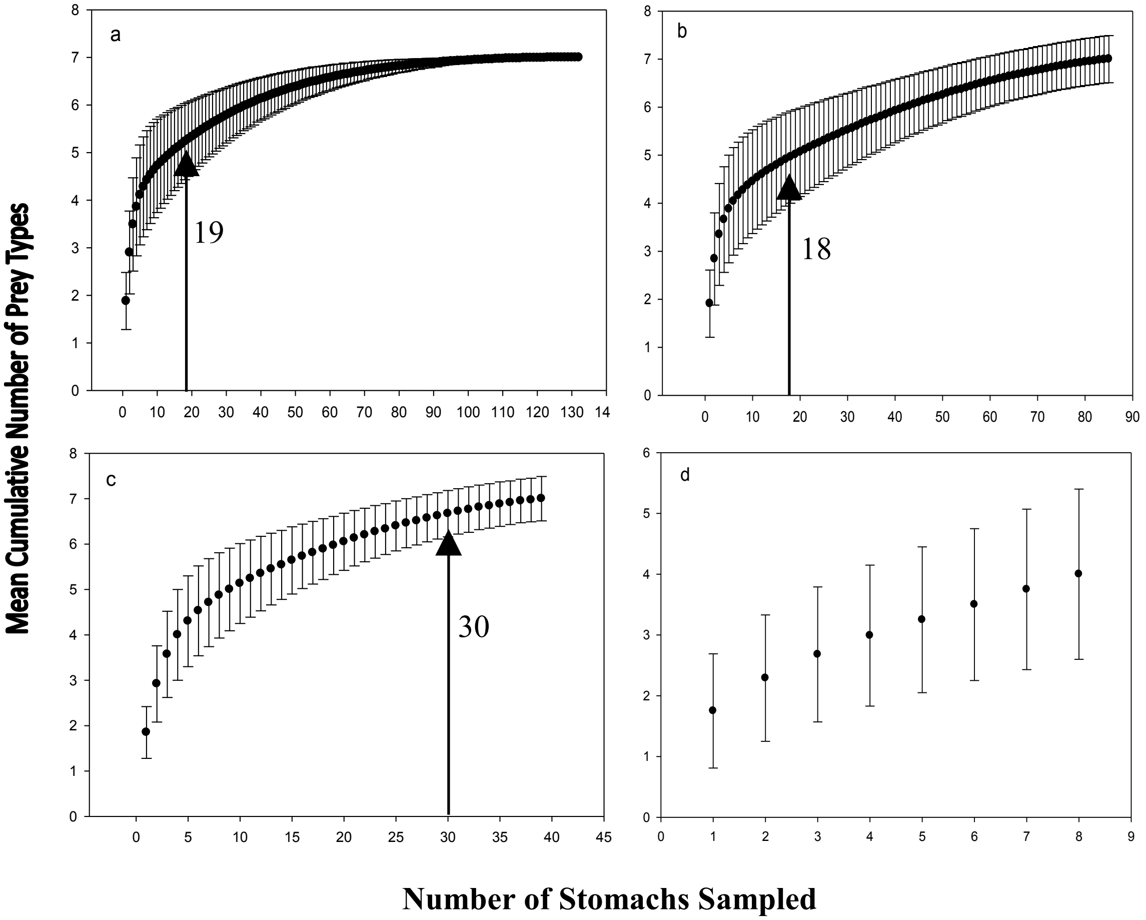

Figure 4: Cumulative Prey Curves for bullnose ray, *Myliobatis freminvillii*, sampled from June-September 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of ray stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from rays ≥40 cm DW, c) stomachs from female rays 41-80 cm DW and male rays 41-60 cm DW, and d) stomachs from female rays >80 cm DW and male rays >60 cm. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

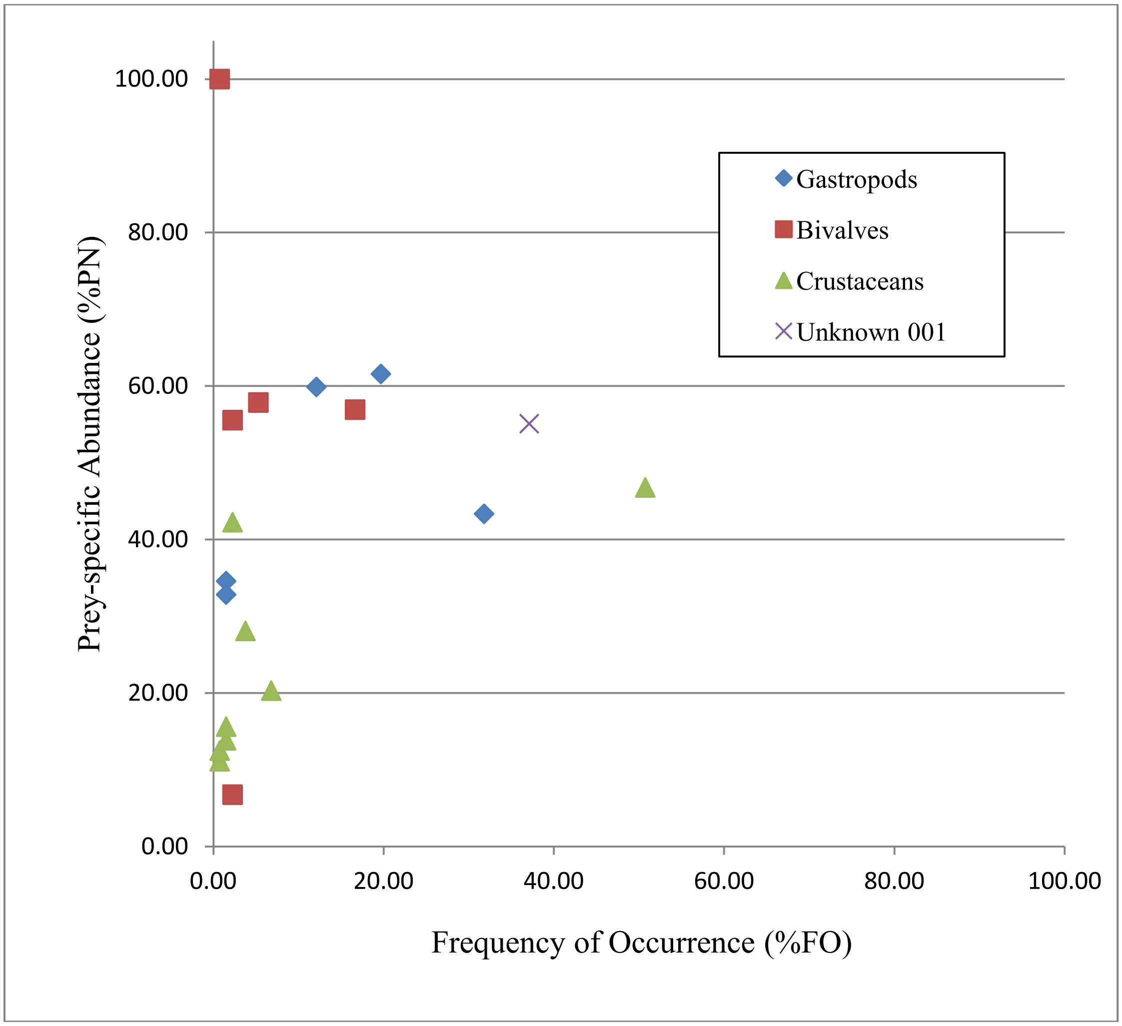

Figure 5: Feeding Strategy diagram of all *M. freminvillii* collected June-September 2009 and 2010 from Delaware Bay (n=133). Each point represents a separate prey species from Table 2, Blue diamonds represent gastropod prey, red squares represent bivalve prey, green triangles represent crustacean prey, and the X represents the unidentified prey item, Unknown 001.

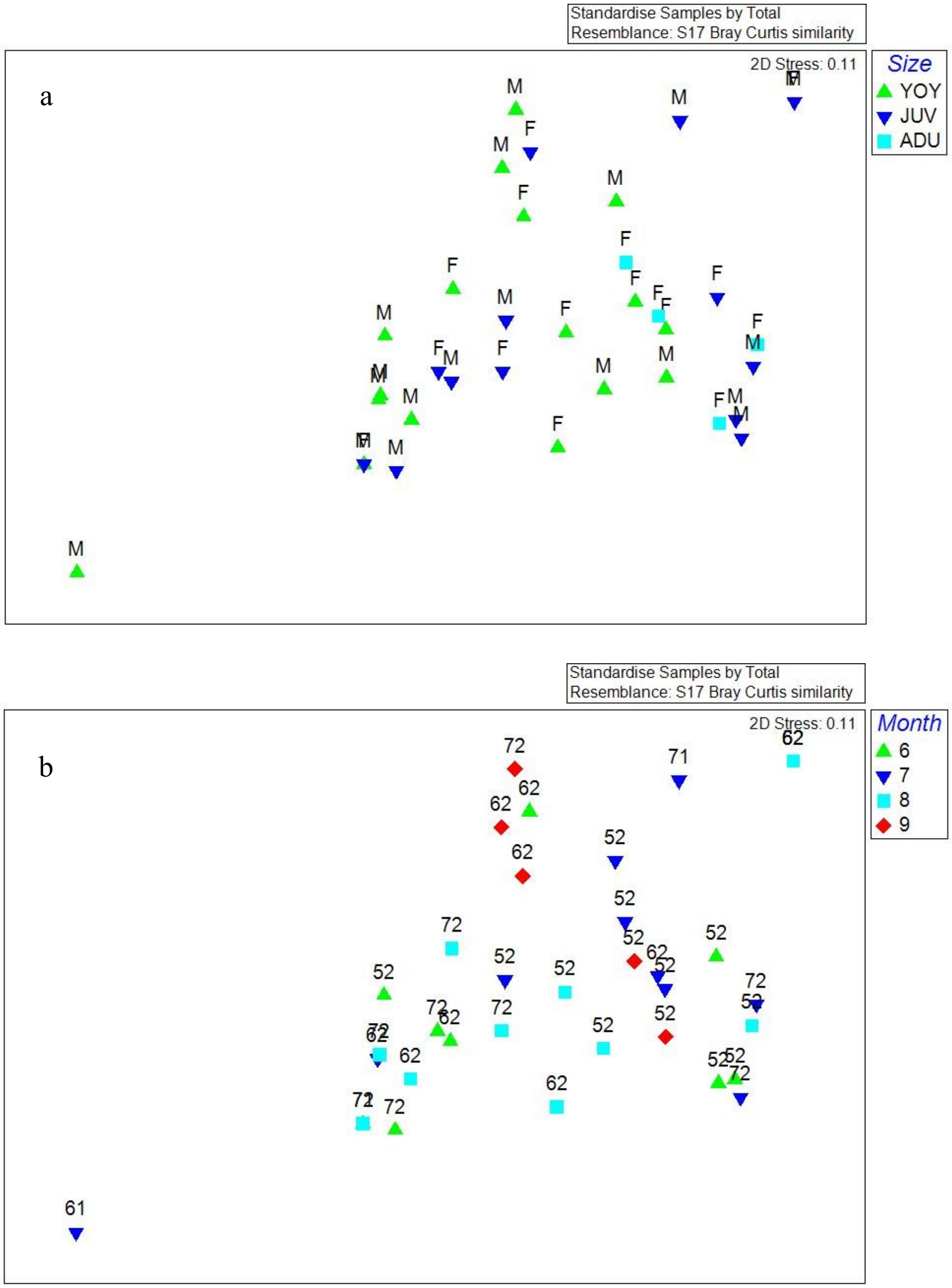

Figure 6: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.).

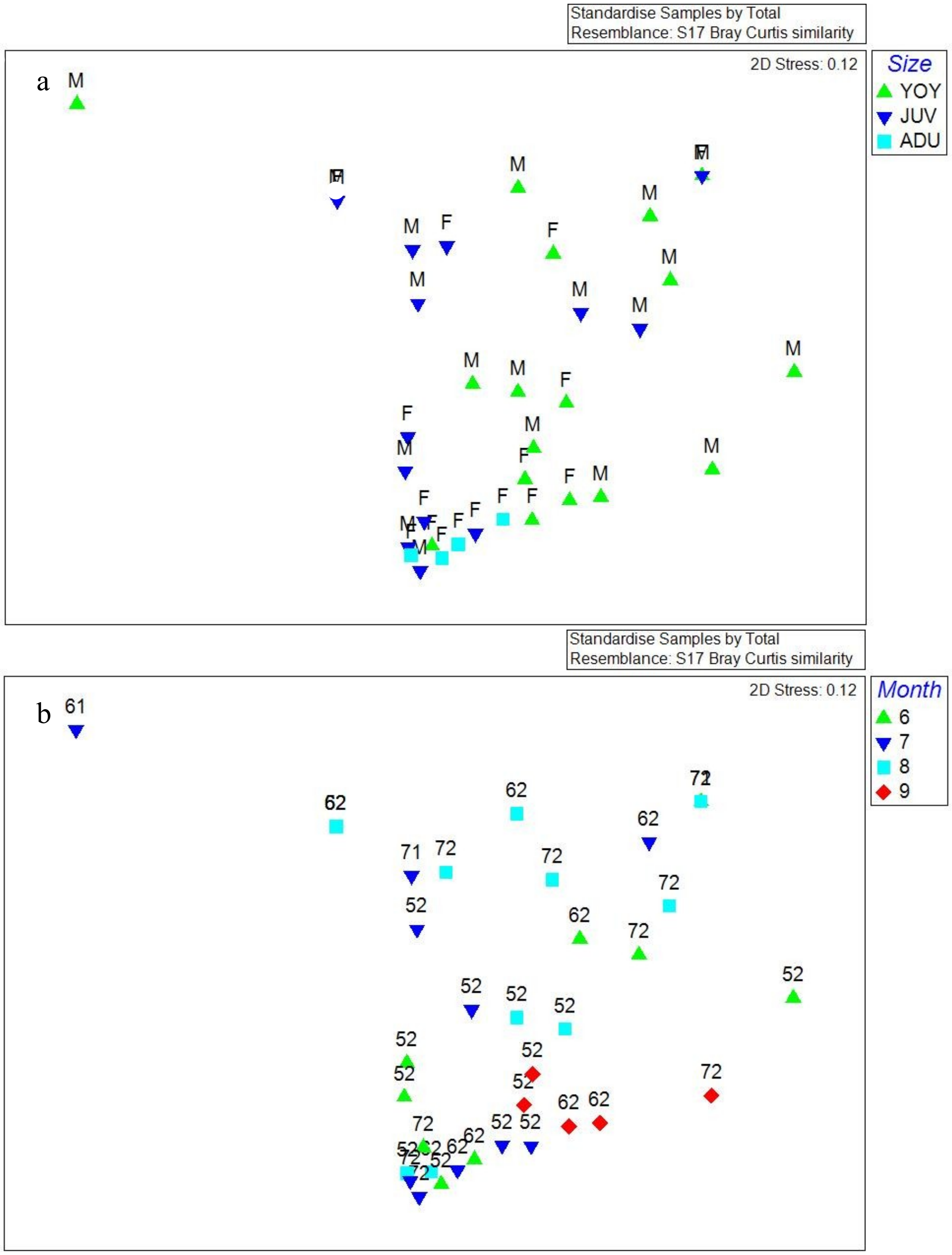

Figure 7: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.).

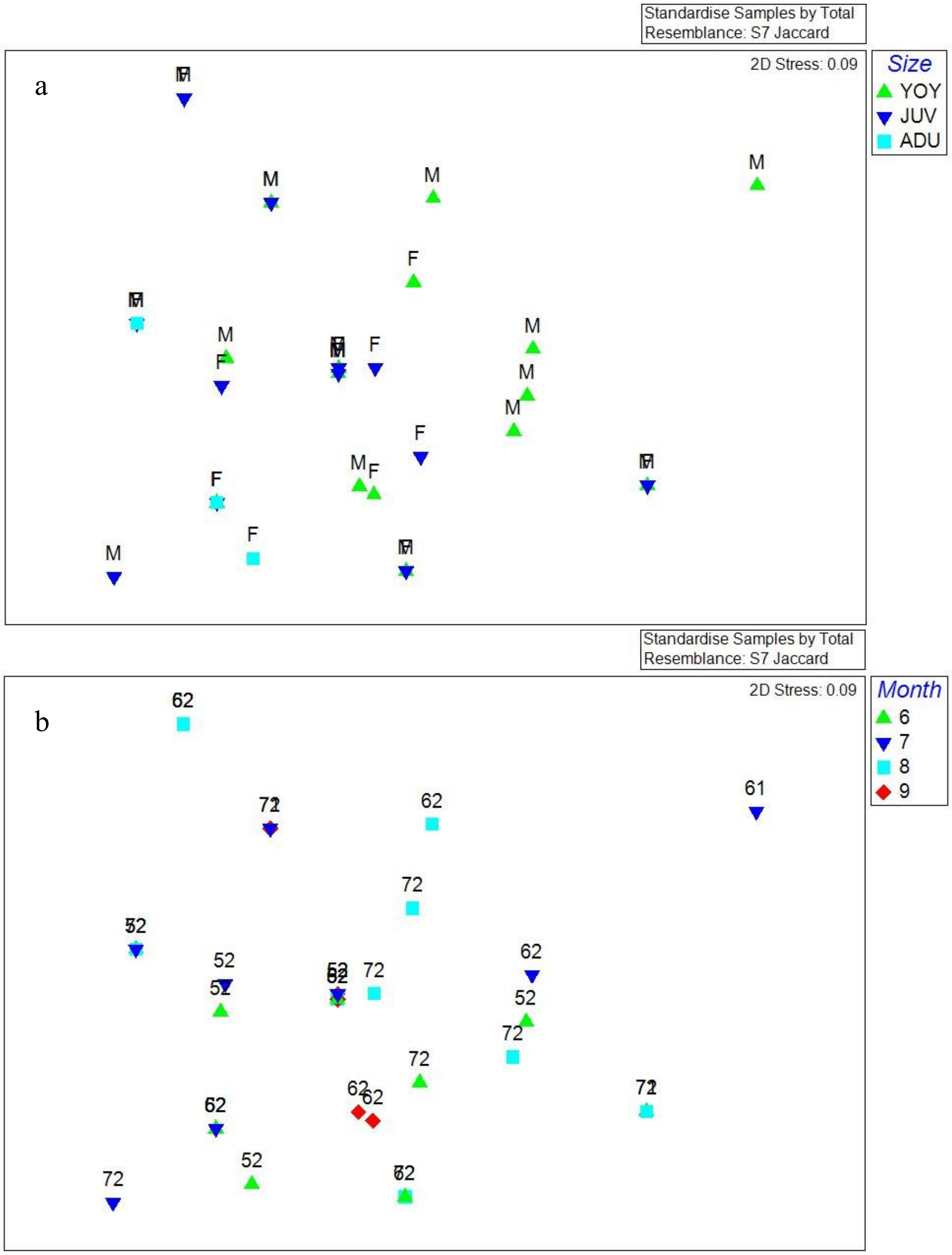

Figure 8: Non-metric multidimensional scaling plots of stomach content from *M. freminvillii* collected June-September 2009-2010. Prey groups (see Table 2 for ‘Prey Categories’) analyzed for proportion of diet by %FO highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) monthly samples labeled by station number; numbers in legend represent months of the year (6=June, 7=July, etc.).

MANUSCRIPT 2

Quantitative food habits of the clearnose skate, *Raja eglanteria,* in Delaware Bay

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ABSTRACT

Feeding habits of many batoid elasmobranchs (skates and rays) have been recorded but diets, prey selection, and resource partitioning within specific populations are not fully understood. Few studies compare diets of a species throughout its entire life history. I used gut content analysis to examine the feeding habits of the clearnose skate, *Raja eglanteria*, to understand the diet and trophic role of this species in the estuarine ecosystem at various life stages. Seventy-five specimens (22 female and 53 male) were collected over the course of two years through fisheries-independent trawl surveys. Decapod crustaceans were the most abundant prey type followed by bivalves and mysids, and then teleost fishes. *Crangon septemspinosa* was found to be the most important prey item in all indices along with *Neomysis americana*, *Ensis directus* and *Cynoscion regalis* in decending order. These skates have a mid-tertiary trophic level and adults have a wider dietary breadth (B = 0.65) than younger, smaller rays which had a dietary breadth less than 0.5. Significant differences were observed between male and female gut contents by relative numerical abundance and weight and among monthly diet by all measures; the only significant spatial differences found were in the frequency of the prey items consumed. The diet data from this study will be used in more comprehensive trophic community analysis and comparisons to elucidate the difference in interactions by similar batoid species in different estuaries and evaluate their role in competition and possible trophic cascades.

INTRODUCTION

Skates, as benthic elasmobranchs, have been an important part of the demersal marine community throughout their history (Compagno, 1990; Cortes, 1999; Szczepanski, ms. 1). Their abundance and widespread occurrence appear to play an influential role in many food webs of coastal shelves (Ebert and Bizzarro, 2007). They prey on benthic invertebrates, often fluidizing sediment to expose prey items and then consuming them, by swimming along the bottom and biting the mollusk parts that remain above the sediment, or by ambushing epibenthic telesots . The skates' benthic lifestyle and feeding habits may impact groundfish by predation and by competition (Murawski, 1991; McHugh, 2001; Link *et al.*, 2002; Orlov, 2004; Ebert and Bizarro, 2007). Despite the fundamental importance of feeding relationships in understanding food web dynamics, community structure, and energy transfer in marine systems, feeding ecology of skates is still poorly understood.

Understanding the biology of skates and their role in the ecosystem has become rather important in recent years. Elasmobranchs, overall, are susceptible to overfishing due to slow maturation, long life span, long gestation and few well-developed offspring (Stevens *et al.,* 2000, Ellis *et al.,* 2005a, b; Dulvy *et al*., 2008). Skates are of special concern since they have recently been targeted directly by more fisheries and have continued to be indirectly impacted in global fisheries as by-catch (Baum *et al.*, 2003; Shepherd and Myers, 2005). They are particularly susceptible to demersal trawling for groundfish (Dulvy *et al*., 2000). Little monitoring had been conducted on skate numbers in the past; some fisheries have reportedly caused declines and local extinctions that went unnoticed for a long period of time (Dulvy *et al.*, 2000).

Anthropogenic pressures on the elasmobranchs have had mixed consequences for skates. Some species have seen marginal increases in abundance, but this has been attributed to predation release associated with the decline of other larger elasmobranch species (Shepherd and Myers, 2005; Ward-Paige *et al.,* 2012). Many species of batoid elasmobranch, like the clearnose skate, have seen increased rates of abundance purportedly in light of decreasing numbers of greater sharks in the Western Atlantic (Myers *et al.,* 2007). As such, skates have been shown to be an integral part of these trophic cascades (Shepherd and Myers, 2005; Myers *et al.,* 2007; Ward-Paige *et al.,* 2012). The actual impact of the cascade is unclear, though, as the study presents no direct evidence that the sharks that are declining in number were the main source of predation pressure on the skates. Nonetheless, understanding the full impact of such trophic relationships requires more accurate knowledge of the diets of the organisms involved.

The clearnose skate, *Raja eglanteria*, is the most abundant skate species in Delaware Bay (Michels and Greco, 2008), but has not been studied in any great detail in this estuarine habitat in recent years. Fitz and Daiber (1963) thoroughly analyzed the stomach contents of 363 skates by basic measures of abundance (number, weight, and frequency) as well as a compound index, but did not use statistical analyses or the more precise compound index (Prey-specific Index of Relative Importance) since it had not been developed yet (Brown *et al.,* 2011). Also, some of their identification of teleosts was lacking in precision (Fitz and Daiber, 1963). The most recent diet data are from offshore studies that include data from large areas of the continental shelf (Bowman *et al.,* 2000; Packer *et al*., 2003). With the advent of ecosystem-based fisheries management (EBFM) and a greater focus on multi-species understanding, trophic data from more specific ecosystems is needed (Link, 2010; Link *et al.,* 2012; Lucey *et al.,* 2012; Pranovi *et al.,* 2012). Delaware Bay is the second largest bay on the East Coast and provides a unique opportunity to study many life history stages within an estuarine ecosystem (Szczepanski ms. 1).

With the concerns of trophic cascades in mind and lack of evidence of its true impact, this research aims to resolve the scarcity of knowledge of batoid feeding habits in an estuarine environment. The principal objective of the current study was to characterize the diet of *Raja eglanteria* in Delaware Bay and specifically to identify how the feeding habits may change ontogenetically, temporally, and spatially within the Bay. These concepts were investigated by testing the null hypotheses that there is no difference in diet among individuals of different sizes, during different months of the year, or at different sampling locations. Differences between male and female diets were also investigated by testing the null hypothesis that there is no difference in stomach contents between individuals of opposite sexes. This research was used to evaluate the ecological role of the clearnose skate and was included in a larger examination characterizing trophic interactions among batoid elasmobranch populations within Delaware Bay and how the dynamics may differ from those of other batoid communities, specifically in Narragansett Bay (Szczepanski, ms. 4).

METHODS

Study Site and Specimen Collection

This study was carried out in the Delaware Bay estuary. Delaware Bay is often described as the portion of the estuary from the mouth of the bay to a point below Artificial Island, where the estuary becomes narrower (Figure 1; Monaco and Ulanowicz, 1997). The surficial sediments of the bay have been characterized as 68% sand and 32% mud (Monaco and Ulanowicz, 1997) and some mixed-sediment bottom with extensive shallow flats and shoals interspersed with deeper sloughs (Kraft, 1988). The bay has little stratification, is well mixed, and has a considerable freshwater input from the Delaware River to the north. Delaware Bay has nutrient-rich waters, but high turbidity results in moderate levels of pelagic phytoplankton productivity (Pennock and Sharp, 1986) and little benthic plant growth. The bay is surrounded by salt marshes with winding rivers and creeks with narrow beaches.

Specimens of *Raja eglanteria* were collected aboard fishery-independent monthly bottom trawl surveys conducted by the Delaware Department of Natural Resource and Environmental Control (DNREC) in March-December of 2009 and 2010. Details about the trawl and the nine stations were outlined by Szczepanski (ms. 1).

Data collected from each specimen on the boat included: disc width (DW, cm), total length (TL, cm), and sex. Gastric lavage was used to remove stomach contents; this technique involves flushing the stomach of the fish with water to rinse out any objects (Hyslop, 1980). Verification samples were taken from 10% of lavaged individuals, and those that did not yield stomach contents, by stomach dissection. Stomachs were excised from the cardiac sphincter to the pyloric sphincter, the contents removed, and then stored on ice until they could be analyzed in the lab.

Stomach Content Analysis

Stomach contents were identified, separated accordingly, counted, and weighed. Prey items were identified to the lowest taxonomic level possible using field guides and taxonomic keys (Smith, 1964; Gosner, 1971 and 1978; Rehder, 1981; Pollock, 1996), and consultation with biologists at the University of Rhode Island (URI), Woods Hole Oceanographic Institute (WHOI), and Virginia Institute of Marine Science (VIMS). Any highly digested items that could not be identified, parasites, and sediments were counted and noted, but not included in statistical testing. The number of each prey item in a stomach sample was estimated using the most conservative count when detached components were present. Items were then weighed (to the nearest 0.01g) after excess moisture was blotted off.

Sample Size Sufficiency

To evaluate whether the sample size was large enough to sufficiently describe the skate's diet, cumulative prey curves (Ferry and Cailliet, 1996) were computed using EstimateS (Version 8.2.0, R.K. Colwell, http://purl.oclc.org/estimates). In this power analysis, the number of possible novel prey items is plotted against an increasing number of stomachs analyzed. The order of the samples was randomized 999 times, with empty stomachs excluded and the mean and standard deviation calculated for each sample size. As the curve reaches an asymptote, the sample size is considered to be sufficient. Visual examination of the curve for an asymptote (Ferry & Cailliet, 1996) is not reliable. To determine if the curve has reached an asymptote, the slope of the linear regression (*b*) of the final four curve endpoints was used as an objective criterion where $b \leq 0.05$ signified an acceptable plateau of the prey curve for diet characterization (Bizzarro *et al.,* 2009; Brown *et al.*, 2011).

Statistical Analysis

Diet Characterization

The contribution of each prey taxon to diet composition was estimated with three relative measures of prey quantity (RMPQ) described by Hyslop (1980). These measures include number (N), wet weight (W), and frequency of occurrence (FO) (Hyslop, 1980). Prey-specific abundance by number (%PN) and by weight (%PW) were calculated to identify each prey item's relative importance independent of the other prey found (Amundsen *et al.,* 1996). Prey-specific abundances are important not only as descriptive indices but also in the construction of a graphical model of specialization and a compound index both described below.

Since relative importance of prey can vary depending on which index is used, composite indices were also used. These were more comprehensive as they incorporated number, weight, and frequency all together. Index of Relative Importance (IRI) was calculated (Pinkas *et al.,* 1971; Cortés, 1997; Koen Alonso *et al.*, 2001) to maintain comparability with published work; this was expressed as a percentage of the total IRI for all species. Prey-Specific Index of Relative Importance, %PSIRI (Brown *et al.*, 2011), was also used as it is more precise than IRI, which can be biased by %FO and over-emphasizes common species (Hansson, 1998) often exceeding 100% (Bizzarro *et al.,* 2007).

Details about RMPQs, compound indices, and their respective calculations can be found in Szczepanski (ms. 1).

Trophic level and dietary specializations were examined to make inferences about the species' potential for dealing with environmental changes in resource availability. Trophic level (*TRL*) was calculated with Cortés' Trophic Level Index (1999). Prey species were combined into higher taxonomic or functional groupings (e.g. - Paguridae or bivalve, etc.) to aid in calculation of trophic level; %W was used in the calculation of *TRL* as the proportion of prey in the diet. Trophic levels of prey items (Table 1) were determined using calculated values from Pauly & Chistensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert & Bizzarro (2007). Dietary breadth was calculated using Levins standardized index (Krebs, 1989):

$$B=\left(\frac{1}{n-1}\right)\left(\frac{1}{\sum p_{ij}^{2}}\right)-1$$

where, B = Levins standardized index for predator i; p_{ij} = proportion of diet of predator i that is made up of prey j; and n = number of prey categories. This index ranges from 0 to 1, low values indicating diets dominated by few prey items (specialist predators) and higher values indicating generalist diets (Krebs, 1989; Fanelli *et al.,* 2009). In order to avoid problems derived by different states of prey digestion the index was calculated with %PSIRI. Dietary specialization was portrayed graphically by plotting %PN against %FO (Amundsen, 1996).

Significance Tests for Variation

Samples were defined as the averaged stomach content proportions for all individuals of a specific size group and sex at each station each month. Size groups were used that reflected life history stages (Packer *et al.,* 2003): young-of-the-year (YOY) comprised individuals < 35 cm TL, juveniles (JUV) included skates from 35-60 cm TL, and adults (ADU) were fish > 60 cm TL. Ontogenetic diet overlap was initially examined using the Schoener dietary overlap index (S_{do}) and simplified Morisita index (C_h) (Clarke and Warwick, 2001; McElroy *et al.,* 2006; Bizzarro *et al.*, 2007; Mabragaña and Giberto 2007). Diet was tested for differences among size classes, sex, sampling months, and sites. Significance testing involved only the 3 RMPQ's (N, W, FO) separately since each indicates different things about the diet and is also susceptible to different types of bias. Prey species were combined into larger groupings as described above for statistical analysis since many groups of uncommon prey were represented by few individuals and unnecessarily skewed the results; these groupings aided in the interpretation of the ecological importance of the results.

Non-metric multidimensional scaling (nMDS) ordination plots were constructed using PRIMER v6.1.13 (Clarke and Warwick, 2001) to look for relative similarities in overall diet for each RMPQ. Differences in diet among size groups, sexes, months, and collecting stations were tested by using permutation tests called analysis of similarities (ANOSIM). Similarity of percent contribution (SIMPER) analysis was used to identify the significantly important dietary categories that contributed to statistical differences in ANOSIM when differences were present. Szczepanski (ms. 1) provides further detail for each step of significance testing.

RESULTS

A total of 75 *Raja eglanteria* individuals was collected (22 females, 53 males) between March 2009 and December 2010. YOY, JUV, and ADU were represented by 9, 34, and 32 individuals, respectively. Out of all the stomachs collected, 74 (99%) contained prey; only 1 (1%) was empty. All of the YOY stomachs had food items present. Of the 34 JUV stomachs examined, 33 (97%) had food, 1 (3%) did not. All individuals from ADU contained prey items. Table 2 summarizes the details of the trawling efforts, presenting data only on skates with prey that were used in analyses. Skates were caught in all months from April to December, with the highest numbers being caught in August and September (Figure 2a). Most skates were caught at the mouth of the bay, specifically at the deepest station (#72 at 17.7m, Figure 2b). Maximum number of prey species found in a single stomach was 7, occurring in two separate skates (TL = 60.6 cm and 68.4 cm, both ADU). The average stomach content weight for all individuals with prey was 7.80 g and increased according to size class: YOY = 0.82 g, JUV = 3.28 g and ADU = 13.01 g.

The cumulative prey curve for all skates accounting for prey identified to lowest possible taxon reached a final slope at the last four points of b = 0.081 (Figure 3a) indicating a nearly, but not fully, sufficient sample size. The curve for YOY reached a final slope of b = 0.348 illustrating that n = 9 was not nearly a sufficient sample size (Figure 3b). The slope for JUV ended in a similar slope (Figure 3c, b = 0.36) despite the sample size more than tripling, indicating an increase in novel prey by this size class. The sample size to characterize the diet of ADU was also insufficient, as evidenced by the slope of the curve b = 0.29 (Figure 3d). To examine sample size sufficiency for statistical tests, curves were generated using the corresponding larger prey groupings (Figure 4a-d). For all stomachs together (Figure 4a), the asymptote was achieved at 40 stomach samples since there were only 14 distinct categories, with a final slope of $b = 0.015$. The slope for YOY concluded with a slope of $b = 0.418$ and was not sufficient for comparison (Figure 4b). The slope of the JUV curve achieved an asymptote at n = 25 (Figure 4c). The slope for ADU approached but did not reach an asymptote with $b = 0.068$ (Figure 4d).

The overall diet for *R. eglanteria* was characterized by 31 items identified to species, 2 more identifiable to family, and 2 items identified only to order or higher (Table 3). Food items were mostly decapod crustaceans, bivalves, mysids and teleost fishes. Decapods were found in 79% of stomachs and contributed to the diet most by both number and weight (51.2 %N, 52.29 %W). Bivalves were found frequently, approximately 31 %FO (though only contributing to 6.5 %N and 7.62 %W). Mysids were the next most frequent item in stomachs. Found in 26% of stomachs, mysids contributed 18.5 %N and 12.13 %W. The diet of the skate also included a considerable amount of teleost fish occurring in 22.08% of stomachs (15.3 %N, 20.38%W). %IRI for each prey type was 83.28%, 3.4%, 10.53%, and 6.09%, respectively. Gastropods, cephalopods, portunid crabs, and stromatid crustaceans were also found in stomachs of the clearnose skate, but not in notable abundance.

Crangon septemspinosa was the most abundant species overall (41.5 %N, 36.18% W) occurring in 73% of stomachs followed by *Ensis directus* (6.5%N, 7.26 %W), which was found in approximately 30% of the samples, and *Neomysis americana* (18.5 %N, 12.13 %W), which occurred in 26% of the samples. Other prevalent prey species included *Cancer irroratus* (14 %FO, 4.1 %N, 6.68 %W) and *Cynscion regalis* (9 %FO, 6.1 %N, 7.19 %W). With respect to %IRI, *C. septemspinosa* had the highest value (76.03%); *N. americana* (10.53%) and *E. directus* (5.47%) also made considerable overall contributions to the diet. *Doryteuthis pealeii* was found in only 4% of stomachs. There were many crustaceans in the diet including pagurids (mostly *P. longicarpus), Ovalipes ocellatus,* and *Squilla empusa.* Fish found in samples but in low abundance included the small schooling fish *Anchoa mitchillii,* and some flatfish, *Trinectes maculatus* and *Scophthalmus aquosus.* Also there were traces of plant matter, sediment, and driftwood.

Of all the relative measures of importance, %PSIRI accounted for individual preferences along with species-wide prey abundances. Decapods contributed 53.85% by PSIRI, while teleost fish and mysids had PSIRI values of 18.55% and 15.30%, respectively, and bivalves with %PSIRI of 7.31%. *Crangon septemspinosa* contributed 38.87% to PSIRI, *N. americana* contributed 15.30%, *E. directus* contributed 6.86%, *C. regalis* contributed 6.62%, and *C. irroratus* contributed 5.32%.

When the general diets of the different size classes were compared (Table 4), epibenthic crustaceans as well as krill were most important to the smallest skates, and then portunid crabs and epibenthic fish; pagurids and bivalves were found in the diet but were rare. The variety of prey consumed by JUV skates increased, though this size of skate still ate mostly epibenthic crustaceans. Those prey were followed closely in general abundance by krill and then portunids at approximately the same respective proportions, though krill consumption slightly increased and portunid consumption slightly decreased. The proportion of bivalves and pagurids in the diet increased while benthic crustaceans and small schooling fish began to appear. Adult skates had the diet with the widest variety. The proportion of epibenthic crustaceans increased again as did the proportion of epibenthic fish, with a substantial portion of portunids and bivalves. Among the other prey types consumed by the other sized skates, flatfish were found in only the diets of ADU skates while not in the diets of the rest.

The overall Trophic Level (*TRL*) of the clearnose skate was calculated to be 3.61, with YOY having a *TRL* = 3.60 and JUV and ADU having *TRL's* of 3.50 and 3.72, respectively. This is evidenced by the higher proportion of krill and lower proportions of higher trophic level arthropods eaten by juvenile skates.

Overall dietary breadth of the clearnose skate was calculated as $B = 0.66$; YOY, JUV, and ADU had dietary breadths of $B = 0.40$, 0.44 and 0.65, respectively. To examine feeding strategy for all *Raja eglanteria*, prey-specific abundance (%PN) was plotted against frequency of occurrence (Figure 5), indicating a moderate degree of specialization for a crustacean species (*C. septemspinosa*). Many of the other items found in the diet, like some other crustaceans and fish species, occurred infrequently, indicating more individual specialization for those items. However as a whole, the degree of variety in the diet with most species being eaten infrequently at varying levels of prey-specific abundance characterizes the clearnose skate as a generalist feeder, with a preference for *C. septemspinosa*.

To investigate any ontogenetic differences, Schoener's dietary overlap index (S_{do}) and simplified Morisita index (C_h) were calculated. The highest degree of overlap was between YOY and JUV ($S_{do} = 0.80$, $C_h = 0.95$). The least overlap by S_{do} was between YOY and ADU (0.61) and by C_h was between JUV and ADU (0.78). All iterations of overlap by either index were calculated to show more than 55% overlap.

Examination of the nMDS plots based on %N for each factor (size, sex, month, and station) for all stomach samples illustrated groupings in some areas but mostly high variability (Figure 6). There does seem to be a clustering of male diets with some degree of variation, whereas female diets were relatively varied with no clear clustering; size groups show an increasing level of similarity but with a high degree of overlap overall (Figure 6a, stress = 0.13). There was also some grouping by month with a slight degree of overlap but no clustering by site (Figure 6b, stress = 0.13). ANOSIM tests run on each of the factors resulted in relatively high degrees of overlap for all factors ($R_{size} = 0.004$, $R_{sex} = 0.14$, $R_{month} = 0.19$, and $R_{station} = 0.05$). There were significant differences between diets of the sexes and sampling month ($p_{sex} = 0.04$, $p_{month} \ll 0.01$) but not for diets of the different sizes or collection sites ($p_{size} = 0.46$, $p_{site} = 0.25$).

Similarity plots of samples based on %W exhibited more distinct groupings (Figure 7, stress = 0.14). Female and male diets did exhibit some variability but less overlap while sizes did not separate cearly (Figure 7a). Months seemed to group more clearly with some overalp while station 72 was the mostly tightly grouped of the stations while diets from the other locations were slightly more varied (Figure 7b). Statistical testing resulted again in a high degree of overlap for all factors ($R_{size} = -0.04$, $R_{sex} = 0.12$, $R_{month} = 0.15$, and $R_{station} = 0.09$) with significant differences among different sexes ($p = 0.04$) and months ($p = 0.01$). Sampling site differences approached significant ($p = 0.09$) and there was no difference in diets of each size ($p = 0.67$).

Diets plotted based on %FO indicated some possible groupings but a considerable amount of overlap (Figure 8, stress = 0.15). JUV samples seemed to cluster close together, while YOY showed little similarity and ADU samples overlapped each other group; female and male diets also exhibited high overlap and little internal similarity (Figure 8a; R_{size} = -0.01, R_{sex} = 0.06). Samples from different months did form some similarity groupings with slight overlapping, with the exception of March and October which displayed wide separation; samples from station 72 clustered while most other stations seemed widely dispersed (Figure 8b; R_{month} = 0.11, $R_{station}$ = 0.25). ANOSIM tests resulted in month and station differences being significant (p_{month} = 0.04, $p_{site} \ll 0.01$) while there were no differences between diets of different sizes (p = 0.51) or sexes (p = 0.14).

To assess the main factors involved in creating the differences between diets, SIMPER tests were run. The differences between male and female diets were related to the abundance and proportion of *Crangon septemspinosa* as well as the frequency of *Neomysis americana* (Table 5). The prey that was calculated to be responsible to for differences in diet among months can be attributed to the numerical abundance of *N. americana* and the weight and frequency of *C. septemspinosa* (Table 6).

DISCUSSION

This study presents a comprehensive diet analysis for *Raja eglanteria* within Delaware Bay. This species of skate was found to eat mostly decapod crustaceans as well as krill, several species of fish, and bivalves. Most prey items were identified to species with a few that were not identified that precisely. The whole-species cumulative prey curve approached but may not have fully reached sufficiency due to some lack of taxonomic resolution in prey items. That lack of precision could have resulted in redundant counts of prey items; the sample size therefore may well be sufficient. This possibility coupled with the low final slope lends confidence that the diet characterization is a good fit for *R. eglanteria*. Many prey species share similar niches and serve similar biological roles in the ecosystem. Prey items were combined into larger taxonomic and functional groups for this reason. When prey species were aggregated, the sample size was found to be sufficient to clearly describe at least the general trophic role of the clearnose skate in the Delaware Bay ecosystem.

Past studies attempted to describe the diet of the clearnose skate in Delaware Bay and those data were similar in some aspects to this study, but lacked precision in some aspects of analysis. Fitz and Daiber (1963) studied the overall biology of *Raja eglanteria* in Delaware and did include a dietary analysis. They recorded similar proportions of prey items for %N and %FO with *Crangon septemspinosa* being the most important by both measures (71 %N, 60 %FO) and *Neomysis americana* second by %N (11.6%) and *Ensis directus* second by %FO (36.0%). Weight was calculated differently so comparisons of this measure are less meaningful, however *E. directus*, *Pagurus pollicaris*, and *Ovalipes ocellatus* were ranked as important. Other species found in stomachs in 2009-2010 were found frequently in stomachs analyzed in the 1963 study, including *P. longicarpus* and *Cynscion regalis*. It was noted that “Fish (unident.)” made up almost as much of the diet content as identified fish. Fitz and Daiber also recorded some items in the diet of *R. eglanteria* that were not found in stomachs from 2009-2010: *Neopanope* (now *Dyspanopeus*) *texana* was found in 20.3% of stomachs analyzed and *Lubinia dubia* 13.2%, each contributing to the %N and weight of food in the diet. Polychaetes were also found, but not to any great extent. Fitz and Daiber (1963) analyzed 363 stomachs containing food so it is reasonable to expect some novel prey items in their analysis to not necessarily be found in this one (n = 74). The crustaceans unique to the 1963 diet study could have decreased in abundance since then and not be found in the diet any longer giving some indication of *R. eglanteria*’s ability to exhibit feeding plasticity.

Bowman *et al.* (2000) reported very little *C. septemspinosa* and almost no *N. americana*, but did find substantial amounts of *O. ocellatus* and *Cancer irroratus* along with high abundance of *C. regalis* and fish from the family, Soleidae. Their study only included data from 44 stomachs and was likely not statistically sufficient for full diet characterization. Those data were also only reported in percentage of stomach content by weight and may have been distorted by different levels of digestion that were not described. Packer *et al.* (2003) also found *C. septemspinosa* and *N. americana* to be substantial prey items along with various crabs, fish, some bivalves, and polychaetes. However, some of their data were reported from other sources and some was quantified in a more general way (pie charts of abundance by % occurrence). Though they did analyze 83 stomachs, their study area (as well as the area sampled by Bowman *et al.*,

2000) included much of the Western Atlantic coast (Packer *et al.*, 2003) so it included diets of fish from other habitats that likely had different prey abundances.

The trophic level of this skate indicates that it is an upper level predator, though not fully apex. The dietary breadth was intermediate with small immature rays having a more narrow dietary breadth increasing with age and size. %PN and %FO for the different prey species indicate that *Raja eglanteria* is a generalist feeder with a preference for *Crangon septemspinosa* and could have a size-dependent specialization for krill. The shift of importance of *Neomysis americana* after maturity is indicated by the difference in composition of the diet made up by krill; there was a drastic drop in krill from JUV to ADU, despite a similar size sample. The readily available krill would provide an abundant source of nutrition for growth into maturity. The variety of prey that the skates consume enables them to be versatile and likely will not be adversely affected by changes in the environment that consequently affect the benthic invertebrate community. This is particularly evident since there are a fair number of teleosts in the skate's diet, like *Cynscion regalis* as well as various pleuronectids and some small schooling fishes. The skate would likely not be as affected by changes in fish populations since they were not a large part of the diet, but could use them as an alternative source of food if crustacean populations changed. *Ensis directus* was the only bivalve consumed in any great frequency. Its abundance in the bay, particularly at the specific trawl stations, implies that *R. eglanteria* selects food based on availability; however, detailed abundance data for all prey items are not available and therefore preclude this claim from being fully supported.

The trophic level of these skates in Delaware Bay is somewhat lower than that reported for the whole species (for its entire range). Most skates' trophic level appears to vary between, and within, different ecosystems (Ebert and Bizzarro, 2007). *Raja eglanteria* from other regions likely have varied trophic levels lending support to the hypothesis that it feeds based on prey availability. The main point of Ebert and Bizzarro's study (2007) was to assess the ecological role of all skates, compare them to each other, and compare them to other top predators. However, their data had come from other past studies (Fitz and Daiber, 1953; Bowman *et al.*, 2000; Packer *et al.*, 2003) and revitalized the older data with a new comparative perspective.

No other study has included statistical comparisons of the diets across life history stages. Based on larger functional prey groupings, JUV was sufficient enough for comparison while the sample size for ADU was very close to sufficient. The comparison between these two groups is of particular importance since any difference would help in our understanding of the skates' transition into maturity. Though there were no overall differences in diet across sizes, size-related differences may have been coupled with other factors like sex or season. Another factor affecting significance level is the low sample size of YOY.

The current study is the first to statistically compare diets from different life history stages of the clearnose skate. Bowman *et al.* (2000) did list %W data by size of skate, starting at 31-35 cm TL and increasing at 5 cm intervals until 61-65 cm TL. If the data were combined to form the same life history stages analyzed in this study, there would have been 1 YOY, 36 JUV, and 7 ADU to compare with the 9 YOY, 33 JUV, and 32 ADU analyzed here. The single YOY stomach did not have anything that could be identified past 'Animal Remains/Misc.' JUV (n = 36) were reported to have high proportions of *Ovalipes ocellatus* and *Cancer irroratus* with increasing variety with greater size increments; this is illustrated by the appearance of amphipods and *Crangon septemspinosa* from 41-55 cm TL, polychaetes at 46 cm TL, and a wide variety of fish (particularly Soleidae) from 51 cm TL. Adults greater than 60 cm TL (n = 7) fed mostly on *Cynoscion regalis*, other unidentified fish, and *C. irroratus*. These data are not completely reliable for comparison of life history stages for the same reasons mentioned for its analysis of overall diet: wide sampling area and use of highly variable weight data (which can be skewed by varying levels of digestion, hindering not only accurate abundance but also identification).

Diets were clearly spearated by sex. The nMDS plot based on numerical abundance of prey types shows the stark contrast between females and males, regardless of size. Most males had very similar diets while ADU females seemed to have a diet that varied from the other sizes perhaps indicating that egg production may have an influence on diet composition. The low *R*-statistic revealed a high degree of similarity, but the *p*-value showed that the little separation was significant. The marginal separation was due not only to the abundance of *C. septemspinosa* but also *N. americana*, and the frequency of *C. septemspinosa* and *E. directus*. Interestingly, there was no difference in diet between sexes within size groups, perhaps due to low sample size for YOY as suggested for the lack of overall difference in size alone. The weights and frequencies of the prey types in the diet also had a significant effect on the difference in diet between sexes. The plot based on weight showed YOY males had different diets from the other males, likely due to the fact that the sizes of prey consumed by these individuals would be much smaller (though the sample for YOY size was also somewhat smaller). ADU females had different diets from other females by frequency of items likely for the same reason that the number of items was different. The plot of frequency appeared to have the effect of each size having a unique diet within each sex except for JUV skates. This could indicate that male and female YOY select different types of prey (suggesting a level of intra-specific competition, albeit small), their diets overlap as they reach an age where more food is accessible due to larger mouth size and then diverge again through maturity when there are different nutritional demands for separate male and female gamete production. No past studies on *Raja eglanteria* life history or diet have looked for dietary differences between sexes.

Weight of prey eaten differed seasonally. Also, the analysis of catch- frequency of skates by month confirms that the clearnose skate is a year-round resident of Delaware Bay (Figure 2a) with some seasonal movements (Fitz and Daiber, 1963; Packer, *et al.*, 2003). The increase in catch into the summer and then a drop in presence in the catch may be due to deeper areas not being sampled by the trawl (Michels and Greco, 2009, 2010); but the decrease of younger skates later in the year could be due to recruitment (Packer *et al.,* 2003) and growth of individuals into the next size stage.

Some studies have shown a degree of seasonality to the diet of *Raja eglanteria*, but never tested its significance. Fitz and Daiber (1963) showed a comparison of diets between fall of 1954 and spring of 1955 by %N and a comparison of diet through season starting summer 1954 to fall 1955 (excluding winter). The number of *Crangon septemspinosa* and *Ensis directus* increased from fall 1954 to spring 1955 while most other prey consumption decreased (mysids, crabs, hermit crabs, and fish). Weights of prey mostly increased slightly from summer to fall 1954 and then decreased into spring 1955, with the exception of *C. septemspinosa*, *Neopanope* (*Dyspanopeus*) *texana* and *E.*

directus which increased from fall 1954 to spring 1955. Most items increased again through summer and fall 1955. Despite these trends, Fitz and Daiber made little mention of them as compared to the variation in the diet of *Leucoraja erinacea*. Their only claim regarding seasonality is that *R. eglanteria* ingests a more or less consistent amount of food throughout its time in the bay, since the available number of prey items varies with the amount of available dry weight of prey (when prey are in low abundance, they are consumed at greater weights and when prey species are in greater abundance they can be consumed at lower weights). Bigelow and Schroeder (1953) noted that for this skate in the Block Island, Rhode Island region, squid was commonly found in the stomachs through early summer while "butterfish (*Poronotus*) [*Peprilus triacanthus*] and scup (*Stenotomus [chrysops])* are a dominant food during September and October." However, this was the extent of the discussion on seasonal variation.

Most skates were caught at the deepest station (#72, Figure 2b), though they did range into the northern half of the bay. The area where the stations were located did have community assemblages dominated by prey species that were found in abundance in the diet (Maurer *et al.*, 1978; Raineault *et al.*, 2012), specifically *Ensis directus*, *Cancer irroratus*, and *Pagurus* spp. There were some species found in these habitats that were not found in the diet (such as *Mytilus edulis*, *Ilynassa trivitatta*, various species of whelk, polychaetes, and bivalves) potentially indicating a level of preference. The only spatial difference that was significant was the difference based on frequency of each prey species consumed. There was likely not a sufficient enough sample size from each station to show any clear separation of diet for the other metrics if it existed between them. Also, these skates are generalist and would likely eat whatever was available at a given site.

There may not have been enough difference in site community composition (Raineault *et al.*, 2012) or not enough distance between sites for differences to be evident in the diet; a skate could have fed in multiple sites and had food items from each in them prior to being collected and analyzed.

Spatial variation was also a topic not thoroughly examined by other studies, though substrate preferences were mentioned (Packer *et al.*, 2003) and some of the prey items are associated with distinct sediment types (Maurer *et al.*, 1978; Raineault *et al.*, 2012). However there has been no other formal comparison of the diets from different collection sites within Delaware Bay, or in any other estuary, likely due to the lack of enough spatial separation between sites as mentioned earlier. There is some indication that the diet of the clearnose skate varies with latitude, though. Hildebrand and Schroeder (1927) reported that *Raja eglanteria* in Chesapeake Bay consumed mostly crabs and shrimp with some fish, though no actual quantities or abundance values were given. The current study showed less of an emphasis of crabs in the diet and more emphasis of shrimp still with some fish. Even further north, Bigelow and Schroeder (1953) identified squid and fish like butterfish and scup as playing important roles in the diet of *R. eglanteria*, with crustaceans not considered. Fitz and Daiber (1963) remarked that fish do not play as much of a role in the Delaware skate diet as they do in New England skate diets. However, fish occurred in approximately 22% of stomach samples (ranking 4th) in Delaware and contributed to approximately 18% of the diet as measured by %PSIRI (ranking 2nd). Though some stomach samples have been collected from JUV *R. eglanteria* within Narragansett Bay (n = 3) which included only *Doryteuthis pealeii* or *Menidia menidia* (unpublished data), more data need to be gathered for comparison of regional variations. The most recent analysis of skate diet composition and trophic level in skates (Ebert and Bizzarro, 2007) found *Raja eglanteria*, as a whole species, to have a trophic level of 3.68. They also reported that decapod crustaceans comprised approximately 57% of their diet, fish at 27%, and mollusks at about 8%; all other prey types were relatively minor.

This study provides a comprehensive diet profile of *Raja eglanteria* characterizing it as a trophic generalist with a strong preference for *Crangon septemspinosa* and *Neomysis americana* but also feeding on fish and bivalves. The first recorded diet components for yearling skate (YOY) are presented in this study as well as more complete and detailed life history stage comparisons. The most pronounced differences in diet are found between males and females, between months of the year, and spatially by frequency of prey. This species of skate is not considered overfished and is not on the International Union for Conservation of Nature (IUCN) Red List. It is likely that *R. eglanteria* can tolerate environmental and trophic community change well as a generalist feeder. Though these skates could derive substantial nutrients from razor clams and crabs, they are still mostly removing shrimp and mysids from the trophic economy of the bay (Fitz and Daiber, 1953). In the event of released top-down predation pressure, an increase in skate abundance may have a greater impact on these prey species and, consequently, have negative effects on the growth and survival of other fish that feed on the same prey (Herrington, 1948; Ebert and Bizzarro, 2007). Packer *et al.* (2003) reported *R. eglanteria* as a regular prey item of many sharks like *Carcharias taurus*, and are therefore a crucial link in the Delaware Bay food web and possible future trophic cascades.

Quantify levels of competition with other species of batoid elasmobranchs in Delaware Bay is the next step in progressing the knowledge of these batoids. Some work has been done involving taxa that can be found in Delaware Bay, but none included all possible species. *Raja eglanteria* and *Leucoraja erinacea* were compared by Fitz and Daiber (1963) and McEachran *et al.* (1976) compared *L. erinacea* and *Leucoraja ocellata* but not *R. eglanteria*. In light of ecosystem-based fisheries management taking a more multi-species analysis approach, even pair-wise species comparisons seem inadequate (Link 2010). The data from this study and other similar diet studies on batoid elasmobranchs are compiled and compared for just such a purpose (Szczepanski, ms.4).

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Table 1: Prey categories used to calculate trophic levels of clearnose skate, *Raja eglanteria* in Delaware Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007).

Group Code	Description	Trophic Level
MOLL	Bivalves, Gastropods and other molluscs excluding Cepahlopods	2.1
KRILL	Euphausid and mysids	2.25
CRUST	Decapod and other crustaceans	2.52
FISH	Misc. marine fish	2.8
FLAT	Pleuronectids	2.9
AMPH	Amphipods and isopods	3.18
CEPH	Squid	3.2
CLUP	Small schooling fish like anchovies and herring	3.2
GAD	Cod, hake, and haddock	3.8

Table 2: Detailed breakdown of *Raja eglanteria* collecting efforts from April-December 2009 and 2010 in Delaware Bay.

Number of Skates	**Size Class**						**Total**
	1		**2**		**3**		
Catches at Trawl Site by Month	**f**	**m**	**f**	**m**	**f**	**m**	
4							
51				1		1	2
62						1	1
71						1	1
5							
41				1		1	2
51						1	1
52					1	4	5
62						2	2
72					1	1	2
6							
41						1	1
52				1		1	2
62				2			2
71						1	1
72			2			2	4
7							
71	1	1					2
72		4		6			10
8							
52					1		1
62						1	1
72	1		4	4	1	2	12
9							
51				1	1	1	3
52			1				1
71						1	1
72	2		4	3		4	13
10							
51						1	1
71						1	1
11							
51					1		1
12							
72					1		1
Total	**4**	**5**	**11**	**19**	**7**	**28**	**74**

Table 3: Overall diet composition of 74 clearnose skate, *Raja eglanteria*, from Delaware Bay collected from April-December 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI.

Class	Order	Family	Species	Prey Category	%FO	%PN	%N	%PW	%W	%IRI	%PSIRI
Gastropoda					3	3.3	0.1	0.84	0.02	<0.01	0.06
	Cephalaspidea	Cyclichnidae	*Acetocina sp.*	Gastropod	1	5.3	0.1	1.42	0.02	<0.01	0.05
	Littorinimorpha	Unidentified Littorinimorpha	Unidentified	Gastropod	1	1.2	0.0	0.27	<0.01	<0.01	0.01
Bivalvia					31	20.8	6.5	24.44	7.62	3.40	7.34
	Mytiloida	Mytilidae	*Mytilus edulis*	Bivalve	1	0.8	0.0	1.14	0.02	0.00	0.01
	Nuculoida	Yoldiidae	*Yoldia sp.*	Bivalve	1	20.0	0.3	48.09	0.65	0.02	0.46
	Veneroida	Pharidae	*Ensis directus*	Bivalve	30	21.8	6.5	24.42	7.26	5.47	6.86
Cepahlopoda	Teuthida	Loligindae	*Doryteuthis pealeii*	Cephalopod	4	70.0	2.8	67.09	2.72	0.30	2.78
Crustacea					83	86.4	71.8	81.94	68.11	90.03	72.81
	Amphipoda	Gammaridae	Unidentified	Amphipod	1	50.0	0.7	1.77	0.02	0.01	0.35
	Decapoda				79	64.6	51.2	66.00	52.29	83.28	53.85
		Callianassidae	*Callianassa atlantica*	Benthic Crustacean	5	23.2	1.3	29.89	1.62	0.21	1.44
		Cancridae	*Cancer irroratus*	Epibenthic Crustacean	14	30.1	4.1	48.69	6.58	1.93	5.32
		Crangonidae	*Crangon septemspinosa*	Epibenthic Crustacean	73	57.0	41.6	49.58	36.18	76.03	38.87
		Epialtidae	*Libinia emarginata*	Epibenthic Crustacean	1	1.1	0.0	75.99	1.03	0.02	0.52
		Hippidae	*Emerita talpoida*	Benthic Crustacean	1	4.3	0.1	7.76	0.10	<0.01	0.08
		Paguridae			26	10.1	2.6	8.25	2.14	1.70	2.49
			Pagurus acadianus	Paguridae	1	6.3	0.1	14.47	0.20	0.01	0.14
			Pagurus longicarpus	Paguridae	22	8.0	1.7	8.12	1.76	1.01	1.75
			Pagurus pollicaris	Paguridae	4	22.7	0.9	6.89	0.28	0.07	0.60
		Pandalidae	*Stylopandalus richardi*	Epibenthic Crustacean	1	10.0	0.1	1.88	0.03	<0.01	0.08
		Pinnotheridae	*Pinnixa chaetopterana*	Benthic Crustacean	8	8.1	0.7	6.48	0.53	0.13	0.59
		Portunidae			10	25.8	2.7	56.64	5.88	1.22	4.46
			Callinectes sapidus	Portunidae	1	6.7	0.1	76.03	1.03	0.02	0.56
			Carcinus maenas	Portunidae	1	20.0	0.3	14.50	0.20	0.01	0.23
			Ovalipes ocellatus	Portunidae	8	13.3	1.1	43.76	3.55	0.50	2.31
			Unidentified	Portunidae	1	100.0	1.4	100.00	1.35	0.05	1.35
	Mysida	Mysidae	*Neomysis Americana*	Krill	26	71.9	18.5	47.24	12.13	10.53	15.30
	Stromatidae	Squillidae	*Squilla empusa*	Benthic Crustacean	5	42.9	2.3	79.67	4.31	0.48	3.31
Actinopterygii					22	69.2	15.3	92.31	20.38	6.09	18.55
	Atheriniformes	Atherinopsidae	*Menidia menidia*	Small schooling fish	1	100.0	1.4	100.00	1.35	0.05	1.35
	Clupeiformes	Engaulidae	*Anchoa mitchillii*	Small schooling fish	3	1.2	0.0	17.21	0.47	0.02	0.25
	Gadiformes	Gadidae			5	39.0	2.0	84.01	4.36	0.46	3.33
			Gadus morhua	Epibenthic fish	3	25.0	0.7	94.74	2.56	0.12	1.62
			Urophycis regia	Epibenthic fish	3	53.0	1.4	73.29	1.98	0.12	1.71
	Perciformes				12	67.5	7.9	88.08	10.30	2.16	9.46
		Gobiidae	*Gobiosoma bosc*	Misc. Teleost	1	100.0	1.4	100.00	1.35	0.05	1.35
		Pomatomidae	*Pomatomus saltatrix*	Epibenthic fish	1	50.0	0.7	84.09	1.14	0.03	0.91
		Sciaenidae	*Cynoscion regalis*	Epibenthic fish	9	63.9	6.0	75.98	7.19	1.68	6.62
		Stromateidae	*Peprilus triacanthus*	Small schooling fish	1	10.0	0.1	76.83	1.04	0.02	0.59
	Pleuronectiformes				10	38.2	4.0	100.00	10.39	1.52	3.97
		Achiridae	*Trinectes maculatus*	Flatfish	7	56.7	3.8	52.95	3.58	0.67	3.70
		Scophthalmidae	*Scophthalmus aquosus*	Flatfish	4	7.5	0.3	5.73	0.23	0.03	0.27
	Syngnathiformes	Syngnathidae	*Syngnathus fuscus*	Misc. Teleost	1	3.0	0.0	3.96	0.05	0.00	0.05
	Unidentified Tele	Unidentified		Misc. Teleost	1	1.2	0.0	20.09	0.27	0.01	0.14
Plant Matter				Other Prey	18	6.7	1.2	6.75	1.19	0.36	1.19
Driftwood				Other Prey	1	33.3	0.5	1.36	0.02	0.01	0.23
Sediment				Other Prey	5	7.5	0.4	1.24	0.07	0.03	0.24

Table 4. Diet composition for 3 different size classes of clearnose skate, *Raja eglanteria*, collected April-December 2009 and 2010. RMPQs and PSIRI expressed as percentages for larger prey categories.

		Amphipod	Benthic Crustacean	Bivalve	Cephalopod	Epibenthic Crustaceans	Epibenthic Fish	Flatfish	Gastropod	Krill	Misc. Teleost	Other Prey	Paguridae	Portunidae	Small Schooling Fish
%N	YOY	0.0	0.0	0.5	0.0	52.8	1.9	0.0	0.0	32.0	0.0	1.0	0.7	11.1	0.0
	JUV	0.0	2.4	6.4	0.3	38.3	7.2	0.0	0.0	35.3	0.0	0.9	2.6	6.2	0.4
	ADU	1.4	2.1	8.7	0.0	46.7	12.0	8.7	0.2	3.4	3.7	3.3	3.4	6.3	0.0
%W	YOY	0.00	0.00	0.56	0.00	60.48	10.82	0.00	0.00	16.14	0.00	0.41	0.48	11.11	0.00
	JUV	0.00	3.33	7.46	0.04	36.10	9.85	0.00	0.00	24.19	0.00	2.50	3.97	9.95	2.62
	ADU	0.05	1.90	10.22	0.00	41.32	15.98	8.06	0.05	0.76	3.63	0.44	1.19	15.47	0.93
%FO	YOY	0	0	11	0	78	11	0	0	44	0	22	22	11	0
	JUV	0	20	43	3	83	10	0	0	43	0	20	33	20	7
	ADU	3	11	29	0	69	20	23	6	6	11	26	23	31	3
%PSIR	YOY	0.00	0.00	0.51	0.00	56.65	6.34	0.00	0.00	24.07	0.00	0.71	0.61	11.11	0.00
	JUV	0.00	2.87	6.92	0.19	37.20	8.53	0.00	0.00	29.73	0.00	1.72	3.29	8.06	1.49
	ADU	0.74	2.01	9.45	0.00	44.03	13.99	8.40	0.12	2.08	3.66	1.85	2.28	10.90	0.49

Table 5: SIMPER Test results for discriminating species of overall diet that contribute to the significant differences between sexes for RMPQ's %N, %W, and %FO. Species that contribute most to the dissimilarity between sexes are denoted by an asterisk; SD is Standard Deviation.

	Female x Male, %N				
	Average dissimilarity = 80.72%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Crangon septemspinosa*	24.08	1.32	29.83	29.83
*	*Neomysis americana*	19.05	0.9	23.6	53.43
	Trinectes maculatus	5.9	0.41	7.31	60.74
	Cynoscion regalis	5.9	0.45	7.31	68.05
	Ensis directus	5.01	0.47	6.21	74.26
	Cancer irroratus	4.07	0.45	5.05	79.31
	Squilla empusa	2.97	0.3	3.67	82.98
	Urophycis regia	2.33	0.22	2.88	85.86
	Female x Male, %W				
	Average dissimilarity = 84.78%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Crangon septemspinosa*	21.16	1.21	24.96	24.96
	Neomysis americana	14.98	0.82	17.67	42.62
	Cynoscion regalis	7.55	0.47	8.91	51.53
	Cancer irroratus	6.11	0.45	7.21	58.74
	Trinectes maculatus	5.35	0.37	6.31	65.05
	Ensis directus	5.27	0.48	6.22	71.27
	Squilla empusa	4.48	0.34	5.28	76.55
	Ovalipes ocellatus	3.67	0.33	4.33	80.88
	Female x Male, %FO				
	Average dissimilarity = 92.83%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Crangon septemspinosa*	9.87	0.8	13.08	13.08
	Ensis directus	7.18	0.74	9.51	22.59
	Neomysis americana	7.03	0.7	9.32	31.91
	Trinectes maculatus	6.74	0.52	8.93	40.84
	Pagurus longicarpus	5.35	0.62	7.1	47.93
	Cynoscion regalis	4.83	0.47	6.41	54.34
	Cancer irroratus	4.81	0.58	6.37	60.72
	Vegitation	3.93	0.53	5.2	65.92
	Squilla empusa	2.8	0.39	3.72	69.64
	Ovalipes ocellatus	2.46	0.38	3.26	72.89
	Pinnixa chaetopterana	2.11	0.38	2.79	75.69

Table 6: SIMPER Test results for discriminating species that contribute to the significant monthly differences in overall diet between YOY and ADU, and site differences between JUV and ADU; both tests based on %N data. Species that contribute most to the dissimilarity between sexes are denoted by an asterisk; SD is Standard Deviation.

	Significant Differences by Month				
	YOY x ADU, %N				
	Average dissimilarity = 95.09%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Neomysis americana*	43.86	13.74	46.12	46.12
	Cynoscion regalis	15.28	0.79	16.07	62.18
	Ensis directus	6.6	0.41	6.94	69.12
	Crangon septimspinosa	5.95	0.66	6.26	75.38
	Gobiosoma bosc	5.56	0.34	5.84	81.22
	Squilla empusa	5.56	0.34	5.84	87.07
	Trinectes maculatus	5.56	0.43	5.84	92.91
	Significant Differences by Month				
	JUV x ADU, %W				
	Average dissimilarity = 84.21%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Crangon septimspinosa*	20.81	1.18	24.72	24.72
	Neomysis americana	19.91	0.88	23.64	48.36
	Ensis directus	11.05	0.65	13.13	61.49
	Cynoscion regalis	7.23	0.45	8.58	70.07
	Trinectes maculatus	6.7	0.43	7.95	78.02
	Cancer irroratus	4.11	0.51	4.88	82.91
	Gobiosoma bosc	3.8	0.29	4.51	87.41
	Portunidae	1.9	0.2	2.25	89.67
	Pagurus longicarpus	1.38	0.32	1.64	91.31
	Significant Differences by Month				
	JUV x ADU, %FO				
	Average dissimilarity = 84.21%				
	Species	Average Dissimilarity	Diss/SD	Species % Contribution to Dissimilarity	Cumulative % Dissimilarity
*	*Crangon septimspinosa*	20.01	1.18	24.7	24.7
	Neomysis americana	18.91	0.87	23.74	48.44
	Ensis directus	11.02	0.66	13.15	61.59
	Cynoscion regalis	7.53	0.46	9.01	70.6
	Trinectes maculatus	6.9	0.4	7.95	78.95
	Cancer irroratus	4.15	0.52	4.86	83.41
	Gobiosoma bosc	3.3	0.28	4.55	87.96
	Portunidae	1.7	0.21	2.23	90.19

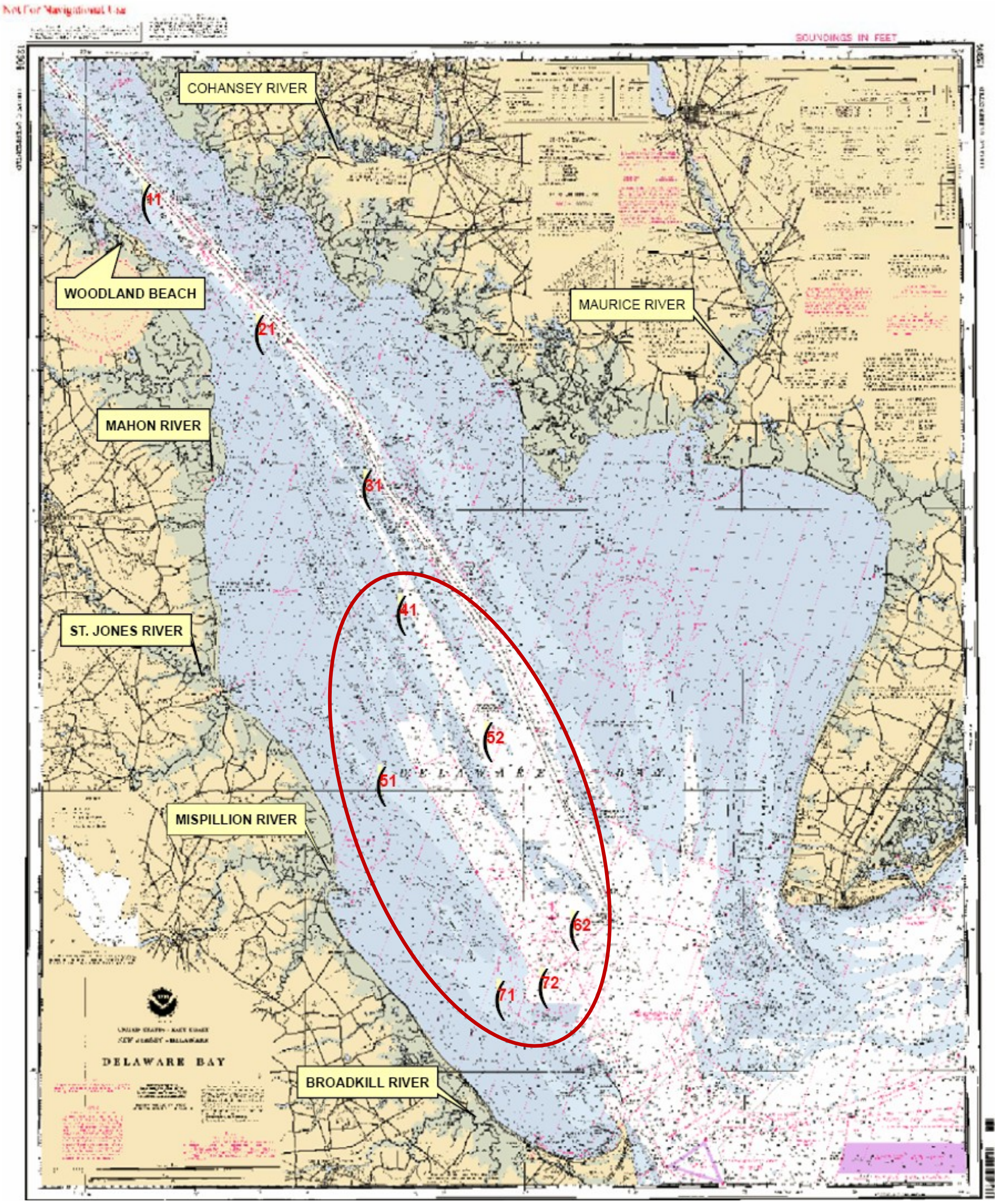

Figure 1: Stations sampled in Delaware Bay during the 2009-2010 DNREC otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red circle indicates the stations where *R. eglanteria* were caught. Average depth in meters for those stations is as follows: 41=8.1 m, 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors.

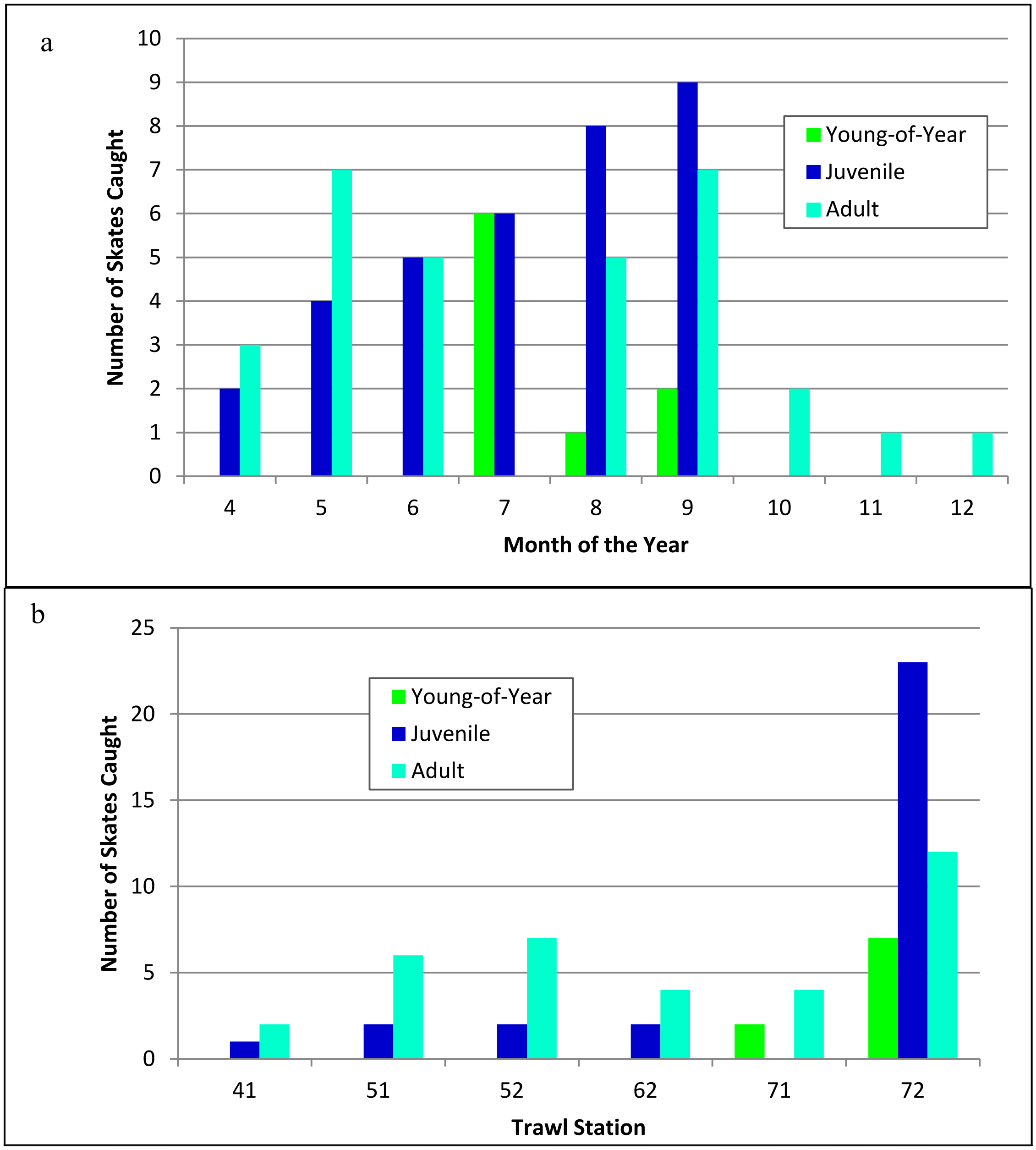

Figure 2: Frequency of *R. eglanteria* caught in Delaware Bay by DNREC monthly finfish trawl surveys in 2009-2010. Graphs profile catch by a) month of the year, March-December, and b) trawl station.

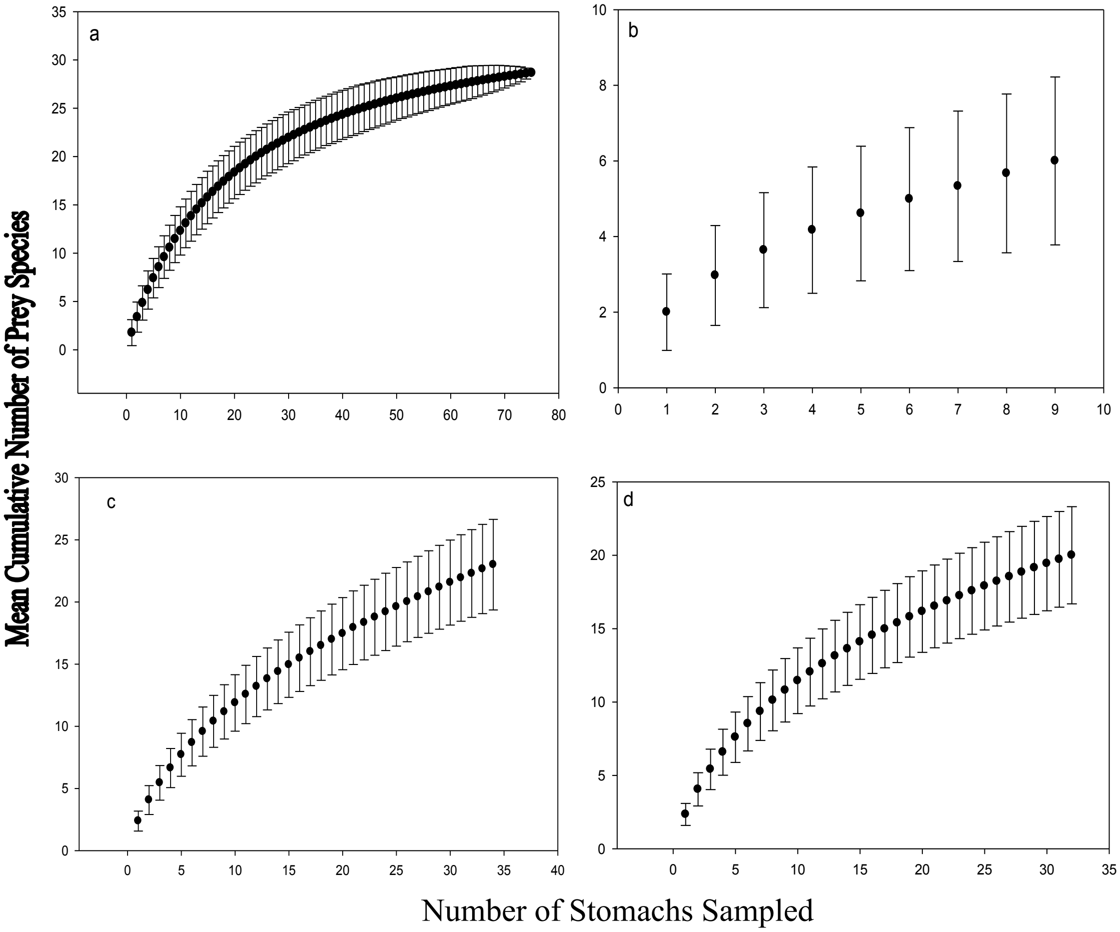

Figure 3: Cumulative Prey Curves for clearnose skate, *Raja eglanteria*, sampled from April-December 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates ≥35 cm DW, c) stomachs from 35-60 cm DW, and d) stomachs from skates >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

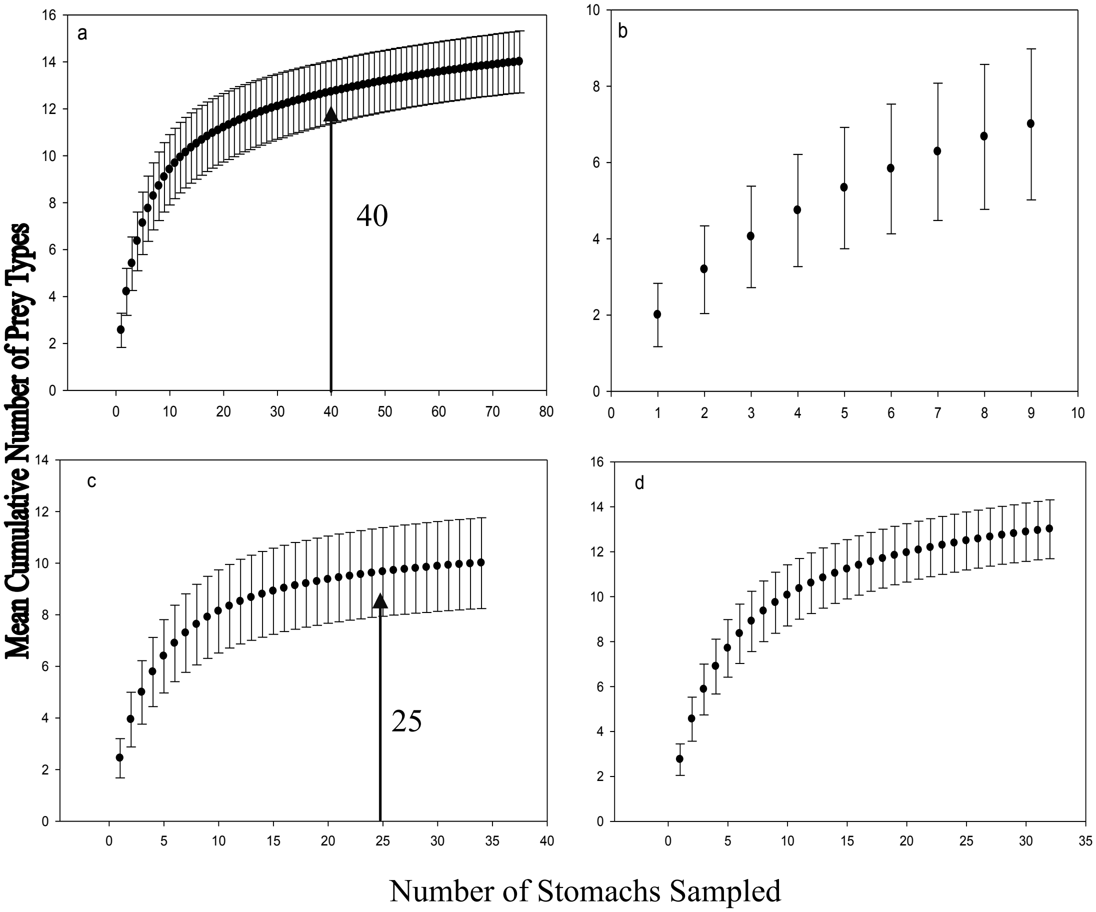

Figure 4: Cumulative Prey Curves for clearnose skate, *Raja eglanteria*, sampled from April-Deceember 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates ≥35 cm DW, c) stomachs from 35-60 cm DW, and d) stomachs from skates >60 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

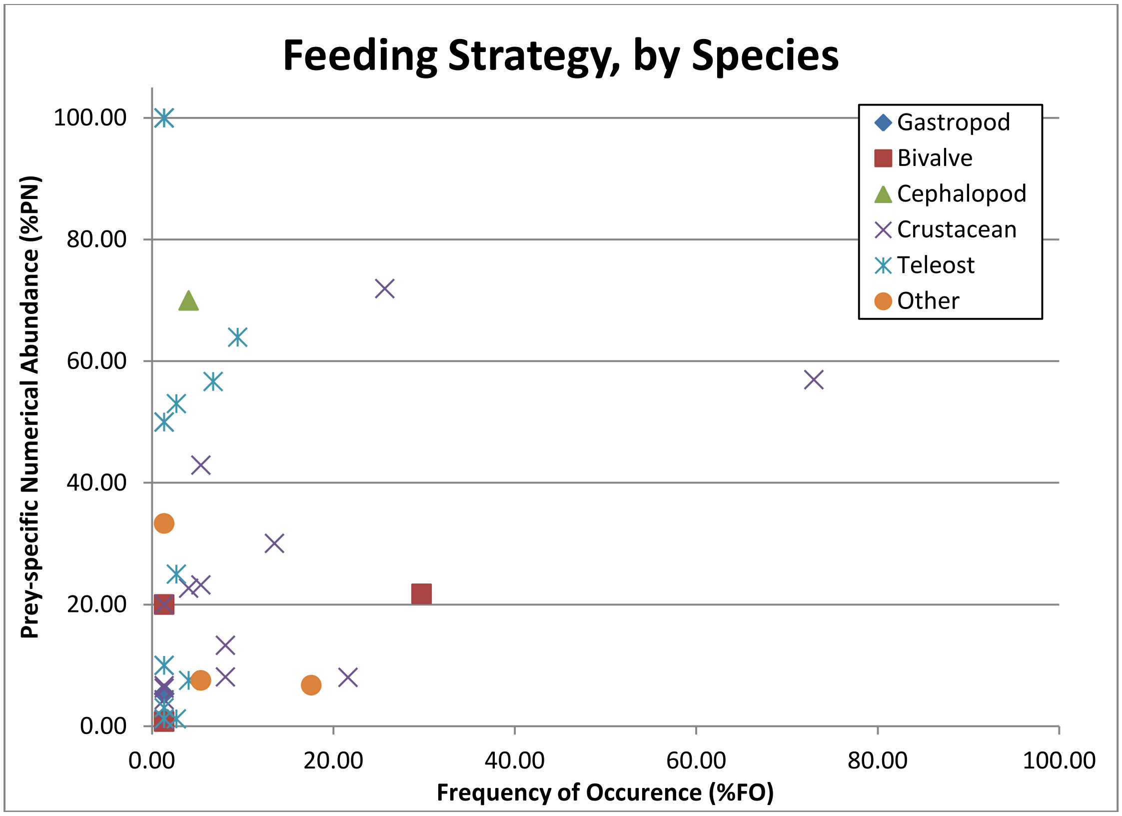

Figure 5: Feeding Strategy diagram of all *R. eglanteria* collected April-December 2009 and 2010 from Delaware Bay (n=74). Each point represents a separate prey species from Table 2, symbols represent different prey categories used in statistical analyses.

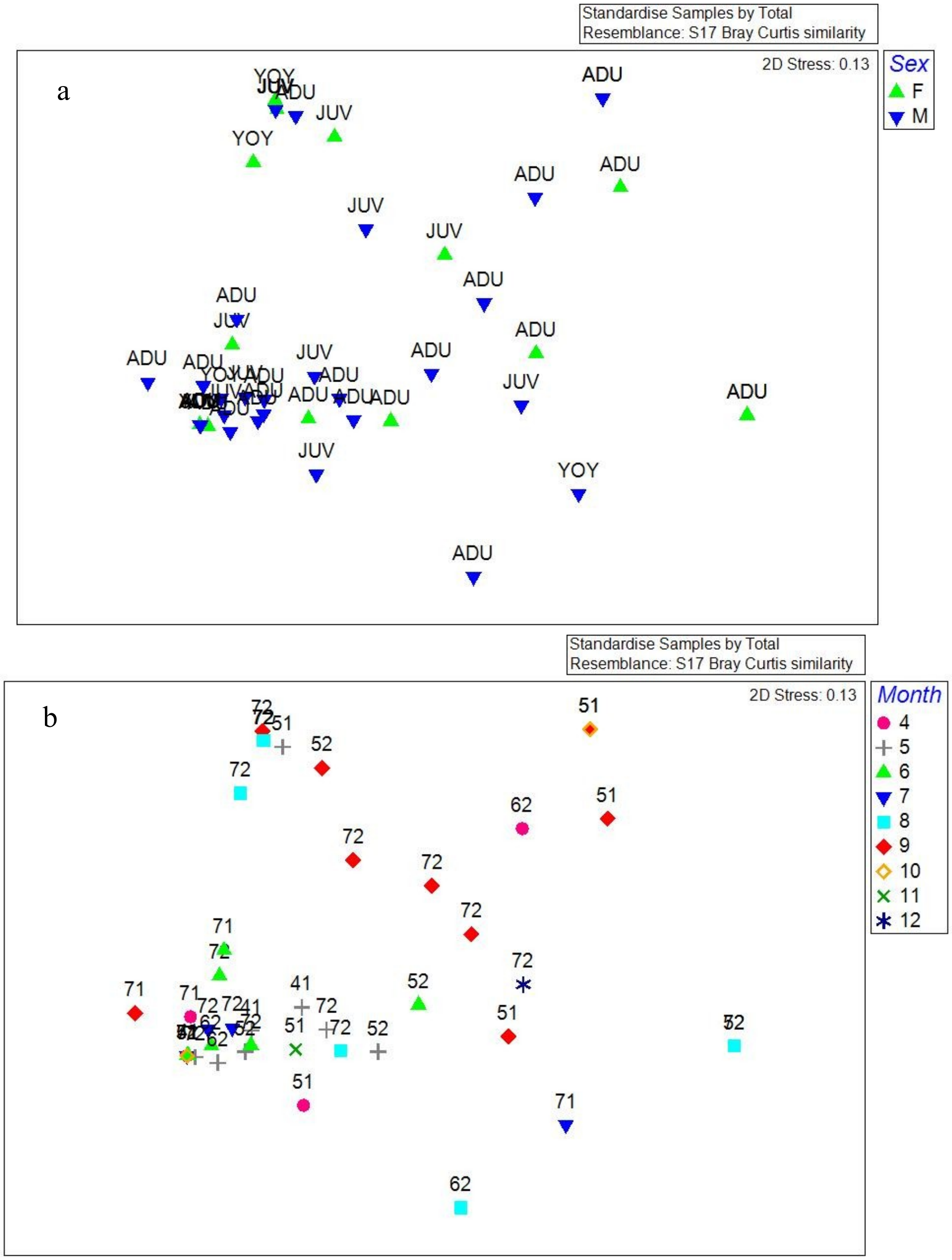

Figure 6: Non-metric multidimensional scaling plots of stomach content from *R. eglanteria* collected April -December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.).

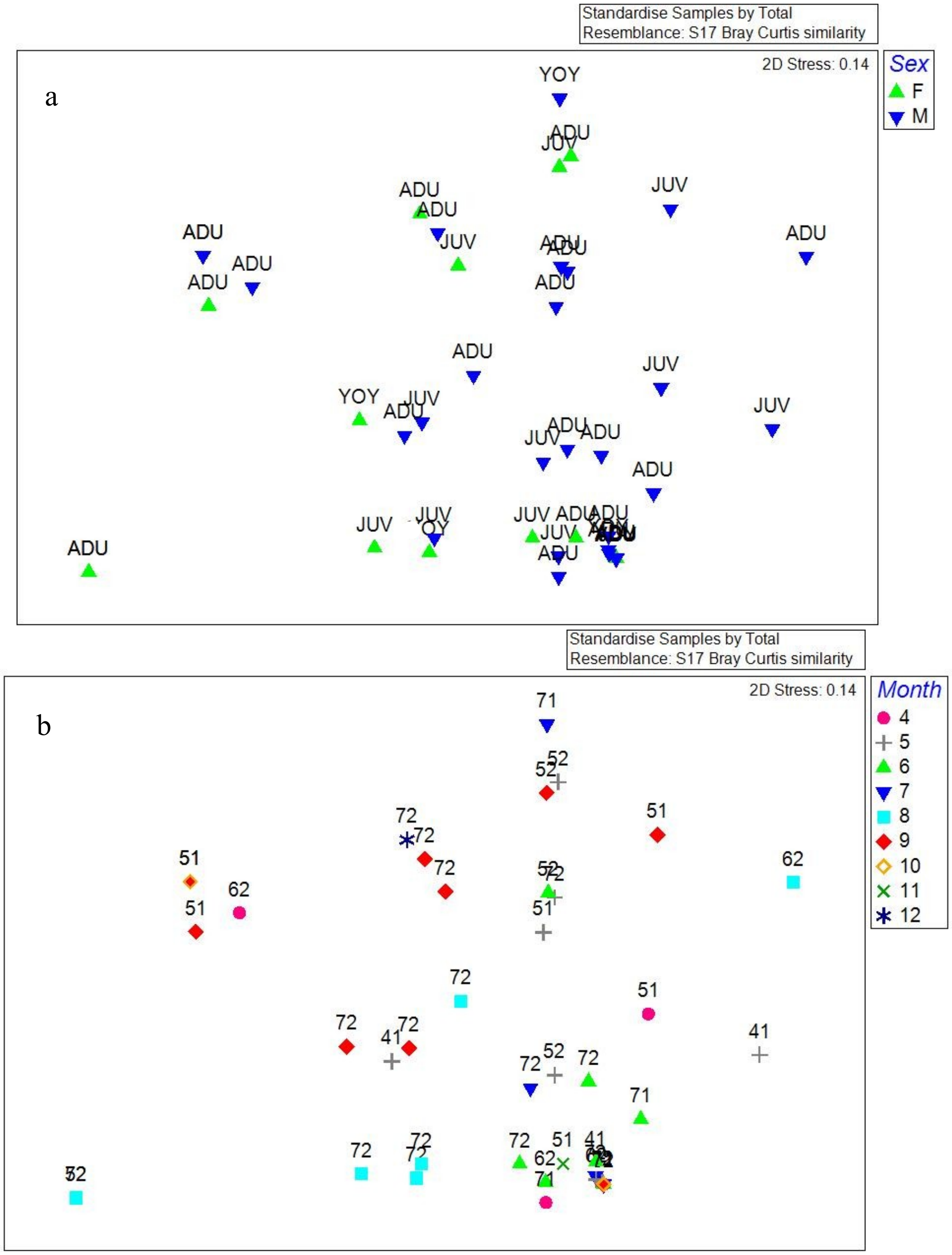

Figure 7: Non-metric multidimensional scaling plots of stomach content from *R.egalnteria* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.).

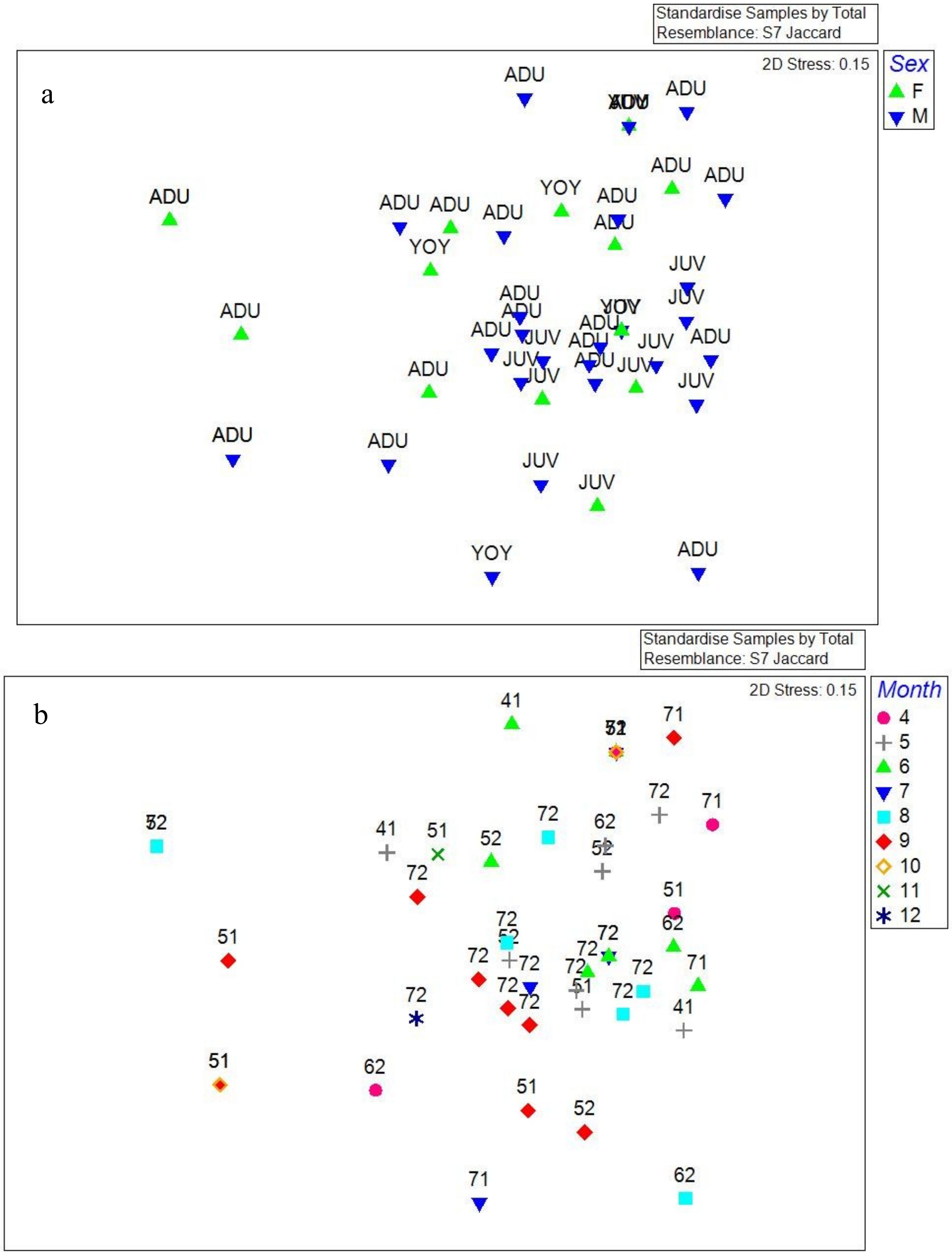

Figure 8: Non-metric multidimensional scaling plots of stomach content from *R. eglanteria* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %FO highlighting factors of a) sex groups labeled by size class (▲represents females, ▼ represents males) and b) monthly samples labeled by station number; numbers in legend represent months of the year (4=March, 5=April, etc.).

MANUSCRIPT 3

Quantitative food habits of the little skate, *Leucoraja erinacea*, in Narragansett Bay

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ABSTRACT

Skates play an important role in marine ecosystems as upper level predators, but are vulnerable to over-exploitation by fisheries due to slow growth to maturity and few offspring. These elasmobranchs are particularly vulnerable to commercial trawling due to their demersal life style. Proper management and conservation of these fish require a better understanding of their trophic ecology. Through gut content analysis, I evaluated the dietary habits of the little skate, *Leucoraja erinacea*, to understand the trophic role of this species within Narragansett Bay at various life stages. Three-hundred eighty-nine specimens (185 females, 204 males) were collected over the course of two years through fisheries-independent trawl surveys. Amphipods and decapod crustaceans were the most abundant prey types with polychaetes, crabs, bivalves, and fish also occurring in the diet. *Leptocheirus pinguis* was the most important prey item by any measure, followed by *Crangon septemspinosa*, *Ensis directis*, *Callianassa atlantica*, *Cancer irroratus*, and *Pherusa affinis* in descending order. *Leucoraja erinacea* consumed a wide variety of prey and were characterized as generalist predators with an overall trophic level of 3.86. There were no statistically significant ontogenetic differences in this population of skates, nor was there a difference between the diets of the sexes. Numerical abundance, weight and frequency of prey in the diets were significantly different over time and also among trawl sites. Based on cross referencing current diet data with past prey abundance data, it is deduced that little skates likely feed by availability of prey, particularly in areas where the preferred food items were not histoically abundant. The diet data from this study will be used in a more comprehensive community analysis to elucidate trophic relationships among batoid elasmobranchs within and between different estuaries.

INTRODUCTION

Elasmobranch fisheries, like those of most teleosts, have been under much anthropogenic pressure in recent years. Many populations of sharks have been heavily exploited (Stevens *et al.*, 2000; Bizzarro *et al.*, 2007; Dulvy *et al.*, 2008). Though there have been conservation efforts to aid in recovery (Baum *et al.*, 2003; Ward-Paige *et al.,* 2012), elasmobranchs still struggle to rebuild their numbers due to certain life history traits (Pauly *et al.*, 1998a; Stevens *et al.,* 2000; Ellis *et al.*, 2005a, b; Dulvy *et al.,* 2008). Despite being one of the more common components of by-catch fisheries and vulnerable to trawl fisheries due to their demersal life-style on soft bottom substrates, skates are generally overlooked relative to the more charismatic shark fisheries (Ebert and Sulikowski, 2007). More recently, skates have been targeted and kept for the market as other historically valuable species have declined (Frisk *et al.*, 2002).

Many elasmobranchs serve as predators near, or at, the top of marine food chains and impose top-down control on ecosystems they occur in (Stevens *et al.*, 2000), but as the abundance of the larger sharks decreases, there is the potential for predation release on the trophic levels below them, often smaller elasmobranchs termed “mesopredators” (Myers *et al.*, 2007). Skates fall into this category and contribute to cascade effects. Trophic cascades reported in some marine communities show a slight increase in skate populations as larger sharks decrease (Shepherd and Myers, 2005). Though cascades have been reported involving batoid elasmobranchs, the studies do not provide direct evidence that the decline of the sharks is what caused the change in skate populations and therefore remain speculative. Nonetheless, in order to anticipate the effects of the potential cascades and fully understand the role they play in the ecosystem, one needs to know the skates' complete diet.

Skates, as benthic elasmobranchs, have been an important part of the demersal marine community throughout their history (Compagno, 1990; Cortes, 1999; Szczepanski, ms. 2). Their abundance and widespread occurrence appear to play an influential role in many food webs of coastal shelves (Ebert and Bizzarro, 2007). They prey on benthic invertebrates, often fluidizing sediment to expose prey items and then consuming them, by swimming along the bottom and biting the mollusk parts that remain above the sediment, or by ambushing epibenthic telesots. The skates' benthic lifestyle and feeding habits may impact groundfish by predation and by competition (Murawski, 1991; McHugh, 2001; Link *et al.*, 2002; Orlov, 2004; Ebert and Bizarro, 2007). Despite the fundamental importance of feeding relationships in understanding food web dynamics, community structure, and energy transfer in marine systems, feeding ecology of skates is still poorly understood.

Little skate, *Leucoraja erinacea*, is a relatively well studied species making it a good model for studying trophic relationships (Fitz and Daiber, 1963; McEachran *et al.*, 1976; McEachran and Martin, 1977; Bowman *et al.*, 2000, McHugh, 2001; Frisk *et al.*, 2002; Packer *et al.*, 2003; Alvarado Bremer *et al.*, 2005) and has had documented impacts on fisheries or commercially fished species (Garrison, 2000; Stevens *et al.*, 2000; Shepherd and Myers, 2005; Frisk *et al.,* 2008). As more fish stocks are subjected to ecosystem-based fisheries management (EBFM), there is a need for more focused studies, particularly on trophic ecology, within specific ecosystems (Link, 2010; Link *et al.,* 2012; Lucey *et al.,* 2012; Pranovi *et al.,* 2012).

Narragansett Bay is a well studied estuary in southern New England (Monaco and Ulanowicz, 1997; Desbonnet and Costa-Pierce, 2008); *Leucoraja erinacea* is found in high abundance here year-round (Packer *et al.*, 2003). Despite the extensive amount of information recorded about the ecology of Narragansett Bay, specific diet data for *L. erinacea* within this estuary are lacking. In order to fully assess the trophic relationships of this ecosystem for more effective ecosystem-based fisheries management (EBFM; Link, 2010) and to compare the trophic interactions in this system to ones of the same species in other habitats, these data are necessary (Szczepanski, ms. 4). The continuous presence of the skate in the bay provides for a critical opportunity to investigate possible seasonal and ontogenetic shifts in diet.

With the concerns of trophic cascades in mind, lack of evidence of their proposed negative effects, and need for more complete data to contribute to EBFM, this research aims to resolve the lack of knowledge of batoid feeding habits in an estuarine environment. The objectives of this study were similar to those for other species studied by Szczepanski (ms. 1, 2). The principal objective of the current study was to characterize the diet of *Leucoraja erinacea* in Narragansett Bay, as a species and for each life history stage. Another specific goal of this study was to identify how the feeding habits may change ontogenetically, temporally, and spatially within the Bay. The study tested the null hypotheses that there is no difference in stomach contents among individuals of different sizes, during different months of the year, or at different sampling locations. Differences in diets between males and females were also investigated by testing the null hypothesis of no difference in diet between individuals of different sexes. This research was used to evaluate the ecological role of the little skate and was included in a larger examination characterizing trophic interactions among batoid elasmobranch populations within Narragansett Bay and how the dynamics may differ from those of other batoid communities, specifically in Delaware Bay (Szczepanski ms. 4).

METHODS

Study Site and Specimen Collection

The study was conducted in the Narragansett Bay estuary complex. This coastal embayment lies north-south on the Rhode Island coast starting at the mouth of the Providence River and the head of Mount Hope Bay to the mouth marked by Narragansett Town Beach on the western shore and Sakonnet Point on the eastern shore. Overall, the superficial sediments of Narragansett Bay were characterized as 50% mud and 50% sand by Holliday *et al.* (1993). In general, silt-clay sediments dominate the upper bay, with fine sands near the mouth. The bay is a well mixed system resulting in vertically homogenous stratification with water temperatures ranging from approximately 1 to 25°C with no thermocline and salinities ranging from 24-32 ppt (Kremer and Nixon 1978, Monaco and Ulanowicz, 1997, Calabretta and Oviatt, 2008). There are strong seasonal cycles and sharp gradients in the distribution of biologically important nutrients, including ammonia, nitrite, nitrate, phosphate, and silicate (Nixon, 1987). The bay is characterized as a high phosphorous-low nitrogen system that is probably nitrogen limited (Nixon, 1987). Another important characteristic of the bay is that the water is relatively clear compared to other East Coast estuaries (Bricker *et al.,* 1995). With its nutrients and high water transparency, Narragansett Bay can be classified as a phytoplankton-based system with a strong winter-spring diatom bloom often beginning as early as December (Kremer and Nixon, 1978). Narragansett Bay has very few seagrass beds and some limited areas of kelp in the lower bay (Bricker *et al.,* 1995).

Specimens of *Leucoraja erinacea* were collected aboard fishery-independent monthly bottom trawl surveys conducted by the Rhode Island Department of Environmental Management (DEM) in March-December of 2009 and 2010. The twelve haul stations were randomly stratified between depths of 3-37 m throughout the bay; specimens were also collected by rod-and-reel from a seawall above Narragansett Town Beach, Narragansett, RI. (Figure 1). Across sites, salinities ranged from 21-32‰ and bottom temperatures of 31.-26.0° C.

Data collected from each specimen on the boat included: disc width (DW, cm), total length (TL, cm), and sex. Gastric lavage and stomach dissection were used to remove stomach contents as described by Szczepanski (ms. 2) and collected items were then stored on ice until they could be analyzed in the lab.

Stomach Content Analysis

Stomach contents were identified, separated accordingly, counted, and weighed. Prey items were identified to the lowest taxonomic level possible using field guides and taxonomic keys (Smith, 1964; Gosner, 1971 and 1978; Rehder, 1981; Pollock, 1996), and consultation with biologists at the University of Rhode Island (URI), Woods Hole Oceanographic Institute (WHOI), and Virginia Institute of Marine Science (VIMS). Any highly digested items that could not be identified, parasites, and sediments were counted and noted, but not included in statistical testing. The number of each prey item in a stomach sample was estimated using the most conservative count when detached components were present. Items were then weighed (to the nearest 0.01 g) after excess moisture was blotted off.

Sample Size Sufficiency

To evaluate whether the sample size was large enough to sufficiently describe the skate's diet, cumulative prey curves (Ferry and Cailliet, 1996) were computed using

EstimateS (Version 8.2.0, R.K. Colwell, http://purl.oclc.org/estimates). In this power analysis, the number of possible novel prey items is plotted against an increasing number of stomachs analyzed. The order of the samples was randomized 999 times, with empty stomachs excluded and the mean and standard deviation calculated for each sample size. As the curve reaches an asymptote, the sample size is considered to be sufficient. Visual examination of the curve for an asymptote (Ferry & Cailliet, 1996) is not reliable. To determine if the curve has reached an asymptote, the slope of the linear regression (*b*) of the final four curve endpoints was used as an objective criterion where $b \leq 0.05$ signified an acceptable plateau of the prey curve for diet characterization (Bizzarro *et al.,* 2009; Brown *et al.*, 2011).

Statistical Analysis

Diet Characterization

The contribution of each prey taxon to diet composition was estimated with three relative measures of prey quantity (RMPQ) described by Hyslop (1980). These measures include number (N), wet weight (W), and frequency of occurrence (FO) (Hyslop, 1980). Prey-specific abundances by number (%PN) and by weight (%PW) were calculated to identify each prey item's relative importance independent of the other prey found (Amundsen *et al.,* 1996). Prey-specific abundances are important not only as descriptive indices but also in the construction of a graphical model of specialization and a compound index both described below.

Since relative importance of prey can vary depending on which index is used, composite indices were also used. These were more comprehensive as they incorporated number, weight, and frequency all together. Index of Relative Importance (IRI) was calculated (Pinkas *et al.,* 1971; Cortés, 1997; Koen Alonso *et al.*, 2001) to maintain comparability with published work; this was expressed as a percentage of the total IRI for all species. Prey-Specific Index of Relative Importance, %PSIRI (Brown *et al.*, 2011), was also used as it is more precise than IRI, which can be biased by %FO and over-emphasizes common species (Hansson, 1998) often exceeding 100% (Bizzarro *et al.,* 2007).

Details about RMPQs, compound indices, and their respective calculations were given by Szczepanski (ms. 1).

Trophic level and dietary specializations were examined to make inferences about the species' potential for dealing with environmental changes in resource availability. Trophic level (*TRL*) was calculated with Cortés' Trophic Level Index (1999). Prey species were combined into higher taxonomic or functional groupings (e.g.- Paguridae or bivalve, etc.) to aid in calculation of trophic level; %W was used in the calculation of *TRL* as the proportion of prey in the diet. Trophic levels of prey items (Table 1) were determined using calculated values from Pauly & Chistensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert & Bizzarro (2007). Dietary breadth was calculated using Levins standardized index (Krebs, 1989):

$$B=\left(\frac{1}{n-1}\right)\left(\frac{1}{\sum p_{ij}^{2}}\right)-1$$

where, B = Levins standardized index for predator i; p_{ij} = proportion of diet of predator i that is made up of prey j; and n = number of prey categories. This index ranges from 0 to 1, low values indicating diets dominated by few prey items (specialist predators) and higher values indicating generalist diets (Krebs, 1989; Fanelli *et al.,* 2009). In order to avoid problems derived by different states of prey digestion the index was calculated with %PSIRI. Dietary specialization was portrayed graphically by plotting %PN against %FO (Amundsen, 1996).

Significance Tests for Variation

Samples were defined as the averaged stomach content proportions for all individuals of a specific size group and sex at each station each month. Size groups were used that reflected life history stages (Packer *et al.,* 2003): young-of-the-year (YOY) comprised individuals < 30 cm TL, juveniles (JUV) included skates from 30-45 cm TL, and adults (ADU) were fish > 45 cm TL. Ontogenetic diet overlap was initially examined using the Schoener dietary overlap index (S_{do}) and simplified Morisita index (C_h)(Clarke and Warwick, 2001; McElroy *et al.,* 2006; Bizzarro *et al.*, 2007; Mabragaña and Giberto 2007). Diet was tested for differences first among just size classes and then with the following independent variables: sex, sampling months, and sites. Significance testing involved only the 3 RMPQ's (N, W, FO) separately since each indicates different things about the diet and is also susceptible to different types of bias. Prey species were combined into larger groupings as described above for statistical analysis since many groups of uncommon prey were represented by few instances and unnecessarily skewed the results; these groupings aided in the interpretation of the ecological importance of the results.

Non-metric multidimensional scaling (nMDS) ordination plots were constructed using PRIMER v6.1.13 (Clarke and Warwick, 2001) to look for relative similarities in overall diet for each RMPQ. Differences in diet among size groups, sexes, months, and collecting stations were tested by using permutation tests called analysis of similarities

(ANOSIM). Szczepanski (ms. 1) provides further detail for each step of significance testing.

RESULTS

Little skates were caught in Narragansett Bay from April to December in 2009-2010, at nine of the twelve trawl stations and at the Narragansett Bay seawall (Figure 1). Most skates were collected close to the mouth of the bay, though some specimens were caught at the mouth of Mount Hope Bay (station #25, northeast corner of Narragansett Bay; Figure 2). A total of 396 individuals was collected (185 females, 204 males; Table 2) of which only ten were under 30 cm TL. The JUV size class was represented by 120 individuals and ADU by 266. All ten YOY stomachs contained food items, 118 JUV contained prey leaving only 2 empty stomachs (2%), and 261 ADU out of the 266 samples contained food (2% empty). The maximum number of prey species found in a stomach was 8; this occurred in six individuals, 3 JUV and 3 ADU. The average stomach content weight for all individuals with prey was 3.70g and varied by size class: YOY = 1.40 g, JUV = 3.80 g and ADU = 2.46 g.

The sample size used in this study was sufficient to characterize the diet of the little skate species as a whole based on prey species or lowest taxonomic level. The cumulative prey curve reached a slope of *b* = 0.05 when n = 261 (Figure 3a). The sample size of n = 10 for YOY was not sufficient to describe the diet fully, with the cumulative prey curve reaching a final slope of *b* = 0.66 (Figure 3b). The slope for JUV also indicated that the sample size was not sufficient for full diet characterization for this size class with a final slope of *b* = 0.13 (Figure 3c). There were enough ADU skates to fully characterize the diet of skates larger than 45cm TL; sufficiency was achieved at n = 251 (Figure 3d). When prey were grouped into larger categories, as with statistical analysis, there were overall enough samples for comparison shown by a cumulative prey curve that reached *b* = 0.05 at n = 59 (Figure 4a). Again, 10 YOY stomachs was not a sufficient number for full diet description shown by a curve that ended with *b* = 0.25 (Figure 4b). There were enough skates in the JUV and ADU size groups for confident comparison, with prey curves reaching sufficiency at n = 63 and n = 54, respectively (Figure 4c and 4d).

Leucoraja erinacea in Narragansett Bay were found to eat a wide variety of prey, with 54 items identified to species, 6 items identified to genus, 1 identified only to family and 2 items were only distinguishable to order (Table 3). Crustaceans were a major part of the skates' diet, especially amphipods and shrimp, together with polychaetes and bivalves comprising a bulk of the prey items as well as some crabs and fish. Decapods occurred in 81% of the samples (contributing 24.4 %N and 34.6 %W) and amphipods were found in 74% of stomachs examined (56.5 %N and 39.0 %W). Polychaetes were found relatively frequently (28 %FO) comprising only 5.0% of the numerical abundance of prey and 8.8% abundance by weight. Bivalves contributed more by number and weight (8.6 %N and 10.5 %W) than did polychaetes, but were only found in 22% of stomachs. The teleost fish that were found occurred in 15% of the samples and only contributed 2.3% of the total number of prey items and 4.3% of the total weight of prey consumed. Taking all metrics into consideration with the compound index %IRI, amphipods contributed to 56.8% of the diet, decapods contributed 38.3%, bivalves only 2.7% and polychaetes only 2.6%. Some gastropods, cephalopods, krill, and other prey items were found in stomachs, but not in any notable abundance.

When one considers the diet metrics of the prey items relative to only the stomachs that contained that specific prey, as %PSIRI, the same pattern emerged.

Amphipods made up almost half (47.8 %PSIRI) of the prey in the stomachs that contain them, whereas decapods made up a third (28.9 %PSIRI) of the diet in the skates that ate them; bivalves and polychaetes were a part of the diet but not very large (9.5 and 6.9 %PSIRI, respectively).

Leptocheirus pinguis was the most frequently found prey item in little skate stomachs, (61 %FO) followed closely by *Crangon septemspinosa* (56 %FO). Both were also most abundant by %N and %W with *L. pinguis* contributing 37.1 %N and 34.0 %W to the diet and *C. septemspinosa* contributing 14.5 %N and 12.7 %W. *Callianassa atlantica* occurred in 21% of stomach samples, as did *Pherusa affinis* and *Pinnixa sayana* independently. Though they each were found in the same number of stomachs, *P. affinis* had the highest numerical abundance (2.8 %N, 5.1%W) while *C. atlantica* had the highest gravimetric abundance (2.3 %N, 6.1 %W) of the three items; *P. sayana* only accounted for 1 %N and 1.3 %W. Other relatively frequently occurring species included *Ensis directus* (19 %FO, 7.7 %N, 9.8 %W), *Cancer irroratus* (18 %FO, 2.9 %N, 5.2 %W) and *Ampelisca verrillii* (16 %FO, 3.0 %N, 1.4 %W). When all metrics were compounded into IRI, *L. pinguis* was the most important prey item at 64.98%. *Crangon septemspinosa* contributed 19.98 %IRI, *E. directus* was 4.47 %IRI, *C. atlantica*, *P. affinis* was 2.10 %IRI, and *C. irroratus* was 1.91 %IRI.

When each prey species was analyzed independently of the others by prey-specific measures, *Leptocheirus pinguis* remained the highest ranking prey item in the diet with 40.54 %PSIRI. *Crangon septemspinosa* also maintained the role as second most important prey, but only contributing to 13.60 %PSIRI. *Ensis directus* had 8.73 %PSIRI, *Callianassa atlantica* contributed 4.53 %PSIRI, *Cancer irroratus* was 4.06 %PSIRI, and

Pherusa affinis was 3.91 %PSIRI.

When prey items were grouped into larger categories and skates were grouped into size classes (Table 4), it was evident that YOY consumed mostly amphipods and some epibenthic crustaceans, with some polychaetes. Benthic crustaceans, epibenthic fish, bivalves, krill, and small schooling fish also contributed to the diets of YOY skates. Skates in the JUV size category had diets with very similar proportions of those prey categories with the exception of benthic crustaceans (which more than doubled in frequency), small schooling fish (which declined by half), and krill (which disappeared from the diet). This intermediate size category had a more diverse diet including cephalopods, flatfish, gastropods, isopods, all categories of fish, pagurids and portunids. The weight of the amphipods in the diet of JUV did decline more than the number. The largest size skates, ADU, also ate mostly amphipods and epibenthic crustaceans, with considerable amounts of benthic crustaceans, polychaetes, and bivalves. Epibenthic and large schooling fish remained in the diet while cephalopods, flatfish, gastropods, isopods, krill, pagurids, portunids, and small schooling fish were absent.

The little skate in Narragansett Bay, as a whole species, was calculated to have a trophic level (*TRL*) of 3.86. When sizes were figured separately, YOY had a *TRL* = 3.93, while JUV and ADU were lower with *TRL*s of 3.82 and 3.87, respectively.

Overall dietary breadth of the little skate was rather broad and calculated at B = 0.78; YOY and ADU respectively had dietary breadths of B = 0.77 and B = 0.75 while JUV had a greater dietary breadth of B = 0.83.

To examine feeding strategy for all *Leucoraja erinacea*, prey-specific abundance (%PN) was plotted against frequency of occurrence (Figure 5). There was a moderate degree of specialization for one amphipod species (*L.pinguis*) and a high frequency of one crustacean species (*C. septemspinosa*). Many of the other items found in the diet, like some other amphipod, crustacean, bivalve, and fish species, occurred infrequently indicating more individual specialization on those items and less preference. However as a whole, the degree of variety in the diet with most species being eaten infrequently at varying levels of prey-specific abundance characterizes the little skate as a broad generalist feeder, with a preference for *L. pinguis* and *C. septemspinosa*.

Overlap indices were used to detect the possibility of ontogenetic differences in the chosen size categories. There was an extremely high degree of overlap among all sizes, with all iterations of Schoener's Dietary Overlap, S_{do}, greater than 0.939 (with 1.0 being complete overlap). Overlap between diets of different sexes was also high, $S_{do} = 0.975$. The Simplified Morista index, C_h, was calculated to be a complete overlap for the all combinations of sizes, and between the diets of the different sexes.

Analysis with nMDS plots to examine the differences in %N among all the samples showed little separation in either size or sex (Figure 6a, stress = 0.11). ANOSIM also resulted in high overlap and no significance ($R_{size} = -0.012$, $p_{size} = 0.64$; $R_{sex} = -0.01$, $p_{sex} = 0.67$). Stomach samples seemed to group a bit more by month and station, particularly with station 197 along the bottom of the space and stations 158, 161, and 205 in the dense cluster toward the top (Figure 6b). Month was calculated to have very little separation but significant differences ($R = 0.091$, $p \ll 0.01$), while stations were not as overlapping and also significantly different ($R = 0.25$, $p \ll 0.01$).

An nMDS plot of the %W for each stomach showed even more dispersion (Figure 7, stress = 0.2). Again, diets of different sizes and sexes did not form distinguishable groups and were not significantly different per ANOSIM testing ($R_{size} = 0.02$, $p_{size} = 0.21$; $R_{sex} = -0.01$, $p_{sex} = 0.75$). Months seemed to separate noticeably with earlier months closer to the top left and later months lower and to the right, though still a considerable amount of overlap. Stations were also clearly clustered particularly 132 and 158 at the bottom of the space, 161 through the middle, 194 and 205 mostly in the bottom right, 197 located vertically along the left. ANOSIM tests confirmed these relationships with high overlap but significant differences for both factors ($R_{month} = 0.1$, $p_{month} \ll 0.01$; $R_{station} = 0.2$, $p_{station} \ll 0.01$).

The nMDS plot based on %FO across all samples seemed the most varied with no clear groupings of sizes or sexes (Figure 8a, stress = 0.17). No ANOSIM test indicated any separation or significant differences for those factors ($R_{size} = 0.03$, $p_{size} = 0.14$; $R_{sex} = -0.02$, $p_{sex} = 0.51$). Though there was considerable overlap when comparing diets by months and stations (Figure 8b), there were some distinct groups of points, particularly from stations 99, 158, 161, and 205. Calculated R-values confirmed little separation for either factor ($R_{month} = 0.05$, $R_{station} = 0.18$) but significant differences among diets from different months ($p = 0.02$) and at different sampling stations ($p \ll 0.01$).

DISCUSSION

This study presents a comprehensive diet analysis of *Leucoraja erinacea* from within the Narragansett Bay estuary. *Leucoraja erinacea* utilizes a broad resource base, including at least 54 different prey items. Based on the results of the cumulative prey curves, the data used in the diet characterization of the whole species were more than sufficient. Decapods and amphipods were the most important prey items, though polychaetes and bivalves were also found to be important. Specifically, *Leptochierus pinguis* and *Crangon septemspinosa* were preferred along with other crustaceans like *Callianassa atlantica* and the polychaete *Pherusa affinis*. These organisms are common throughout Narragansett Bay and provide an abundant food source (French *et al.,* 1992; NBNERR, 2009). The pea crab *Pinnixa sayana* was found somewhat frequently in the diet of *L. erinacea,* but is likely to be an incidental item; *P. sayana* is found in muddy substrates and are known to be commensal burrow-dwellers (Gosner, 1978; Pollock, 1998). This crab is found with the same frequency as *C. atlantica* and *P. affinis* (21 %FO), both soft sediment burrowers (Gosner, 1978). Coupled with low %IRI and %PSIRI values (0.63 and 1.13, respectively), it is reasonable to conclude that this prey (as well as other *Pinnixa* sp.) is accidentally ingested while the skate is targeting and excavating other benthic prey species.

Sample sizes of the larger two size groups of skate (JUV and ADU) provided for confident comparison between skates that are maturing and skates that fully mature and ready to reproduce. There were very few YOY samples collected so any comparisons made with this group are not fully sufficient, however specimens from this group were harder to come by due to the size collecting gear used and therefore any samples collected provided meaningful data as very few studies include data from this size class at all. The increasing variety of prey items in the diet can be attributed to decrease in morphological size limitations. Krill was consumed less by YOY than expected for smaller individuals with greater prey size limitations, but this is an instance in which low sample size may have been a factor.

Other investigators have analyzed the diet of *Leucoraja erinacea*, but none have characterized the diet of this species within Narragansett Bay. Bigelow and Schroeder (1953) remarked that the little skates from the Woods Hole region preferred sand or gravel substrates and less often mud and that *L. erinacea* ate crabs and hermit crabs, shrimp, amphipods, nereid worms, razor clams, and fragments of squid. There were also notes that diets from Long Island Sound were dominated by amphipods, crabs, shrimp, and small fishes (Bigelow and Schroeder, 1953). Almost no other quantitative data are presented that would be comparable to what is presented here.

Fitz and Daiber (1963) compared the diet of the clearnose skate and little skate from the Delaware Bay and found mostly *Crangon septemspinosa* (74 %N,72 %FO), with *Nereis limbata (*4 %N, 26 %FO)*, Ensis directus* (5 %N, 34 %FO), and *Euceramus praelongus* (4 %N, 15 %FO) as major prey items for *L. erinacea*. Though these findings were similar to those of Narragansett, *C. septemspinosa* played a greater role in the more southern diet overall while *E. directus* played a lesser role by number. The other two dominant species were not specifically found in the Narragansett diet, however there were certainly counterparts (other polychaetes to fulfill the role of the burrowing worm prey and amphipods fulfilled the role that the burrowing crustacean *E. praelongus* played). The diet of skates in Delaware Bay had fewer prey species (22 spp.) than in

Narragansett Bay (60 spp.), therefore indicating these skates could be feeding due to prey availability; Fitz and Daiber (1963) also came to that conclusion. Though Fitz and Daiber (1963) did do rather comprehensive diet characterization and comparisons, the study did lack a complete set of size classes. The 1963 study had a sample size of 185, which may have been sufficient based on the number of prey species found but did not include any individuals smaller than 32cm TL, 93 individuals presently considered JUV, and 92 presently considered ADU. That n-value may have been sufficient for comparison; however, no clear comparison in size was made and statistical comparisons were not done. It is also clear that, even though the two species shared many common prey items, there was some partitioning of resources. Competition for razor clams and various mud and hermit crabs was reported; the consumption of polychaetes distinguished the diet of the *L. erinacea* from the consumption of fish by *R. eglanteria* (Fitz and Daiber, 1963) and a similar case of partitioning could occur in Narragansett Bay with the presence of the winter skate, *Leucoraja ocellata* (Szczepanski, ms. 4), though how the resources are partitioned would be different.

The overall trophic level of the little skate within Narragansett Bay indicates that it is an upper level marine predator and the dietary breadth was calculated to be very high and therefore very diverse. The *TRL* was high due to skates mostly eating crustaceans. The feeding strategy graph indicated high preference for *Leptocheirus pinguis* and somewhat for *Crangon septemspinosa*, with a slight degree of individual specialization. These results imply a preference for small crustaceans but a generalist feeding strategy based on availability in a patchy environment. Any variations as a result of individual specialization that were based on external factors would be seen in multivariate analyses.

Ebert and Bizzarro (2007) determined the trophic levels of all skates, at varying taxonomic levels. For all skates combined, *TRL* = 3.8 while *Leucoraja erinacea* as a species had *TRL* = 3.7. The overall trophic level of *L. erinacea* in the Narragansett Bay was calculated by the current study to be 3.96, considerably higher (though not tested for significance). The same prey trophic levels were used in the current study as were used by Ebert and Bizzarro (2007) so the difference is likely due to a higher proportion of decapod crustaceans and perhaps fish in the diet of the skates in the estuary relative to the proportion of amphipods and polychaetes in many other skates' diets. The 2007 study used a sample size of 19,738 individuals from other studies along the entire Western Atlantic Coast.

This study is the only one to statistically test the diets of different life-history stages of *L. erinacea* within an estuary. No difference in size was detected among any RMPQ. This may have been due to the lack of YOY samples and the fact that JUV and ADU have highly diverse diets as calculated by Levin's Index. Different sexes also did not present differences in diet, likely due to high prey diversity found in the stomachs. The different size groups within sexes had nearly significantly different frequencies of prey items in their diets, suggesting that there were ontogenetic differences coupled with different life history nutritional requirements. The lack of significance can be attributed to low YOY sample size; it is unlikely that YOY would share more similarity (in any of the RMPQs measured) with ADU than JUV if the differences were a gradient. The high similarity in male and female JUV may be due to the increase in diet breadth. The lack of similarity of female ADU to the other groups in any of the plots may be indicative of having different dietary needs for egg production. A similar difference was seen in another skate species in Delaware Bay (Szczepanski, ms. 2).

Most studies have incorporated data from along the continental shelf. McEachran *et al.* (1976) compared the diet of *Leucoraja erinacea* with that of *L. ocellatta,* in addition to comparing their trophic interrelationship with that between *Raja radiata* and *R. senta*. The 1976 study did detect differences in diet relative to size, just as the current study noted some variations with size. However, the McEachran group did not do comparable multivariate statistical testing to evaluate the significance of these differences. They did report that *Crangon septemspinosa* was the only decapod in skates >30 cm TL and that haustorid amphipods, copepods, and cumaceans were not seen in larger specimens. The latter organisms were not seen in diets of Narragansett Bay skates, likely due to the fact that the former study collected from offshore and from a large latitiudinal range; McEahran *et al.* (1976) counted 97 prey taxa from 785 samples. Interestingly enough, *Leptocheirus pinguis* was found to be highly important in the diet of skates in Block Island Sound; other areas revealed similar species ranking high in the diet but at different levels of importance (McEachran *et al.*, 1976). This further indicated feeding by availability.

Bowman *et al.* (2000) also sampled little skate from along most of the Western Atlantic coast and reported similar results to those of McEachran *et al.* (1976). Amphipods and *Crangon septemspinosa* were of great importance to the diet throughout the skates' lives. Cumaceans were mostly found only in skates <30 cm TL and the items that were most important decreased in importance as the skates grew and their diet diversity increased, most notably to include larger crabs and fish. The data were separated by region and differences were noticeable, but data were only reported by weight and no statistical testing was done. The abundance of prey items for Southern New England corresponded with the importance by weight as calculated in the current study.

Packer *et al.* (2003) reviewed many relevant studies including the ones already mentioned. That report further confirmed that little skates feed based on availability and the high importance of decapod crustaceans and amphipods decreases as skates' size increases and dietary diversity increases to include polychaetes. This size difference was not statistically apparent in Narragansett Bay, but there were not nearly enough YOY individuals to make a valid comparison; the studies reviewed by Packer *et al.* (2003) together comprised a more than sufficient sample size for all size groupings.

Monthly differences were noted for numerical abundance of prey items in the diets and size differences of weight and frequency of items in the diets within months. This pattern would indicate that the prey abundance varies throughout the year so the actual number of items ingested changes but the preference for which items they choose and the size of those items varies for each size class. Benthic seasonal changes do occur in Narragansett Bay (Frithsen, 1988), and may contribute to temporal variations in skate diets. Other species of skate in the Northwest Atlantic have been reported to exhibit seasonal movements (Frisk *et al.*, 2008, 2010) and *L. erinacea* engages in seasonal movements in Delaware Bay (Fitz and Daiber, 1963). It is reasonable to conclude that the population of skate sampled in this study also move seasonally. Data from this study would indicate a similar monthly movement of little skate in Narragansett Bay provided the prey availability in different places along the skate's route varied.

Diets were noted to differ significantly by number, weight, and frequency at the different collection sites. These differences add confidence to the previous assessment that differences in monthly diet may correspond to skate movement through the bay and, thus, skates find varying prey abundances as they travel. French *et al.* (1992) reported habitat patterns throughout the bay (Figure 9). When the trawl stations from the current study are overlaid onto a map of the habitats, a general idea of what the habitat is like and benthic prey availability can be inferred. Station 25 lies within an area considered "Upper Bay Soft Bottom" and is characterized by soft sediments and low-diversity, mid-estuarine species like *Mediomastus* sp. and *Nephtys* sp. polychaetes and *Nucula* sp. and *Yoldia* sp. bivalves. Stations 132, 138, and 151 are found in an area known as the "Mid-Bay Complex" where the bottom is deeper, covered in clay-silt or clay-sand-silt, and is inhabitated by similar organisms as station 25 with the addition of *Mulinia* clams. Stations 99, 161, and 194, are in the "Marine Silty Sand" habitat with fine sands and the presence of *Spisula* clams, the sand dollar *Echinarachnius* and *Spiophanes* polychaetes; however, station 99 was directly adjacent to anthropogenic structures and exposed to constant human disturbance so natural distributions of characteristic organisms may not have been consistent with past data. Station 197 was characterized as "Lower Bay Complex" with a variety of mixed sediments containing sand and organisms including *Mytilus*, *Crepidula*, *Pherusa affinis*, *Aricidea*, and *Ampelisca* while Station 205 was characterized as "Marine Sand" with silty sand and organisms including *Astarte*, *Cyclocardium,* and *Arctica* clams, and the amphipod *Byblis serrata*. French *et al.* (1992) also showed amphipods to be abundant throughout the bay but in highest abudance in areas where I found stomachs that had high proportions of amphipods in them. Diets were different at stations that were not known to have high amphipod abundance and tended to correspond with the abundant organisms at a given location (Figure 9; French *et al.*, 1992).

McHugh (2001) looked at 2 specific sites on Georges Bank to evaluate differences in little and winter skate diets as well as those of haddock. That study determined statistical differences in diet across sites and linked them to availability of polychaetes at one station over another. All *Leucoraja erinacea* ate polychaetes, cancrid crabs, and shrimp, but in different proportions at the different stations, resulting in high overlap values. The current study revealed similar patterns: though dietary overlap within the bay was high, proportion of the different prey species eaten differed depending on prey availability (either from seasonal changes in prey abundance of location in the estuary).

The little skate will likely not be affected adversely by environmental changes or shifts in benthic community structure. They are versatile feeders adjusting to prey availability on smaller scale variability (spatial and temporal). However, if changes adversely affected decapod shrimp or amphipods in Narragansett Bay, then survivorship of young may be compromised and lower recruitment would result. YOY could move to other places to feed but this could make them more vulnerable to predation (Packer *et al*, 2003).

On the other hand, *L. erinacea* might have an effect on other fish populations by shifting to feed on their prey or larvae. The latter is less likely since few small fish were found in the little skate's diet. Herrington (1948) suggested that predation by skates resulting in the removal of large numbers of small shrimp from the estuarine system could affect the growth and survival of haddock. Langston (1982) reported dietary overlap for Atlantic cod and silver hake with other fish including little skate. Though some overlap was noted for each species, the values were low and did not exceed 40% and could be attributed to a wide variety of crustaceans consumed, in both cases. McHugh (2001) reported that dietary overlap was high among *L. erinacea*, *L. ocellata*, and *Melanogrammus aeglefinnus* (haddock) throughout ontogeny and sites, but resources are partitioned by consuming different proportions of the specific prey types. Though the little skate does feed on many common prey items shared by other skates and commercially important fish, it seems to effectively partition its resources with its cohabitants.

The next step is to quantify levels of competition with other species of batoid elasmobranchs in Narragansett Bay. Some work has been done involving taxa that can be found in the bay, but none included all possible species. McEachran *et al.* (1976) compared *Leucoraja erinacea* and *L. ocellata* but not within the context of an estuarine system. McHugh (2001) also compared the two skates along with the commercially important haddock, but in Georges Bank. Since the little skate is a commensurate generalist and feeds relative to prey availability, comparison to diets of *L. erinacea* in other regions would prove rather informative. In light of ecosystem-based fisheries management taking a more multi-species analysis approach, even pair-wise species comparisons seem inadequate (Link, 2010). The data from this study and other similar diet studies on batoid elasmobranchs are compiled and compared for just such a purpose (Szczepanski, ms. 4).

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Table 1: Prey categories used to calculate trophic levels of little skate, *Leucoraja erinacea* in Narragansett Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007).

Group Code	Description	Trophic Level
MOLL	Bivalves, Gastropods and other molluscs excluding Cepahlopods	2.1
KRILL	Euphausid and mysids	2.25
CRUST	Decapod and other crustaceans	2.52
POLY	Polychaetes and other marine worms	2.6
FISH	Misc. marine fish	2.8
FLAT	Pleuronectids	2.9
AMPH	Amphipods and isopods	3.18
CEPH	Squid	3.2
CLUP	Small schooling fish like anchovies and herring	3.2
GAD	Cod, hake, and haddock	3.8

Table 2: Detailed breakdown of *Leucoraja erinacea* collecting efforts from April-December 2009 and 2010 in Narragansett Bay.

Trawl Station by Month	**YOY**		**JUV**		**ADU**		**Grand Total**
	f	**m**	**f**	**m**	**f**	**M**	
April							
158			1	2	3	4	10
161		1	6	6	5	13	31
197				2	5	1	8
205			2	2	2	11	17
May							
138			2		4		6
161			2	1	1	2	6
194	2	1	2	1		1	7
197	1	2	1	1	2	2	9
205		1	2	1	2	2	8
June							
99				1		2	3
158			4	7	5	9	25
194			3	2	1	2	8
205			6	2	5	8	21
July							
25					1		1
161			1		2	3	6
194			1		1	2	4
197			1	1	1	1	4
205			4	10	6	11	31
August							
205			2	1	6	9	18
September							
99			1	2	2	1	6
132					1		1
194			2			1	3
197			1		1	1	3
205			1	3	9	6	19
October							
132					2	4	6
138			1		1		2
158			1	4	8	7	20
161				1	3	2	6
194					1	1	2
197			2		1	1	4
205			1	3	4	7	15
November							
132			2	1	3	4	10
161			1		6	4	11
197			1	2	1	1	5
205			1		2	6	9
December							
132			1				1
158					9	1	10
194				1	4	2	7
197	1		2		1	3	7
205	1		3		8	7	19
Grand Total	**5**	**5**	**61**	**57**	**119**	**142**	**389**

Table 3 Overall diet composition of 389 little skate, *Leucoraja erinacea*, from Narragansett Bay collected from March-December 2009-2010. RMPQs expressed as percentages; %FO, %N and %W were utilized in calculations of %IRI; %FO, %PN, and %PW were utilized in calculations of %PSIRI.

Class	Order	Family	Species	Prey Category	%FO	%PN	%N	%PW	%W	%IRI	%PSIRI
Tentaculata	Lobata	Bolinosidae	*Mnemiopsis* sp.	Other Prey	1	66.67	0.34	60.00	0.31	<0.01	0.32
Polychaeta					28	17.43	4.96	30.77	8.76	2.57	6.86
	Cirratulida	Paraonidae	*Paraonis* sp.	Polychaete	5	7.52	0.39	15.38	0.79	0.08	0.59
	Eunicida				3	18.13	0.56	38.01	1.17	0.04	0.86
		Oenonidae	*Arabella* sp.	Polychaete	<1	7.69	0.02	28.04	0.07	<0.01	0.05
		Onuphidae	*Diopatra cuprea*	Polychaete	3	19.08	0.54	38.92	1.10	0.06	0.82
	Phyllodocida				4	19.11	0.73	34.73	1.34	0.06	1.04
		Glyceridae	*Glycera dibranchiata*	Polychaete	1	13.75	0.14	26.90	0.28	0.01	0.21
		Nereidae	*Nereis* sp.	Polychaete	2	18.77	0.43	32.93	0.76	0.04	0.60
		Nereididae	*Alitta sucinea*	Polychaete	1	12.10	0.12	17.89	0.18	0.00	0.15
		Polynoidae	*Polynoe sp.*	Polychaete	<1	14.29	0.04	45.45	0.12	0.00	0.08
	Scolecida				4	13.85	0.53	10.45	0.40	0.03	0.47
		Arenicolidae	*Arenicola cristata*	Polychaete	1	8.48	0.07	10.62	0.08	<0.01	0.07
		Maldanidae	*Clymenella torquata*	Polychaete	4	13.03	0.47	8.92	0.32	0.04	0.39
	Terebellida	Flabelligeridae	*Pherusa affinis*	Polychaete	21	13.41	2.75	24.67	5.06	2.10	3.91
Rhyncocoela	Unid. Rhyncocoela		Unidentified	Other Prey	8	10.56	0.84	1.07	0.09	0.10	0.46
Gastropoda					1	13.13	0.07	24.85	0.13	<0.01	0.10
	Neogastropoda	Columbellidae	*Costoanachis avara*	Gastropod	<1	1.27	0.00	0.32	<0.01	<0.01	<0.01
	Littorinimorpha	Littorinidae	*Littorina littorea*	Gastropod	<1	25.00	0.06	49.38	0.13	<0.01	0.10
Bivalvia					22	39.75	8.56	48.58	10.46	2.70	9.51
	Mytiloida	Mytilidae	*Mytilus edulis*	Bivalve	1	25.74	0.33	22.99	0.29	0.01	0.31
	Myoida	Myidae	*Mya arenaria*	Bivalve	<1	70.59	0.18	44.19	0.11	<0.01	0.15
	Pholadomyoida	Pandoridae	*Pandora* sp.	Bivalve	1	31.25	0.16	22.54	0.12	<0.01	0.14
	Veneroida				20	39.45	7.89	49.70	9.94	2.86	8.91
		Pharidae	*Ensis directus*	Bivalve	19	39.46	7.69	50.18	9.78	4.47	8.73
		Solecurtidae	*Tagelus divisus*	Bivalve	<1	75.00	0.19	62.26	0.16	<0.01	0.18
		Veneridae	*Mercenaria mercenaria*	Bivalve	1	1.76	0.01	0.10	<0.01	<0.01	<0.01
Cepahlopoda	Teuthida	Loligindae	*Doryteuthis pealeii*	Cephalopod	3	7.79	0.26	50.82	1.69	0.09	0.98
Crustacea					92	88.61	81.57	79.60	73.28	93.94	77.42
	Amphipoda				74	76.22	56.48	52.66	39.03	56.81	47.75
		Ampeliscidae	*Ampelisca verrilli*	Amphipod	16	18.25	3.00	8.44	1.38	0.94	2.19
		Aoridae			20	13.89	2.78	5.90	1.18	1.02	1.98
			Microdeutopus gryllotalpa	Amphipod	5	37.76	1.74	16.27	0.75	0.15	1.25

Table 3 cont'd.

Class	Order	Family	Species	Prey Category	%FO	%PN	%N	%PW	%W	%IRI	%PSIRI
Crustacea	Amphipoda	Aoridae	*Unicola* sp.	Amphipod	15	6.73	1.03	2.78	0.43	0.30	0.73
		Caprellidae	Unknown Caprellid	Amphipod	<1	12.50	0.03	2.08	0.01	<0.01	0.02
		Cheirocratidae	*Casco bigelowi*	Amphipod	3	4.09	0.10	3.81	0.10	0.01	0.10
		Corophiidae			62	76.43	47.43	54.76	33.98	64.98	40.70
			Corophium volutator	Amphipod	1	29.50	0.30	2.95	0.03	<0.01	0.17
			Leptocheirus pinguis	Amphipod	61	77.22	47.12	55.64	33.95	64.98	40.54
		Gammaridae			2	18.50	0.43	18.18	0.42	0.03	0.42
			Gammarus oceanicus	Amphipod	1	12.05	0.09	6.15	0.05	<0.01	0.07
			Gammarus tigrinus	Amphipod	2	21.73	0.33	24.19	0.37	0.01	0.35
		Ischyroceridae	*Cerapus tubularis*	Amphipod	3	5.55	0.17	2.77	0.09	0.01	0.13
		Oedicerotidae	*Ameroculodes edwardsi*	Amphipod	5	49.64	2.55	36.50	1.87	0.30	2.21
	Decapoda				81	30.23	24.42	42.83	34.60	38.26	28.91
		Axiidae	*Axius serratus*	Benthic Crustacean	2	7.09	0.13	53.95	0.97	0.03	0.55
		Callianassidae	*Callianassa atlantica*	Benthic Crustacean	21	10.71	2.25	32.40	6.81	2.50	4.53
		Cancridae	*Cancer irroratus*	Epibenthic Crustacean	18	16.20	2.91	29.01	5.21	1.91	4.06
		Crangonidae	*Crangon septimspinosa*	Epibenthic Crustacean	56	25.90	14.48	22.75	12.72	19.96	13.60
		Nephropidae	*Homarus americanus*	Epibenthic Crustacean	<1	8.33	0.02	0.98	0.00	<0.01	0.01
		Ogyrididae	*Ogyrides alphaerostris*	Epibenthic Crustacean	<1	1.08	<0.01	0.22	0.00	<0.01	<0.01
		Pandalidae	*Stylopandalus richardi*	Epibenthic Crustacean	2	2.91	0.05	9.60	0.17	0.01	0.11
		Panopeidae	*Panopeus herbstii*	Benthic Crustacean	4	8.64	0.33	12.97	0.50	0.04	0.42
		Parthenopidae	*Heteréocrypta granulata*	Benthic Crustacean	1	3.82	0.02	11.71	0.06	<0.01	0.04
		Paguridae			4	18.48	0.76	18.25	0.75	0.08	0.75
			Pagurus longicarpus	Paguridae	3	18.18	0.56	10.89	0.34	0.04	0.45
			Pagurus pollicaris	Paguridae	1	19.41	0.20	40.35	0.41	0.01	0.31
		Pinnotheridae			23	4.87	1.10	6.24	1.41	0.73	1.25
			Pinnixa chaetopterana	Benthic Crustacean	<1	17.07	0.04	23.53	0.06	<0.01	0.05
			Pinnixa cylindrica	Benthic Crustacean	1	6.18	0.06	7.13	0.07	<0.01	0.07
			Pinnixa sayana	Benthic Crustacean	21	4.66	0.99	5.99	1.28	0.63	1.13
		Portunidae			2	51.72	0.93	63.23	1.13	0.05	1.03
			Callinectes sapidus	Portunidae	<1	5.26	0.01	4.18	0.01	<0.01	0.01
			Carcinus maenas	Portunidae	1	25.88	0.13	31.24	0.16	<0.01	0.15
			Ovalipes ocellatus	Portunidae	1	76.25	0.78	93.98	0.96	0.02	0.87
		Upogebiidae	*Upogebia affinis*	Benthic Crustacean	11	13.36	1.44	34.14	3.68	0.72	2.56

Table 3 cont'd.

Class	Order	Family	Species	Prey Category	%FO	%PN	%N	%PW	%W	%IRI	%PSIRI
Crustacea	Euphausiacea	Euphausiidae	*Meganyctiphanes norvegica*	Krill	1	18.84	0.10	10.74	0.06	<0.01	0.08
	Isopoda	Idoteidae	*Idotea balthica*	Isopod	1	22.50	0.12	15.76	0.08	<0.01	0.10
	Mysida	Mysidae	*Neomysis Americana*	Krill	2	8.70	0.20	4.87	0.11	0.01	0.16
	Stromatopoda	Squillidae	*Squilla empusa*	Benthic Crustacean	2	16.44	0.25	38.71	0.60	0.02	0.42
Actinopterygii					15	15.42	2.25	29.68	4.34	0.63	3.30
	Clupeiformes				3	23.26	0.78	24.55	0.82	0.04	0.80
		Clupeidae	*Clupea harengus*	Large Schooling Fish	1	38.13	0.39	34.64	0.36	0.01	0.37
		Engaulidae	*Anchoa mitchillii*	Small Schooling Fish	2	16.66	0.38	20.06	0.46	0.03	0.42
	Gadiformes	Merlucciidae	*Merluccius bilinearis*	Epibenthic fish	1	2.38	0.01	65.16	0.33	<0.01	0.17
	Perciformes				10	13.87	1.35	29.56	2.88	0.33	2.12
		Ammodytidae	*Ammodytes americanus*	Epibenthic Fish	7	15.24	1.13	23.39	1.74	0.28	1.44
		Carangidae	*Selene setapinnis*	Small Schooling Fish	1	1.15	0.01	48.50	0.25	<0.01	0.13
		Serranidae	*Centropristis striata*	Epibenthic Fish	<1	0.93	0.00	19.33	0.05	<0.01	0.03
		Sparidae	*Stenotomus chrysops*	Epibenthic Fish	<1	50.00	0.13	96.89	0.25	<0.01	0.19
		Stromateidae	*Peprilus triacanthus*	Small Schooling Fish	1	6.43	0.08	46.33	0.59	0.01	0.34
	Pleuronectiformes				1	6.75	0.05	7.03	0.05	<0.01	0.05
		Scophthalmidae	*Scophthalmus aquosus*	Flatfish	1	8.33	0.04	9.47	0.05	<0.01	0.05
		Unidentified Pleuronectid	Unidentified	Flatfish	<1	3.57	0.01	2.14	0.01	<0.01	0.01
	Unidentified Teleost	Unidentified		Misc. Teleost	2	3.48	0.06	13.96	0.25	0.01	0.16
Plant material				Other Prey	7	9.59	0.66	5.52	0.38	0.02	0.52
Sediment				Other Prey	<1	1.61	0.00	1.54	<0.01	<0.01	<0.01
Unidentified Material				Other Prey	1	37.53	0.48	44.24	0.57	0.02	0.52

Table 4. Diet composition for 3 different size classes of little skate, *Leucoraja erinacea*, collected March-December 2009 and 2010 from Narragansett Bay; RMPQs and PSIRI expressed as percentages for larger prey categories.

	%N			%W			%FO			%PSIRI		
	YOY	JUV	ADU	YOY	JUV	ADU	YOY	JUV	ADU	YOY	JUV	ADU
Amphipod	87.09	85.23	90.88	55.77	31.19	55.81	82	73	86	71.43	58.21	73.34
Benthic Crustacean	0.85	1.98	1.32	1.56	15.17	8.42	23	52	43	1.21	8.57	4.87
Bivalve	0.32	1.09	0.29	2.03	8.31	5.92	14	22	14	1.18	4.70	3.11
Cephalopod	0.00	0.09	0.00	0.00	10.85	0.00	0	4	0	0.00	5.47	0.00
Epibenthic Crustacean	9.07	9.01	5.59	23.54	16.56	20.69	68	63	79	16.30	12.79	13.14
Epibenthic Fish	0.64	0.32	0.15	6.33	3.27	1.04	18	8	7	3.49	1.80	0.60
Flatfish	0.00	0.02	0.00	0.00	0.02	0.00	0	1	0	0.00	0.02	0.00
Gastropod	0.00	0.01	0.00	0.00	0.03	0.00	0	1	0	0.00	0.02	0.00
Isopod	0.00	0.01	0.00	0.00	0.03	0.00	0	1	0	0.00	0.02	0.00
Krill	0.11	0.01	0.00	0.14	0.01	0.00	5	<1	0	0.12	0.01	0.00
Large Schooling Fish	0.00	0.02	0.15	0.00	1.00	0.99	0	1	7	0.00	0.51	0.57
Misc. Teleost	0.00	0.04	0.00	0.00	0.16	0.00	0	2	0	0.00	0.10	0.00
Other Prey	0.43	0.66	0.15	0.20	0.70	0.29	14	16	7	0.32	0.68	0.22
Paguridae	0.00	0.14	0.00	0.00	0.58	0.00	0	5	0	0.00	0.36	0.00
Polychaete	1.17	1.19	1.47	5.79	5.02	6.85	36	33	36	3.48	3.11	4.16
Portunidae	0.00	0.11	0.00	0.00	1.62	0.00	0	2	0	0.00	0.86	0.00
Small Schooling Fish	0.32	0.09	0.00	4.64	5.47	0.00	9	4	0	2.48	2.78	0.00

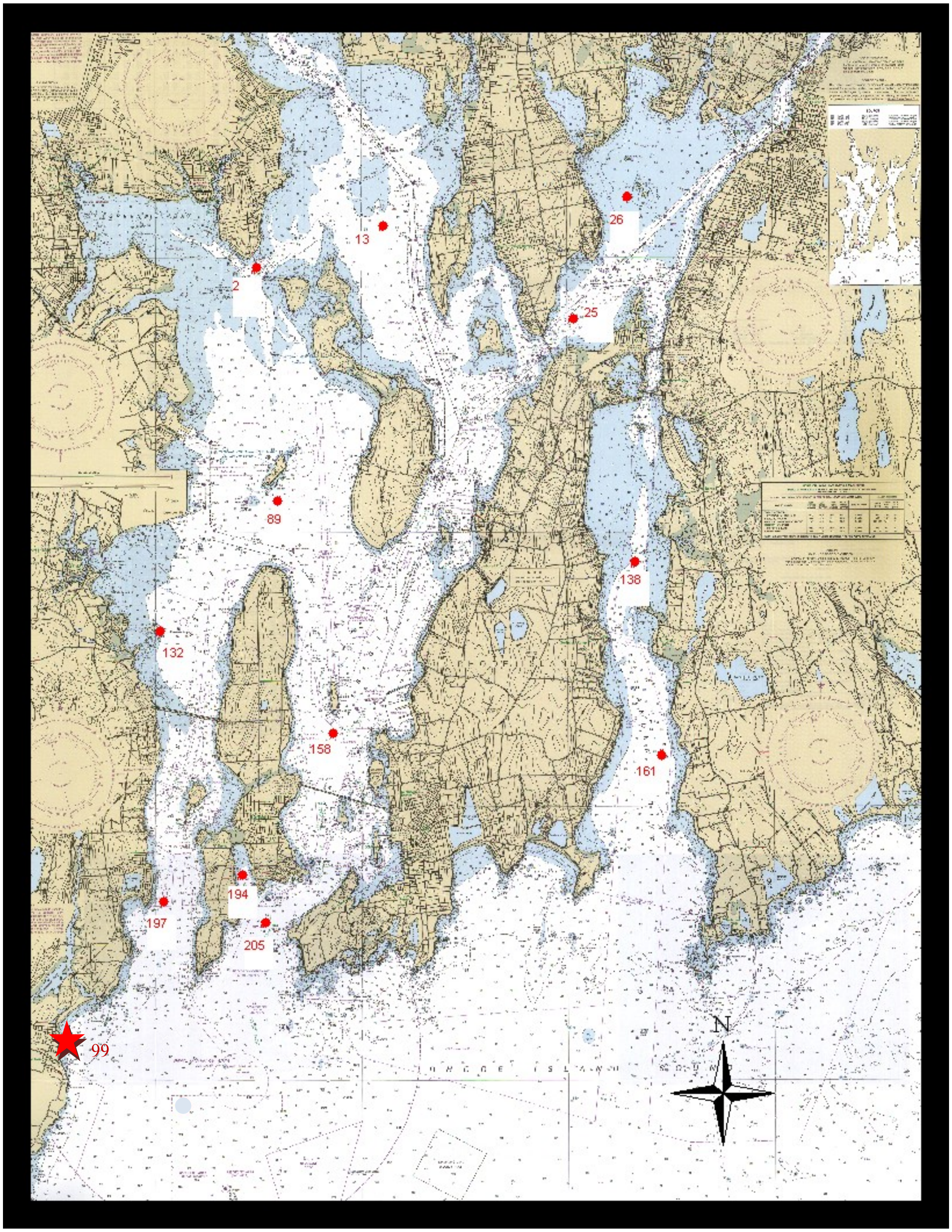

Figure 1: Stations sampled in Narragansett Bay during the 2009-2010 RIDEM otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red star indicates the station where *Leucoraja erinacea* were caught by rod and reel (#99). Approximate depth range in meters for each station is as follows: 1 = 6-9 m, 2 = 9-21 m, 13 = 9-21 m, 25 = 9-21 m, 26 = 3-6 m, 89 = 6-9 m, 99 = 1-3 m, 132 = 12-15 m, 138 = 9-18 m, 158 = 21-34 m, 161 = 6-9 m, 194 = 6-12 m, 197 = 9-15 m, and 205 = 27-37 m.

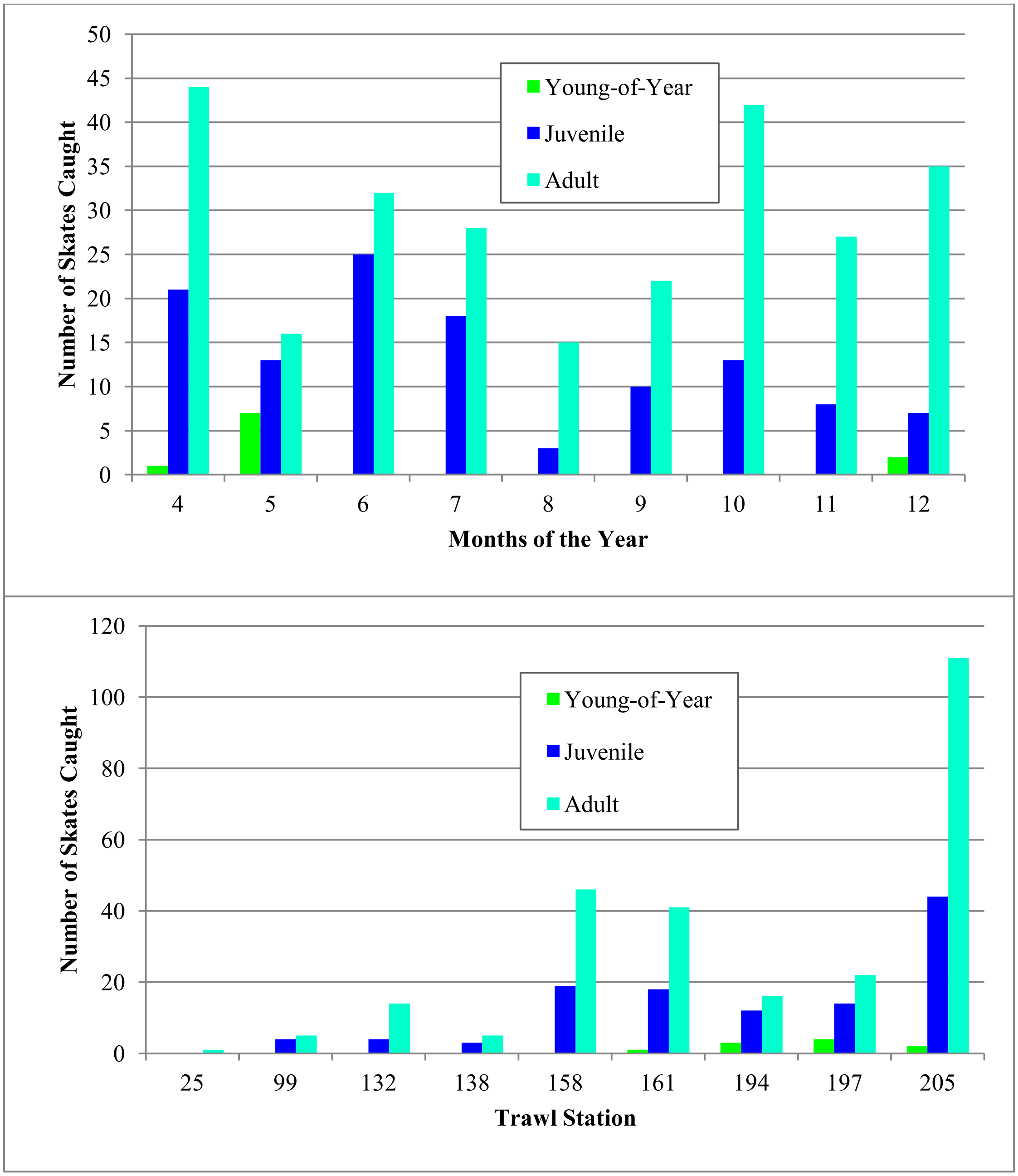

Figure 2: Frequency of *Leucoraja erinacea* caught in Narragansett Bay by rod and reel and by DEM monthly finfish trawl surveys in 2009-2010. Graphs profile catch by a) month of the year, March-December, and b) trawl station.

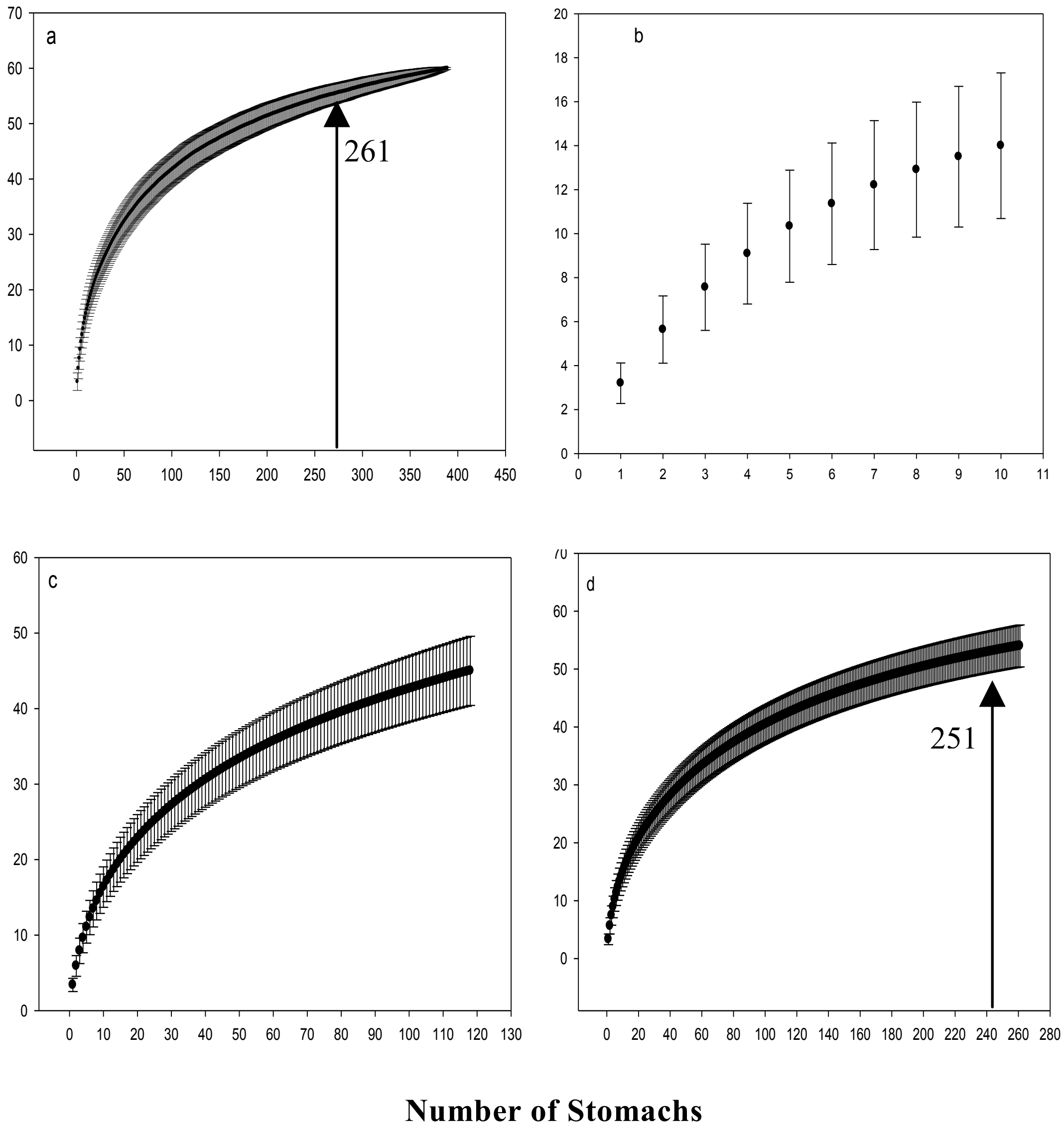

Figure 3: Cumulative Prey Curves for little skate, *Leucoraja erinacea*, sampled from April-December 2009-2010 with prey separated by lowest possible taxon. Mean number of cumulative novel prey species (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates >30 cm DW, c) stomachs from 30-45 cm DW, and d) stomachs from skates >45 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

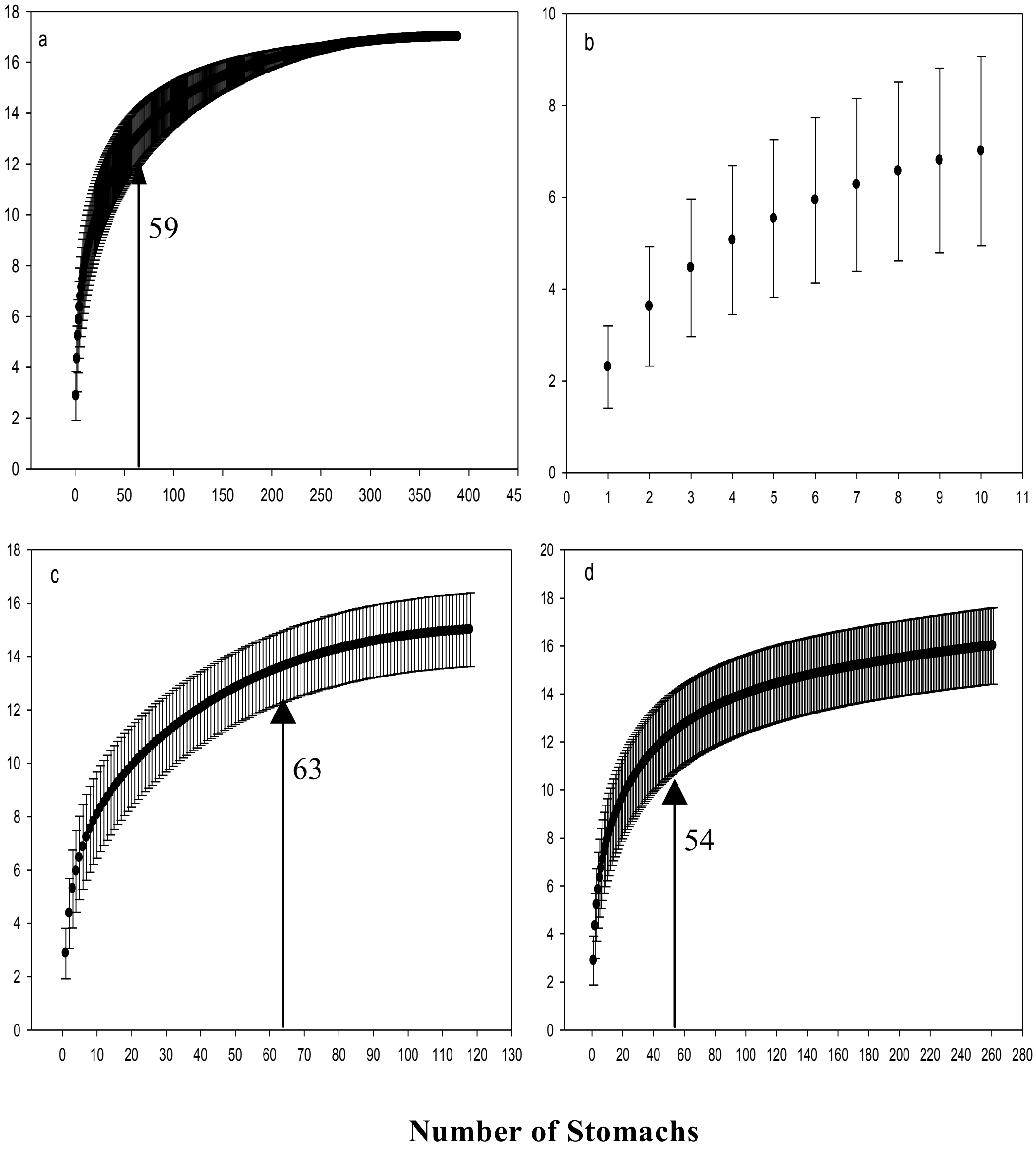

Figure 4: Cumulative Prey Curves for little skate, *Leucoraja erinacea*, sampled from April-Deceember 2009-2010 with prey grouped in categories as done for statistical analysis. Mean number of cumulative novel prey categories (±SD) for increasing number of skate stomachs sampled with order randomized 999 times for a) all stomachs, b) stomachs from skates >30 cm DW, c) stomachs from 30-45 cm DW, and d) stomachs from skates >45 cm DW. The numbered arrow indicates the point at which the curve reaches *b*=0.05 and, therefore, sufficient sample size.

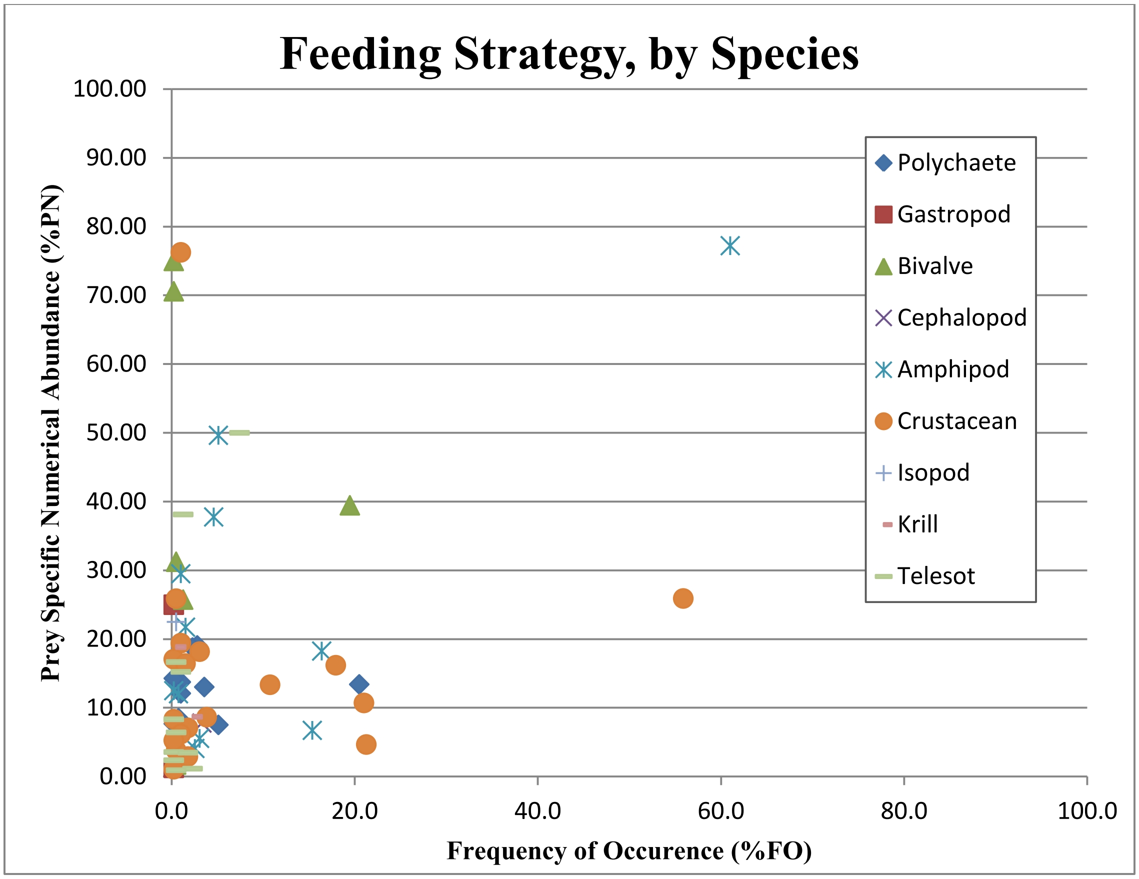

Figure 5: Feeding Strategy diagram of all *Leucoraja erinacea* collected April-December 2009 and 2010 from Narragansett Bay (n=389). Each point represents a separate prey species from Table 3; symbols represent different prey categories used in statistical analyses.

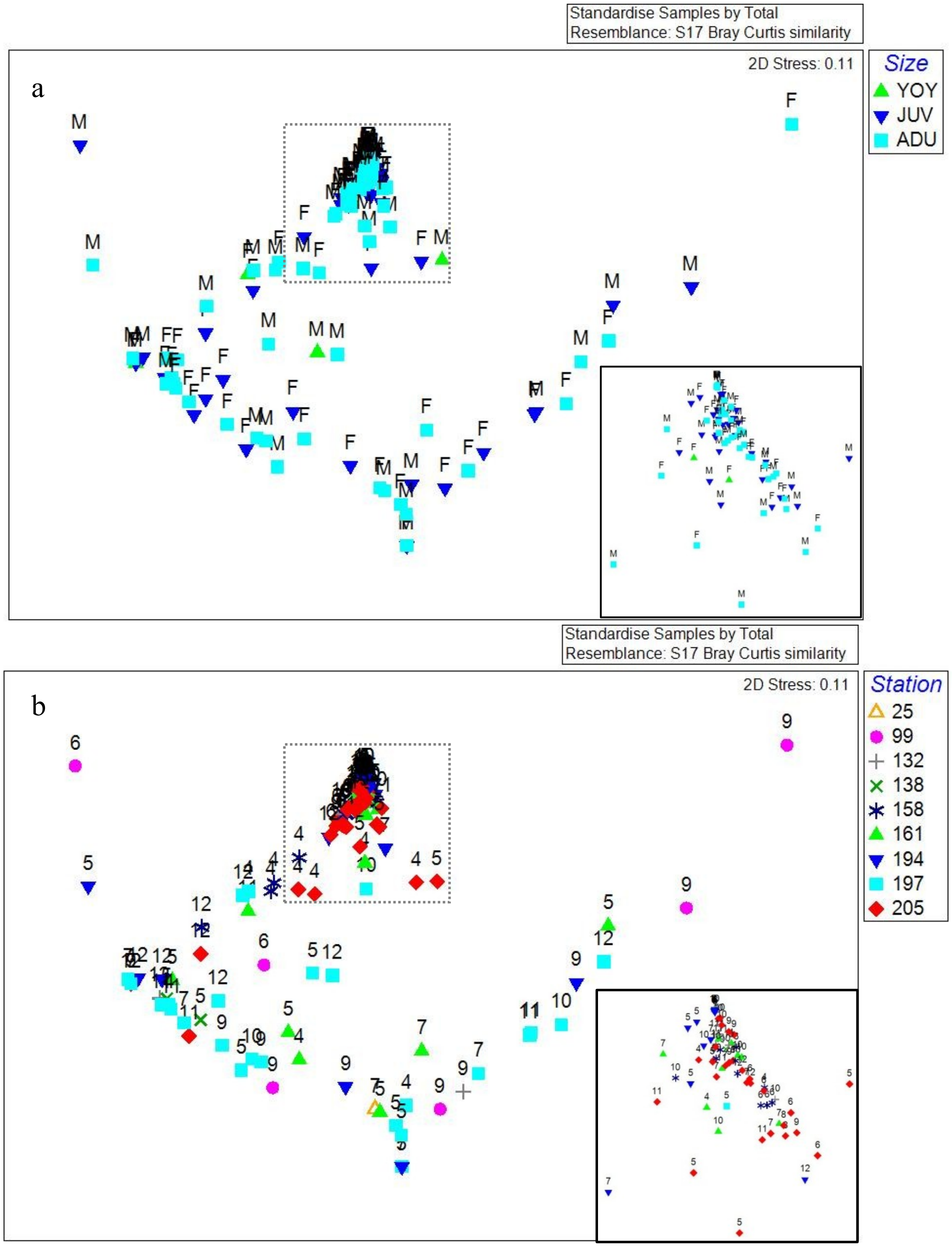

Figure 6: Non-metric multidimensional scaling plots of stomach content from *L.erinacea* collected April -December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %N highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.). To more closely examine the relationship of the dense cluster of points in the nMDS in each plot (denoted by the dashed box), an nMDS subset was configured and superimposed.

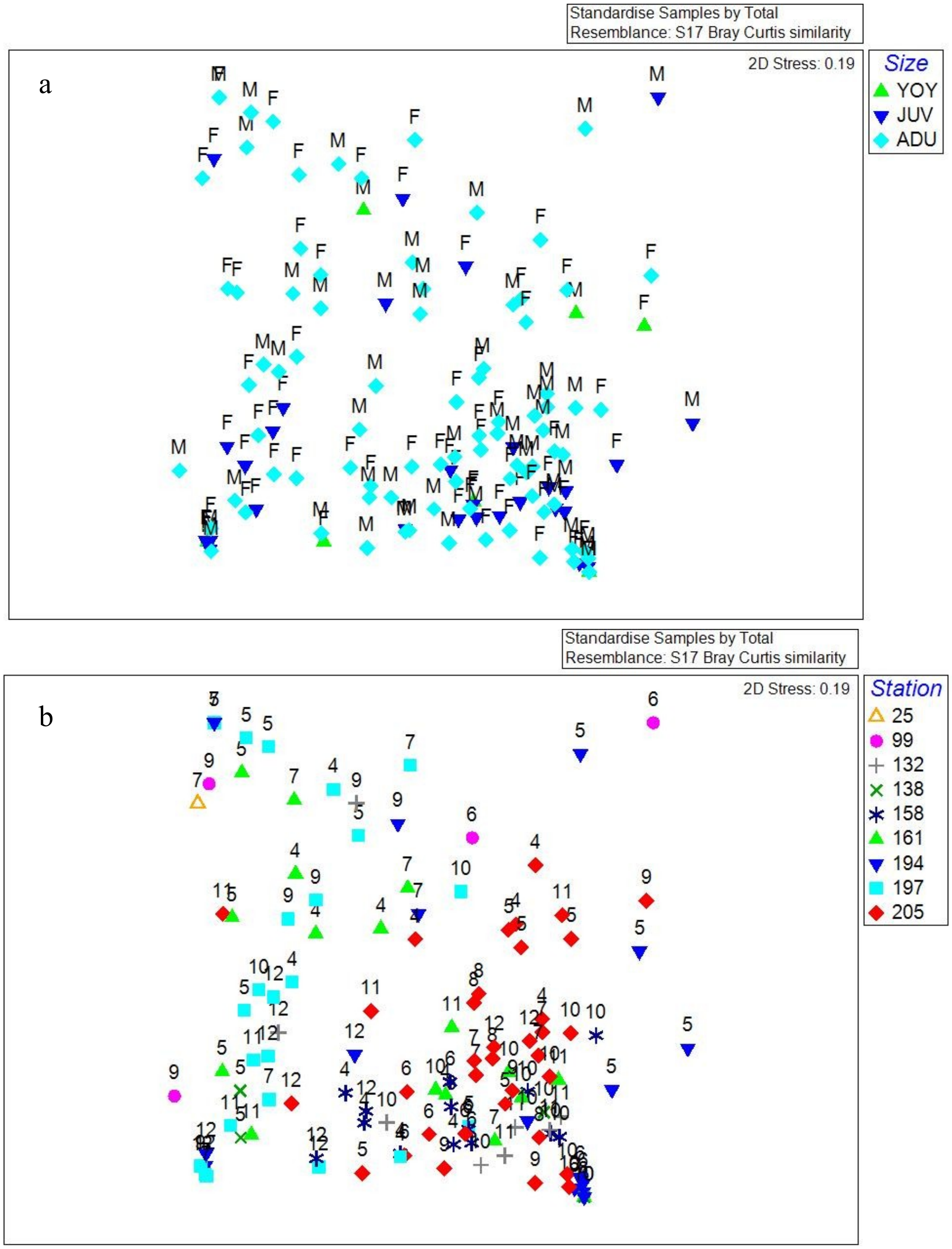

Figure 7: Non-metric multidimensional scaling plots of stomach content from *L.erinacea* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %W highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.).

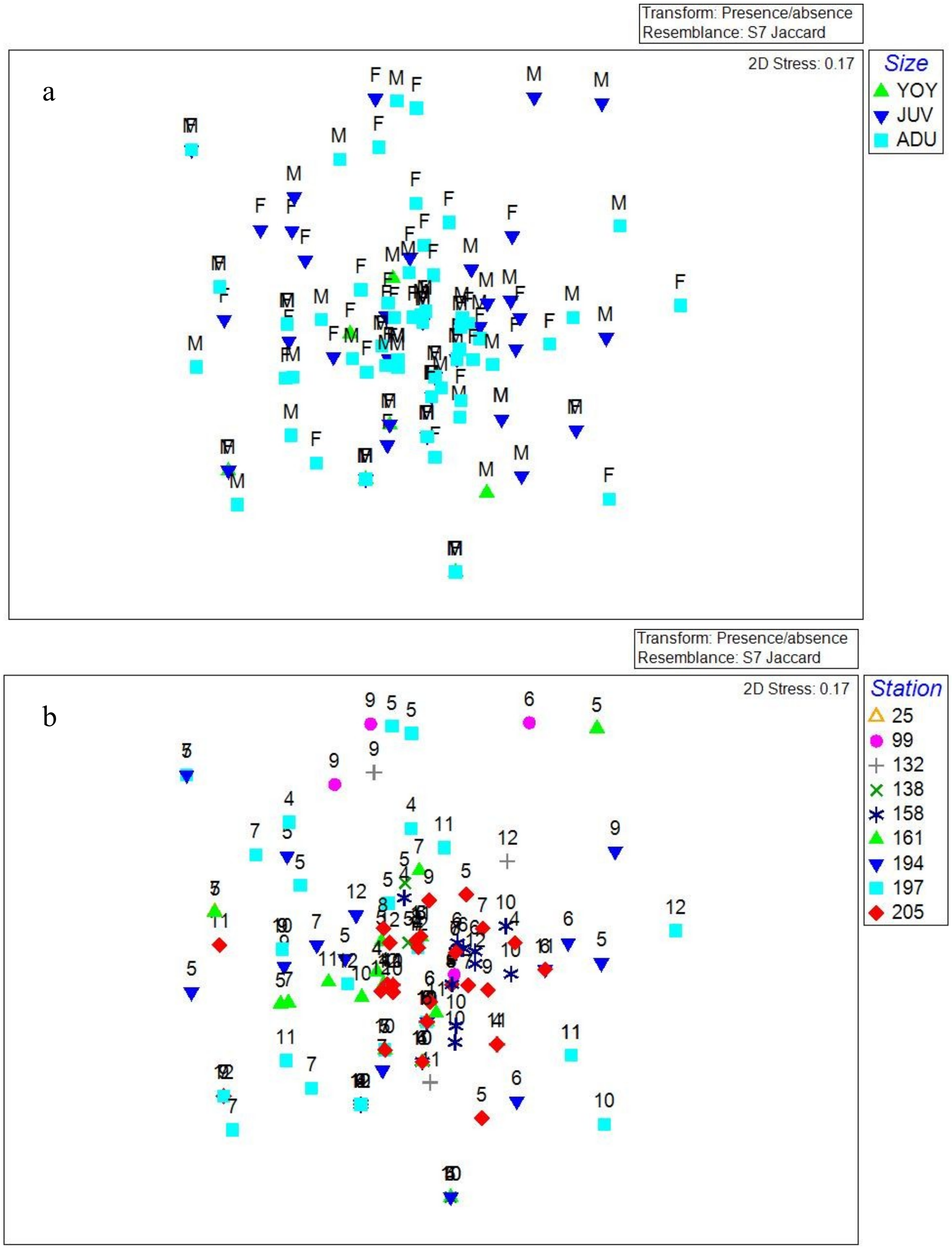

Figure 8: Non-metric multidimensional scaling plots of stomach content from *L. erinacea* collected April-December 2009-2010. Prey groups (see Table 2 for 'Prey Categories') analyzed for proportion of diet by %FO highlighting factors of a) size groups labeled by sex (▲represents YOY, ▼ represents JUV, ■ represents ADU; F=female, M=male) and b) station samples labeled by months of the year (4=April, 5=May, etc.).

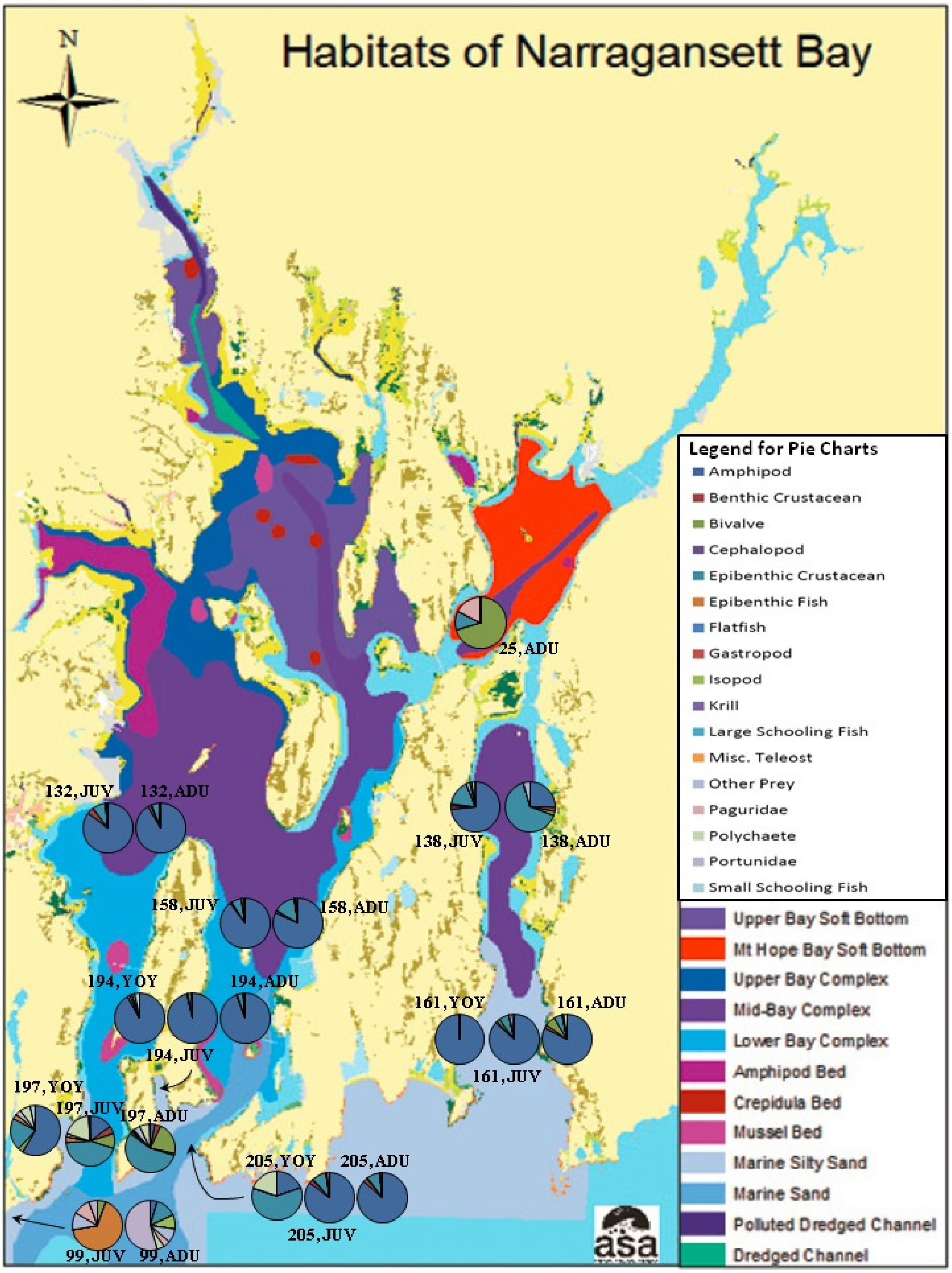

Figure 9: Proportional diet composition for different sizes of *Leucoraja erinacea* at different trawl sites relative to benthic prey abundance. Estuarine habitats map adapted from French *et al.,* 1992. Pie charts are centered over the corresponding station, unless otherwise notedwith an arrow.

MANUSCRIPT 4

Batoid elasmobranch community trophic relationships within and between Narragansett and Delaware Bays: An analysis of resource partitioning

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ABSTRACT

The trophic ecology of batoid elasmobranchs in Narragansett and Delaware Bays was analyzed to determine the degree and mechanism of resource partitioning in each habitat. The diets of each batoid community were also compared with each other to establish the presence of latitudinal or other differences. Single and compound measures were used to examine diet composition, trophic levels and overlap indices of each species were calculated, and multivariate statistical techniques were used to compare all diets. Narragansett Bay species showed a smaller range of overlap than Delaware Bay species did. In both cases, diets of different species differed significantly. The frequencies of prey items in diets of different size individuals within species were significantly different in Narragansett Bay inhabitants. In Delaware Bay, where more species of batoids coexist, diets of size classes within a species differed significantly despite high overlap. Though diets showed some variations based on proportion of prey items consumed, the only statistical difference was between the weights of the prey items in the diets of species groups across different bays.

INTRODUCTION

In recent decades, many of the world's fish stocks have become the focus of concern. Heavy fishing pressure has accelerated the decline of many fisheries and continuing this course can have rather serious consequences (Worm *et al.*, 2006). It has been suggested that population reductions of many fish species are due, in large part, to single-species management and the consequent heavy exploitation, and depletion, of one species at a time with a preferential removal of higher trophic level fish (Pauly *et al.,* 1998a). Additionally, bycatch of species co-occurring with target species has been a significant source of mortality (Alverson *et al.*, 1994; Dulvy *et al.*, 2000; Baum *et al.,* 2003). The large scale removal of species, along with other anthropogenic factors, has been equated with significant losses in marine biodiversity (Sala and Knowlton, 2006; Worm *et al.*, 2006). In order to curtail these trends, policy has begun to shift towards increased use of multi-species and ecosystem-based models in fisheries management (Garrison, 2000; Link & Almeida, 2000; Link, 2010; Link *et al.,* 2012). Ecosystem-based fisheries management (EBFM) policies seek to structure basic units of management along ecological gradients, as opposed to political ones (U.S. Commission on Ocean Policy, 2004; Arkema *et al.*, 2006; Jordaan *et al.*, 2007; Fogarty *et al.,* 2012; Gamble *et al.,* 2012; Link *et al.,* 2012; Lucey *et al.,* 2012; Pranovi *et al.,* 2012).

The stocks of large predatory fish, including many elasmobranch fishes, are of particular concern (Myers and Worm, 2003; Worm *et al.*, 2005; Sibert *et al.*, 2006). Recovery from exploitation is difficult for many of these species due to certain life history traits: slow maturation, long life span, long gestation and few well-developed offspring (Stevens *et al.,* 2000, Ellis *et al.,* 2005a, b; Dulvy *et al.*, 2008). Decline of upper level predators has been reported to trigger top-down trophic cascades (Estes *et al.*, 1998; Myers *et al.,* 2007) and release of smaller elasmobranchs from predation pressure (Peterson *et al.*, 2001; Farhrenthold, 2004; Myers *et al.*, 2007). Consequent changes in batoid elasmobranch (skate and ray) populations could have effects on their prey as well, particularly as these marine organisms are known to play an influential role in shaping benthic invertebrate communities (Smith and Merriner, 1985; Compagno, 1990; Peterson *et al.*, 2001). However, Myers *et al.* (2007) do not provide direct evidence that larger shark declines are clearly the cause for batoid increases. Nonetheless, in order to anticipate any potential effects of such trophic cascades, a comprehensive understanding of batoid elasmobranch trophic ecology is needed.

Some studies have been done examining the trophic interactions of batoid species (Fitz and Daiber, 1963; Holden and Tucker, 1974; McEachran *et al.*, 1976; Langton, 1982; Ellis *et al.*, 1996; McHugh, 2001; Bizzarro *et al.*, 2007; Magrabaña and Giberto, 2007; Link and Sosebee, 2008). EBFM strategies require considerable information about predation rates, though. Improved understanding of batoid trophic relationships is essential to effective assessment and implementation of this type of management (Garrison, 2000; Pranovi *et al.,* 2012). The goal of this study is to analyze the trophic ecology of the batoid elasmobranchs that inhabit the Narragansett and Delaware Bay estuaries and compare the relationships of each community to the other. Specific objectives were to compare intra- and interspecific diet compositions among skate and ray species and test for overall differences across assemblages. Null hypotheses that were tested included that there were no differences in the diet among individuals of sympatric species or of a single species between populations in different geographic locations.

METHODS

Study Site and Specimen Collection

Batoid elasmobranch communities were sampled from Narragansett and Delaware Bays. Both bodies of water are well studied and thoroughly characterized, but exhibit some different biogeophysical traits as well as varying levels of anthropogenic perturbations (Monaco and Ulanowicz, 1997).

From Narragansett Bay, specimens of *Leucoraja erinacea* (Le)*, L. ocellata* (Lo)*,* and *Raja eglanteria* (Re) were collected aboard fishery-independent monthly bottom trawl surveys conducted by the Rhode Island Department of Environmental Management (DEM) in March-December of 2009 and 2010. Details about Narragansett Bay, the trawl, the twelve haul stations, and the rod-and-reel station were outlined by Szczepanski (ms. 3).

From Delaware Bay, specimens were collected aboard fishery-independent monthly bottom trawl surveys conducted by the Delaware Department of Natural Resource and Environmental Control (DNREC) in March-December of 2009 and 2010. Species of interest included the 3 aforementioned skate species as well as 5 species of ray: *Myliobatis freminvillii* (Mf), *Rhinoptera bonasus* (Rb), *Dasyatis centroura* (Dc), *D. say* (Ds), and *Gymnura altavela* (Ga). Details about the Delaware Bay, the trawl, and the nine stations were outlined by Szczepanski (ms. 1).

Sample Processing

Data collected from each specimen on the boat included: disc width (DW, cm), total length (TL, cm), and sex. Gastric lavage and stomach dissection were used to remove stomach contents as described by Szczepanski (ms. 2) and collected prey items were then stored on ice until they could be analyzed in the lab.

Stomach Content Analysis

Stomach contents were identified, separated accordingly, counted, and weighed. Prey items were identified to the lowest taxonomic level possible using field guides and taxonomic keys (Smith, 1964; Gosner, 1971 and 1978; Rehder, 1981; Pollock, 1996), and consultation with biologists at the University of Rhode Island (URI), Woods Hole Oceanographic Institute (WHOI), and Virginia Institute of Marine Science (VIMS). Any highly digested items that could not be identified, parasites, and sediments were counted and noted, but not included in statistical testing. The number of each prey item in a stomach sample was estimated using the most conservative count when detached components were present. Items were then weighed (to the nearest 0.01 g) after excess moisture was blotted off.

Statistical Analysis

Prey species were combined into higher taxonomic or functional groupings (e.g.- Paguridae or bivalve, etc.) for statistical analysis since many groups of uncommon prey were represented by few individuals and unnecessarily skewed the results; these groupings aided in the interpretation of the ecological importance of the results. The contribution of each prey type to diet composition was estimated with three relative measures of prey quantity (RMPQ) described by Hyslop (1980). These measures include number (N), wet weight (W), and frequency of occurrence (FO) (Hyslop, 1980).

Prey-specific abundance by number (%PN) and by weight (%PW) were calculated to identify each prey item's relative importance independent of the other prey found (Amundsen *et al.,* 1996) and was used in constructing the compound index, Prey-Specific Index of Relative Importance, %PSIRI (Brown *et al.*, 2011).

Trophic Level (*TRL*) was calculated using %W; trophic levels of prey items were also needed (Table 1) to calculate the *TRL* of the predators and were determined using calculated values from Pauly and Chistensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007). Details about RMPQs, Prey-specific indices, *TRL*, and their respective calculations were provided by Szczepanski (ms. 1).

Significance Tests for Variation

Samples were defined as the averaged stomach content proportions of each prey category for all individuals of a specific size group and sex at each station each month. Data were separated by size groups which reflect life history stages: young-of-the-year (YOY), juveniles (JUV), and adults (ADU). Size ranges for *Myliobatis freminvillii* were given by Szczepanski (ms. 1), *Raja eglanteria* by Szczepanski (ms. 2), and *Leucoraja erinacea* by Szczepanski (ms. 3). For *Leucoraja ocellata*, YOY were <55 cm total length (TL), JUV were 55-70 cm TL, and ADU were >70 cm TL (Packer, *et al.*, 2003). For both *Rhinoptera bonasus* and *Dasyatis say*, YOY were <40 cm in disc width (DW), JUV were 40-65 cm DW, and ADU >65 cm DW (Hess, 1959; Neer and Thompson, 2005; Snelson and Grubbs, 2006). For *Dasyatis centroura*, YOY were <70 cm DW, JUV were 70-130 cm TL, and ADU were > 130 cm DW (Hess, 1959; McEachran and de Carvalho, 2003). For *Gymnura altavela*, YOY were also <70 cm, but JUV were 70-100 cm DW, and ADU were > 100 cm DW (Capapé *et al.*, 1992).

Diet overlap was initially examined across all species and size classes within each estuary, respectively, using the Schoener dietary overlap index (S_{do}) and simplified Morisita index (C_h) (Clarke and Warwick, 2001; McElroy *et al.,* 2006; Bizzarro *et al.*, 2007; Mabragaña and Giberto, 2007). Significance testing involved each of the 3 RMPQ's (N, W, FO) separately since each indicates different things about the diet and is also susceptible to different types of bias.

Non-metric multidimensional scaling (nMDS) ordination plots were constructed using PRIMER v6.1.13 (Clarke and Warwick, 2001) to look for relative similarities in diet for each RMPQ. Differences in diet among species and size class within each bay were tested by using permutation tests called analysis of similarities (ANOSIM). Diets of each species were also tested between the different geographic regions. Szczepanski (ms. 1) provided further detail for each step of significance testing.

RESULTS

A total of 389 *Leucoraja erinacea* were collected in Narragansett Bay from March 2009-December 2010. Samples from 3 other species were also collected, though very few: 12 *Leucoraja ocellata* (7 YOY, 5 JUV), 3 adult *Raja eglanteria*, and 1 adult *Dasyatis centroura*. Little skate, *L. erinacea*, feeds primarily on amphipods and epibenthic crustaceans at any size (Table 2). Amphipods were 57.4% of the YOY diet based on %PSIRI, 46.8% of JUV diets, and 59.5% for ADU, while epibenthic crustaceans were just under 20 % PSIRI for each size (18.4% YOY, 17.8% JUV, and 19.7% ADU). JUV also consumed benthic crustaceans and bivalves (10.3% and 10.0% PSIRI, respectively) with some pagurids and polychaetes (4.8% and 3.0 %PSIRI, respectively). ADU *L. erinacea* supplemented their diet with pagurids as well (7.5 %PSIRI), bivalves (7.2 %PSIRI) and benthic crustaceans (4.3 %PSIRI). YOY *L. ocellata* fed almost exclusively on epibenthic crustaceans (93.2 %PSIRI) with some amphipods and flatfish (3.7% and 2.2 %PSIRI). JUV *L.ocellata* had a more varied diet with fish as a larger component overall, consuming epibenthic fish (34.6%) and epibenthic crustaceans (23.1%), small schooling fish (18.4%), polychaetes (7.7%), amphipods (6.0%), large schooling fish (2.5%), and cepahalopods (2.2%). The *R. eglanteria* and *D. centroura* collected were all adults with relatively simple diets. *Raja eglanteria* had a large portion of cephalopods in their diet (66.7%) and small schooling fish (33.3%) while *D. centroura* consumed 75% epibenthic fish and 25% other prey (highly digested or unidentified).

Raja eglanteria had the highest calculated trophic level at 4.2, followed by *L. erinacea* samples with 3.93, 3.82, and 3.87 for YOY, JUV, and ADU, respectively. JUV *L. ocellata* had a *TRL* = 3.85 while YOY *L. ocellata* was the lowest with 3.55. *Dasyatis* *centroura* were calculated to have *TRL* = 3.8.

When overlap indices were calculated for the different species of batoids in Narragansett Bay, values ranged from 0-0.38 between both measures, S_{do} *and* C_h (Table 3). The greatest overlap occurred between *Leucoraja erinacea* and *L. ocellata with* a $C_h = 0.38$; the least overlap was between *Raja eglanteria* and *Dasyatis centroura* with no overlap in either measure, though *R. eglanteria* overlapped very little with any species.

Non-metric multidimensional scaling plots were constructed to visualize the relationship of the diets between batoid species based on the different RMPQs (Figure 3). There is a clear distinction between the diets of *Raja eglanteria*, *Dasyatis centoura*, and *Leucoraja* sp. for all the RMPQ analyses. *Leucoraja ocellata* does show a tendency to cluster, though within the large group of *L. erinacea* samples. Diets do not tend to group within a species by size for either %N or %W (Figure 3a and 3b, stress = 0.13 for both) but does somewhat for %FO (Figure 3c, stress = 0.16). ANOSIM tests run on the the different measures confirm that species have significantly different diets with a moderate degree of overlap ($R_{\%N} = 0.343$, $p_{\%N} = 0.02$; $R_{\%W} = 0.527$, $p_{\%W} \ll 0.01$; $R_{\%FO} = 0.676$, $p_{\%FO} = 0.03$) and that different size classes have diets that vary significantly only in the frequency of prey items consumed, not in relative abundances ($R_{\%N} = -0.025$, $p_{\%N} = 0.62$; $R_{\%W} = 0.022$, $p_{\%W} = 0.34$; $R_{\%FO} = 0.206$, $p_{\%FO} \ll 0.01$).

A total of 8 different species of batoid elasmobranch was collected from Delaware Bay between March 2009-December 2010: 8 *Dasyatis centroura* (6 YOY and 2 JUV), 9 *D. say* (2 YOY, 4 JUV, and 3 ADU), 2 *Gymnura altavela* (1YOY and 1 ADU), 37 *Leucoraja erinacea* (2 YOY and 35 JUV), 3 YOY *L. ocellata*, 132 *Myliobatis freminvillii* (85 YOY, 39 JUV, 8 ADU), 3 *Rhinoptera bonasus* (1 YOY and 2 ADU), and 74 *Raja* *eglanteria* (9 YOY, 33 JUV, and 32 ADU). The diets for each species and size class were analyzed using %PSIRI (Table 4). *Dasyatis centroura*, overall, consumed mostly benthic (53.8% and 78.7% for YOY and JUV, respectively) and epibenthic crustaceans (26.6% and 12.7%, YOY and JUV respectively), though YOY also consumed polychaetes (28.4%) while JUV consumed bivalves (5.7%). *Dasyatis say* ate mostly bivalves (71.2%, 43.2%, and 50.2% for YOY, JUV, and ADU, respectively) and polychaetes (28.8%, 30.2%, and 33.3%, for YOY, JUV, and ADU respectively); JUV also included epibenthic (18.6%) and benthic (8.0%) crustaceans in their diets. The 2 *Gymnura altavela* collected had only small schooling fish in their stomachs. All *Leucoraja erinacea* in Delaware Bay consumed epibenthic crustaceans as part of their diet (48.6% and 50.6% for YOY and JUV, respectively), but YOY ate amphipods (48.6%) while JUV consumed more types of prey (17.0% bivalves, 16.8% pagurids, 7.4% benthic crustaceans, 3.6% polychaetes, 1.7% large schooling fish, and 1.0% portinuds). YOY *L. ocellata* that were collected had consumed mostly epibenthic crustaceans (60.7%) and bivalves (36.7%), with some instances of flatfish (2.6%). All *Myliobatis freminvillii* consumed gastropods, pagurids, and bivalves, but in different proportions: YOY were found to have stomach contents that were 25.3% gastropods, 29.7% pagurids, and 11.0% bivalve; JUV had 33.3% gastropods, 8.8% pagurids, and 36.1% bivalves; ADU had 75.1% gastropods, 20.4% pagurids, and 4.4% bivalves. YOY and JUV *M. freminvillii* stomachs also contained an unidentifiable item (recorded as “Unknown 001”) as 28.6% and 20.5% of their diets respectively. YOY *Rhinoptera bonasus* had stomach contents dominated by gastropod remains (92.4%) with some benthic crustacean remains as well (7.6%); ADU *R. bonasus* stomach contents contained a wide variety of items including bivalves (50%), krill (24.9%), isopods

(12.8%), epibenthic (1.3%) and benthic (1.2%) crustaceans, and amphipods (1.1%). All *Raja eglanteria* stomachs contained epibenthic crustaceans (45.0%, 36.9%, and 41.7% for YOY, JUV, and ADU, respectively), krill (28.3%, 22.4%, and 2.8%, for YOY, JUV, and ADU, respectively), polychaetes (10.0%, 6.6%, and 7.6%, for YOY, JUV, and ADU, respectively) and some epibenthic fish (5.7%, 5.6%, and 16.0% for YOY, JUV, and ADU, respectively). JUV and ADU *R. eglanteria* also consumed small proportions of bivalves, benthic crustaceans, pagurids and small schooling fish; adults were the only size found to eat flatfish.

Gymnura altavela had the highest trophic level, calculated to be 4.2 for both sizes. YOY *Dasyatis centroura* had *TRL* = 3.54 while JUV was 3.51. YOY *Leucoraja erinacea* also had relatively high *TRL* of 3.84 while JUV was 3.47. *Raja eglanteria* had trophic levels calculated to be 3.6, 3.49, and 3.72 for YOY, JUV, and ADU, respectively. YOY *L. ocellata TRL* = 3.34. *Myliobatis freminvillii* trophic levels were calculated to be 3.29, 3.13, and 3.14 for YOY, JUV, and ADU, respectively. The lowest trophic level for the Delaware Bay batoids was calculated for YOY *Rhinoptera bonasus* with *TRL* = 3.10, though ADU was found to have *TRL* = 3.44.

When overlap indices were calculated for the different species of batoids in Delaware Bay, values ranged from 0-0.95 between both measures, S_{do} and C_h (Table 5). The greatest overlap occurred between *Leucoraja erinacea* and *L. ocellata* with a C_h = 0.95; *Raja eglanteria* had high overlap with both *L. erinacea* (C_h = 0.86) and *L. ocellata* (C_h = 0.80). The least overlap was between *Gymnura altavela* and *Dasyatis centroura, D. say, L. ocellata, Myliobatis freminvillii,* and *Rhinoptera bonasus,* each, with no overlap in either measure.

Non-metric multidimensional scaling plots were constructed to visualize the relationship of the diets among batoid species based on the different RMPQs (Figure 4). In the nMDS plot constructed with %N (Figure 4a, stress = 0.13), both sizes of *Gymnura altavela* are completely separate from the other clusters as are dasyatid rays and myliobatid rays. *Leucoraja erinacea* and *L. ocellata* samples show a considerable degree of overlap and slightly overlap with *Raja eglanteria* samples, though each species is clearly clustered. Diets within species do not tend to separate by size except for those of *Myliobatis freminvillii*, in which only ADU diets seem to cluster closely within the other samples from smaller sizes. ANOSIM tests showed deep separation between diets of species (*R* = 0.79) but not much between sizes within species (*R* = 0.086), with significant differences seen between species ($p \ll 0.01$) but not size within species (p = 0.07). Plots of species and sizes by %W resulted in similar but more condensed groupings of *R. eglanteria* and more separate clusters of *D. say* and *D. centroura*; and with different sizes of each species clustering with other sizes of that species (Figure 4b, stress = 0.15). Again, ANOSIM confirmed these findings with a high amount of separaton between species (*R* = 0.83) but almost none between sizes within species (*R* = 0.074) and significant differences between diets of each species ($p \ll 0.01$) but not sizes (p = 0.09). The nMDS plot of %FO showed similar taxonomic diet groupings (Figure 4c, stress = 0.13). *Gymnura altavela* was, again, completely separate, with clusters of *M. freminvillii*, *D. say* and *D.centroura*, and *R. eglanteria, L. erinacea, and L. ocellata*. There appeared to be less overlap between species and more between sizes. Again, ANOSIM did result in great separation among species (R=0.82) but not between sizes within species (R=0.11), although both were significantly different ($p \ll 0.01$ between species and p=0.02 between sizes within species).

Diets were analyzed for each species as a whole within each estuary to compare diets across regions (Table 6). *Dasyatis centroura* in Delaware consumed mostly benthic crustaceans (55.8%), epibenthic crustaceans (21.7%), and polychaetes (18.1%), while this species in Narragansett Bay ate mostly epibenthic fish (75%). *Dasyatis say* ate primarily bivalves (55.8%) and polychaetes (30.9%), with some epibenthic crustaceans (8.3%). *Gymnura altavela* diets were entirely made up of small schooling fish. Both *D. say* and *G. atlavela* were collected only in Delaware Bay. *Leucoraja erinacea* in Delaware Bay had a widely varied diet but comprised mostly epibenthic crustaceans (50.1%), bivalves (16.5%), and pagurids (14.8%), while *L. erinacea* in Narragansett Bay had diets composed mainly of amphipods (47.8%), then epibenthic crustaceans (17.9%), benthic crustaceans (9.5%), bivalves (9.5%), and polychaetes (6.9%). *Leucoraja ocellata* in Delaware consumed mostly epibenthic crustaceans (60.7%) and bivalves (36.7%), similar to those in Rhode Island (epibenthic crustaceans 56.1%) though there were no bivalves in those stomachs. Instead, northern *L. ocellata* had stomach contents that included epibenthic fish (14.4%), small schooling fish (12.9%), and amphipods (4.7%). In Delaware Bay, *Myliobatis freminvillii* ate gastropods, pagurids, and bivalves (37.1%, 21.8%, and 19.1%, respectively) and *Rhinoptera bonasus* ate bivalves, gastropods, krill, and isopods (33.3%, 30.9%, 16.6%, and 8.5%, respectively). *Raja eglanteria* in Delaware Bay had stomach contents that included epibenthic crustaceans (41.9%), krill (13.7%), epibenthic fish (11.5%), bivalves (7.6%), polychaetes (7.6%), and flatfish (5.1%); *R. eglanteria* primarily ate cephalopods (66.7%) and small schooling fish (33.3%).

In order to statistically analyze differences among species and between bays, nMDS plots were constructed using the 3 RMPQs (Figure 5). When constructed with %N, a large cluster in the middle of the spaces formed, with *Leucoraja ocellata, L. erinacea,* and *R.eglanteria* from both bays in a dense group (Figure 5a, stress = 0.16). *Myliobatis freminvillii, Rhinoptera bonasus,* and *Raja eglanteria* from Delaware Bay formed separate groups away from the main cluster as did many of the samples of *L. erinacea* from Narragansett Bay. Another group that separated away from the larger cluster consisted of *G. altavela*, *R. eglanteria*, and a *D. centroura* from Delaware Bay and a *L. ocellata* and *D. centroura* sample from Narragansett Bay. ANOSIM tests on these data indicated significant separation of diets among species ($R = 0.441$, $p \ll 0.01$), but not between the diets of any given batoid species from different bays ($R = 0.15$, $p = 0.16$). An nMDS plot constructed with %W resulted in a similar pattern of clustering to %N, though only slightly more condensed for most of the samples with the exception of some *R. eglanteria* samples from both bays and *G. altavela* samples from Delaware Bay (Figure 5b, stress = 0.15). ANOSIM tests show moderate overlap and significant separation by species ($R = 0.53$, $p \ll 0.01$) and also between samples for a given species from different bays ($R = 0.35$, $p = 0.05$). Plots of %FO resulted in more overlap in species diets but apparently distinct groupings by species (Figure 5c, stress = 0.14). Diets of organisms in Narragansett Bay also seemed to cluster more tightly and separately from diets of Delaware Bay inhabitants than in other tests. ANOSIM tests resulted in moderate separation and significant differences in diets between species within a bay ($R = 0.45$, $p \ll 0.01$), as well as for any given species between the two bays ($R = 0.35$, $p \ll 0.01$).

DISCUSSION

This study is the first to analyze the trophic relationships of multiple species of batoid elasmobranch within Narragansett Bay estuary. Relative abundances of prey importance do appear to indicate some difference between species and some slight variations within species by size. However, as indicated by Szczepanski (ms. 3), *Leucoraja erinacea* does not display significant ontogenetic differences in diet composition in this estuary. This is not to say that the other species do not either, however there was not a sufficient sample size to characterize each species to that degree. Each predator species, however small the sample size there was, did seem to focus on certain prey types that were not as heavily consumed as other available prey. The diets recorded here are mostly consistent with previously reported data (Bowman *et al.*, 2000; McHugh, 2001; Packer *et al*., 2003 a,b,c). The diet of *Dasyatis centroura*, however, was different (Bowman *et al.*, 2000) and is likely attributable to the fact that this species is not frequently found in the Narragansett Bay estuary and diet studies are from more southerly habitats (Hess, 1961; McEachran and de Carvahlo, 2002).

Competition with groundfish should be considered due to similar benthic life styles with skates. Atlantic cod and silver hake diets (Langton, 1982) and haddock diets (McHugh, 2001) have been shown to have very little overlap with either little or winter skate diets. Summer flounder diets consist mostly of cephalopods (56% W), small fish (31% W), and small crustaceans (8% W), and sometimes krill (Bowman *et al.,* 2000; Latour *et al.*, 2007). Winter flounder have been reported to consume polychaetes (43% W), anemones (22% W), and amphipods (10% W), and also some krill (Bowman *et al.*, 2000). Scup diets in Narragansett Bay include polychaetes (30%), amphipods (16%), decapod crustaceans (10%) and krill (9%), all measured by weight (Gray, 1991; Bowman *et al.*, 2000). Though many of the prey types are similar to those seen in some skate diets, the combination of prey types and proportions of each consumed do not appear to mimic any of the skates' diets. These fish likely may impart interspecific pressure more on each other than on skates.

The trophic levels calculated for the different groups of batoids reflect their dominant prey types. The clearnose skates collected contained mostly cephalopods and they therefore occupied the highest trophic level. The YOY winter skate was calculated to have the lowest trophic level and consumed mostly epibenthic crustaceans. Each species seemed to occupy a slightly different trophic level; this separation is a good indication that there is clear dietary resource partitioning in this ecosystem.

No other study has calculated overlap indices for these species in this estuary. There was very little overlap between species. It would have been reasonable to expect that since *L. erinacea* and *L. ocellata* are considered generalists (McEachran *et al.*, 1976; McHugh, 2001; Ebert and Bizzarro, 2007; Szczepanski, ms. 3), there would be more overlap. Indeed, these two species did exhibit the highest degree of overlap, but still a relatively low value for the indices involved. Since there are fewer batoid species (relative to other regions, see below), it is likely that there is less interspecific competition for resources and, therefore, less overlap.

The nMDS and ANOSIM tests confirm that the low overlap was indicative of significantly different diets among species. Though size differences may have been more apparent with more samples, this is not likely since the diets of at least one abundant species (*L. erinacea*, Szczepanski ms. 3) have been shown to not exhibit ontogenetic differences.

McHugh (2001) examined diet overlap among little skate, winter skate, and haddock on Georges Bank. Diets of the two species of skate overlapped more greatly than did either skate with the haddock, but the diets of the three species were significantly different. The difference was attributed to proportions of the same prey, therefore, reducing interspecific competition. Shared resources may not be as limiting in this community and benthic production is available in ample supply (McHugh, 2001). This could also be the case in the current study as any degree of overlap still resulted in significantly different diets within either ecosystem.

This study also compares the trophic relationships of the batoid community within Delaware Bay, more than just diet differences between a pair of skates (Fitz and Daiber, 1963). Though interspecific overlap was greater in this system, particularly with many species consuming epibenthic crustaceans, the proportions that were consumed varied. Also, the primary prey items did vary to some extent as did the supplementary prey items. As with the batoids in Narragansett Bay, the diet composition was reflected in the calculated trophic levels. The range of trophic levels recorded was relatively broad.

Overlap indices among species in the Delaware Bay ranged widely. With more species of batoid, it is reasonable to expect a higher chance that some diets will have more similarities. However, most of the observed overlap values were less than 0.5 by these indices. Since more batoid species inhabit this estuary, it was expected that there would be more competition for the available resources and, therefore, more overlap. However, since the number of consumers was greater, resources would need to be rationed more efficiently within the community in order for them all to co-exist. This is only the case if resources are limiting; my study could not fully determine if this is the case, though, since complete resource abundance data were not able to be collected simultaneously.

This study statistically analyzes the diets of the batoids in Delaware Bay for overlap and possible partitioning. The nMDS plots and corresponding ANOSIM showed differences among species and size suggesting that higher levels of interspecific competition may require greater partitioning not only across species but also within a species, depending on the abundance of available resources. The R-value was high among species (indicating high separation of diets) and low among sizes (indicating low separation, higher degree of overlap), but still enough difference in both to not be due to chance. In order for each species to compete effectively, they need to feed efficiently across size classes. *Myliobatis freminvillii* and *Raja eglanteria* did show ontogenetic diet differences (Szczepanski, ms. 1 and 2) and the other species with samples of multiple size classes were trending toward size differences as well. Based on the data collected for my study, this pattern of resource utilization seems to vary by proportional abundance of prey within species and the dominant prey type varying across species.

Fitz and Daiber (1963) had compared the general biology of the clearnose and little skates in Delaware Bay, including their diets. They remarked that both species ate the same prey items, but did report different proportions of those prey eaten. No statistical analysis was involved so actual differences were not fully quantified. Fitz and Daiber (1963) did compare the diets they found with studies from other regions (Chesapeake, Block Island Sound, Long Island Sound) and remarked that the same prey species were found in the stomachs of their fish as in the other studies. This would support the lack of significant differences between bays in the current study. However, those comparisons only make this conclusion based on presence of prey items and not proportional abundance which has been shown to provide enough variation for statistical difference (McEachran *et al.* 1976; Langton, 1982; McHugh, 2001; Magrabaña and Giberto, 2007; Matich *et al.*, 2011).

McEachran *et al.* (1976) examined overlap in two pairs of skate species on the east coast of North America. Overlap values of 50% or more were considered significant (and therefore not different); however some Delaware species in the current study had high overlap but still significantly different diets due to proportional prey abundance in the diet. McEachran et al. (1976) did not use multivariate statistical analysis and may have seen the species differences if they had. Their study did indicate that competition is minimized by differences in proportional abundance of prey in each diet and that corresponding food preferences are influenced by mouth morphology. Differences in diets between the pairs of organisms were reflected in the different benthic communities with which each pair was associated.

The current study compares whole batoid communities from different estuarine systems. Significant differences were detected in diets between species but not across the bay systems. The only differences in species' diets across bays was in prey abundance by weight; the *p*-values for the ANOSIM of abundance by number and frequency of occurence were approaching significance and may have shown differences with greater sample size. This phenomenon may be due to differential size between populations at different latitudes, as size may be a limiting factor in how much food can realistically be consumed (larger individuals are able to consume more food and have larger average stomach content weight, Szczepanski ms.1, 2, and 3). As a specific example, *Leucoraja erinacea* was represented by enough samples and was able to be analyzed separately; diets did differ significantly across bays for all measures (i.e., $R = 0.328$, $p \ll 0.01$, by %N). Nonetheless, it is not too surprising that the diets across bays were not significantly different for some metrics. Statistics only indicate that there was as much variation within each bay as there was between the bays. Though each species eats different prey, as a community they are each still a group of benthic, secondary consumers. Latitudinal differences in batoid diets might be more apparent if one looked at a more specific taxonomic level of the prey.

Other investigators have looked at different batoid communities to examine trophic relationships. In the Northeast Atlantic, Holden and Tucker (1974) analyzed four skates in British waters but only compared percentage of prey occurrence and conducted no statistical tests. They did not find significant differences with species and attributed prey selection to prey availability, speed of predator relative to that of the prey, and mouth morphology; but they also did not consider any overlap measures to verify the degree of non-selective feeding. Ellis *et al.* (1996) examined the same skate species as Holden and Tucker (1974) along with 6 species of shark. Ellis *et al.* (1996) did note species differences with only 7 cases of significant dietary overlap, however 5 of those cases involved skates. Variation in diet was attributed to prey availability and morphology. The current study indicates that even though there may have been overlap, diets can still be significantly different due to proportions of prey consumed. The Ellis et al. (1996) study may have had some different implications if multivariate testing had been employed.

In the southwest Atlantic, Magrabaña and Giberto (2007) studied 2 sympatric skate species and did find that they fed on the same prey species but there were some slight differences in proportions of prey. There were no significant differences between very distinct geographic regions sampled, but there were also no significant differences in diet between the two species. Reduction in interspecific competition is attributed to distinct feeding behaviors. This could certainly be a factor in the Delaware Bay populations since there is a wide variety of morphologies and feeding behaviors (Karl and Obrebski, 1976; Smith and Merriner, 1985; Dean *et al.*, 2007, Bizarro *et al.*, 2007) and with sizes of skates in Narragansett Bay (Packer *et al.,* 2003a, b, c).

Bizzarro *et al.* (2007) analyzed the feeding ecology of 4 skate species off the central California coast and found high dietary overlap though still significant differences between species. These differences were also associated with size of skate and depth. The authors proposed that resource competition is reduced because of declines in upper trophic level groundfish biomass. Such reduction in other competitive species, as has been suggested about the outburst of small elasmobranchs on Georges Bank (Fogarty and Murawski, 1998), could allow the populations in the western Atlantic to partition resources more efficiently. However, an alternative hypothesis has been proposed that suggests that Southern New England populations of skate are connected to neighboring populations and exchange individuals through increased migration (Frisk *et al.*, 2008), minimizing the possibility that declining groundfish provided competitive release.

The results of this study show clear indications of resource partitioning by batoid communities in both Delaware and Narragansett Bays. The skate and ray species residing in each habitat exhibit varying levels of dietary overlap but are still able to maintain different feeding habits from each other by consuming different proportions of the same prey items. With more sympatric species and, therefore, more potential for interspecific competition, resource partitioning occurs to a greater extent between size classes within a species, as was the case in Delaware Bay batoids. Though other studies support these findings, more data on the less abundant species would make comparisons more robust and differences more clear. Considerable recent attention has been devoted to ecosystem based fisheries management (Link, 2010) and the need for resource utilization studies has become more in demand (Bizzarro *et al.*, 2007). Though difference in diet was seen only in the weight of prey items between species of different bays, the impact that each population of batoids has on its respective habitat will likely vary due to differences in environmental factors and other species interactions. In light of the new hypothesis of migratory contributions of skate populations in Georges Bank (Frisk *et al.*, 2008), it will also be important to have a more clear understanding of batoid range shifts (Hoxie, personal communication) and migration patterns to anticipate changes in interspecific competition. Though this study has begun to fill in the gaps in multispecies batoid elasmobranch trophic ecology, it has also emphasized the importance of similar studies from other large estuarine ecosystems in order to fully understand the ecological interactions and potential impacts of batoids on the benthic community.

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Table 1: Prey categories used to calculate trophic levels of little skate, *Leucoraja erinacea* in Narragansett Bay 2009-2010. Mean trophic levels used were from Pauly and Christensen (1995), Pauly *et al.* (1998b), Cortes (1999), and Ebert and Bizzarro (2007).

Group Code	Description	Trophic Level
MOLL	Bivalves, Gastropods and other molluscs excluding Cepahlopods	2.1
KRILL	Euphausid and mysids	2.25
CRUST	Decapod and other crustaceans	2.52
POLY	Polychaetes and other marine worms	2.6
FISH	Misc. marine fish	2.8
FLAT	Pleuronectids	2.9
AMPH	Amphipods and isopods	3.18
CEPH	Squid	3.2
CLUP	Small schooling fish like anchovies and herring	3.2
GAD	Cod, hake, and haddock	3.8

Table 2: The %PSIRI of prey types in the diet of batoids collected from Narragansett Bay, RI between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), and *Raja eglanteria* (Re); each separated by available size class.

Prey Species	DcADU	LeYOY	LeJUV	LeADU	LoYOY	LoJUV	ReADU
Amphipod	0.0%	57.4%	46.8%	59.5%	3.7%	6.0%	0.0%
Benthic Crustacean	0.0%	0.9%	10.3%	4.3%	0.3%	0.0%	0.0%
Bivalve	0.0%	3.2%	10.0%	7.2%	0.0%	0.9%	0.0%
Cephalopod	0.0%	0.0%	1.1%	0.0%	0.0%	2.2%	66.7%
Epibenthic Crustaceans	0.0%	18.4%	17.8%	19.7%	93.2%	23.1%	0.0%
Epibenthic Fish	75.0%	2.9%	1.8%	0.2%	0.0%	34.6%	0.0%
Flatfish	0.0%	0.0%	0.1%	0.0%	2.2%	0.0%	0.0%
Gastropod	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
Krill	0.0%	0.6%	0.1%	0.0%	0.3%	1.0%	0.0%
Large Schooling Fish	0.0%	0.0%	0.4%	0.9%	0.0%	2.5%	0.0%
Misc. Teleost	0.0%	0.0%	0.8%	0.6%	0.0%	0.0%	0.0%
Other Prey	25.0%	0.0%	1.6%	0.0%	0.0%	3.6%	0.0%
Paguridae	0.0%	0.0%	4.8%	7.5%	0.0%	0.0%	0.0%
Polychaete	0.0%	0.0%	3.0%	0.0%	0.4%	7.7%	0.0%
Portunidae	0.0%	0.0%	1.1%	0.0%	0.0%	0.0%	0.0%
Small Schooling Fish	0.0%	0.0%	0.0%	0.0%	0.0%	18.4%	33.3%

Table 3: Dietary overlap indices for batoid elasmobranch species in Narragansett Bay collected March 2009- December 2010. Values range from 0 to 1, with 0 indicating absolutely no overlap and 1 meaning total overlap.

RI Schoener Index, S_{do}				
	Dc	Le	Lo	Re
Dc	****	0.04	0.17	0.00
Le	****	****	0.31	0.01
Lo	****	****	****	0.05
Re	****	****	****	****

RI Simplified Morisita, C_h				
	Dc	Le	Lo	Re
Dc	****	0.04	0.18	0.00
Le	****	****	0.38	0.01
Lo	****	****	****	0.03
Re	****	****	****	****

Table 4: The %PSIRI of prey types in the diets of batoids collected from Delaware Bay between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Dasyatis say* (Ds), *Gymnura altavela* (Ga), *Myliobatis freminvillii* (Mf), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), *Raja eglanteria* (Re), and *Rhinoptera bonasus* (Rb); each separated by available size class.

Prey Species	DcYOY	DcJUV	DsYOY	DsJUV	DsADU	GaYOY	GaJUV	LeYOY	LeJUV	LoYOY	MfYOY	MfJUV	MfADU	RbYOY	RbADU	ReYOY	ReJUV	ReADU
Amphipod	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	48.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.1%	0.0%	0.0%	1.0%
Benthic Crustacean	53.8%	78.7%	0.0%	8.0%	0.0%	0.0%	0.0%	0.0%	7.4%	0.0%	0.0%	0.0%	0.0%	7.6%	1.2%	0.0%	3.5%	2.4%
Bivalve	0.0%	5.7%	71.2%	43.2%	50.2%	0.0%	0.0%	0.0%	17.0%	36.7%	11.0%	36.1%	4.4%	0.0%	50.0%	0.2%	12.4%	8.0%
Cephalopod	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.5%	0.0%
Epibenthic Crustaceans	26.6%	12.7%	0.0%	18.6%	0.0%	0.0%	0.0%	48.6%	50.6%	60.7%	2.5%	0.9%	0.0%	0.0%	1.3%	45.0%	36.9%	41.7%
Epibenthic Fish	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	5.7%	5.6%	16.0%
Flatfish	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	10.6%
Gastropod	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	25.3%	33.3%	75.1%	92.4%	0.2%	0.0%	0.0%	0.2%
Isopod	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	12.8%	0.0%	0.0%	0.0%
Krill	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	24.9%	28.3%	22.4%	2.8%
Large Schooling Fish	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.7%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Misc. Crustacean	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Misc. Teleost	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	2.0%
Other Prey	3.7%	2.9%	0.0%	0.0%	13.0%	0.0%	0.0%	0.0%	0.9%	0.0%	0.0%	0.0%	0.0%	0.0%	8.5%	0.3%	1.1%	1.7%
Paguridae	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	16.8%	0.0%	29.7%	8.8%	20.4%	0.0%	0.0%	0.4%	3.9%	2.0%
Polychaete	28.4%	0.0%	28.8%	30.2%	33.3%	0.0%	0.0%	0.0%	3.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	10.0%	6.6%	7.6%
Portunidae	0.0%	0.0%	0.0%	0.0%	3.5%	0.0%	0.0%	2.8%	1.0%	0.0%	2.9%	0.3%	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%
Small Schooling Fish	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	100.0%	0.0%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	3.6%	0.7%
Unknown 001	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	28.6%	20.5%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%

Table 5: Dietary overlap indices for batoid elasmobranch species in Narragansett Bay collected March 2009- December 2010. Values range from 0 to 1, with 0 indicating absolutely no overlap and 1 meaning total overlap.

DE Schoener Index								
	Dc	Ds	Ga	Le	Lo	Mf	Rb	Re
Dc	****	0.38	0.00	0.45	0.36	0.04	0.09	0.40
Ds	****	****	0.00	0.36	0.38	0.19	0.38	0.23
Ga	****	****	****	0.00	0.00	0.00	0.00	0.00
Le	****	****	****	****	0.73	0.30	0.25	0.60
Lo	****	****	****	****	****	0.18	0.28	0.54
Mf	****	****	****	****	****	****	0.46	0.11
Rb	****	****	****	****	****	****	****	0.30
Re	****	****	****	****	****	****	****	****

DE Simplified Morisita								
	Dc	Ds	Ga	Le	Lo	Mf	Rb	Re
Dc	****	0.36	0.00	0.64	0.54	0.03	0.10	0.54
Ds	****	****	0.00	0.42	0.45	0.28	0.52	0.26
Ga	****	****	****	0.00	0.00	0.00	0.00	0.00
Le	****	****	****	****	0.95	0.21	0.20	0.86
Lo	****	****	****	****	****	0.14	0.23	0.80
Mf	****	****	****	****	****	****	0.58	0.09
Rb	****	****	****	****	****	****	****	0.31
Re	****	****	****	****	****	****	****	****

Table 6: The %PSIRI of prey types in the diets of batoids collected from Narragansett (RI) and Delaware (DE) Bays between March 2009-December 2010. Species include *Dasyatis centroura* (Dc), *Dasyatis say* (Ds), *Gymnura altavela* (Ga), *Myliobatis freminvillii* (Mf), *Leucoraja erinacea* (Le), *Leucoraja ocellata* (Lo), *Raja eglanteria* (Re), and *Rhinoptera bonasus* (Rb); species separated by bay.

Prey Species	Dc, DE	Ds, DE	Ga, DE	Le, DE	Lo, DE	Mf, DE	Rb, DE	Re, DE	Dc, RI	Le, RI	Lo, RI	Re,RI
Amphipod	0.0%	0.0%	0.0%	3.3%	0.0%	0.0%	0.7%	0.4%	0.0%	47.8%	4.7%	0.0%
Benthic Crustacean	55.8%	3.6%	0.0%	6.9%	0.0%	0.0%	3.3%	2.2%	0.0%	9.5%	0.1%	0.0%
Bivalve	1.4%	51.8%	0.0%	16.5%	36.7%	19.1%	33.3%	7.6%	0.0%	9.5%	0.4%	0.0%
Cephalopod	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%	1.1%	0.9%	66.7%
Epibenthic Crustaceans	21.7%	8.3%	0.0%	50.1%	60.7%	0.9%	0.9%	41.9%	0.0%	17.9%	56.1%	0.0%
Epibenthic Fish	0.0%	0.0%	0.0%	0.3%	0.0%	0.0%	0.0%	11.5%	75.0%	1.8%	14.4%	0.0%
Flatfish	0.0%	0.0%	0.0%	0.1%	2.6%	0.0%	0.0%	5.1%	0.0%	0.1%	0.7%	0.0%
Gastropod	0.0%	0.0%	0.0%	0.1%	0.0%	37.1%	30.9%	0.1%	0.0%	0.1%	0.0%	0.0%
Isopod	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%	8.5%	0.0%	0.0%	0.1%	0.0%	0.0%
Krill	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	16.6%	13.7%	0.0%	0.1%	0.6%	0.0%
Large Schooling Fish	0.0%	0.0%	0.0%	1.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.4%	1.0%	0.0%
Misc. Crustacean	0.0%	0.0%	0.0%	0.0%	0.0%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Misc. Teleost	0.0%	0.0%	0.0%	0.2%	0.0%	0.0%	0.0%	1.5%	0.0%	0.2%	0.0%	0.0%
Other Prey	2.9%	4.3%	0.0%	0.8%	0.0%	0.0%	5.7%	1.4%	25.0%	1.8%	2.2%	0.0%
Paguridae	0.0%	0.0%	0.0%	14.8%	0.0%	21.8%	0.0%	2.2%	0.0%	0.8%	0.0%	0.0%
Polychaete	18.1%	30.9%	0.0%	3.5%	0.0%	0.0%	0.0%	7.6%	0.0%	6.9%	6.0%	0.0%
Portunidae	0.0%	1.2%	0.0%	1.4%	0.0%	1.3%	0.0%	0.0%	0.0%	1.1%	0.0%	0.0%
Small Schooling Fish	0.0%	0.0%	100.0%	0.3%	0.0%	0.0%	0.0%	1.4%	0.0%	0.9%	12.9%	33.3%
Unknown 001	0.0%	0.0%	0.0%	0.0%	0.0%	19.5%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%

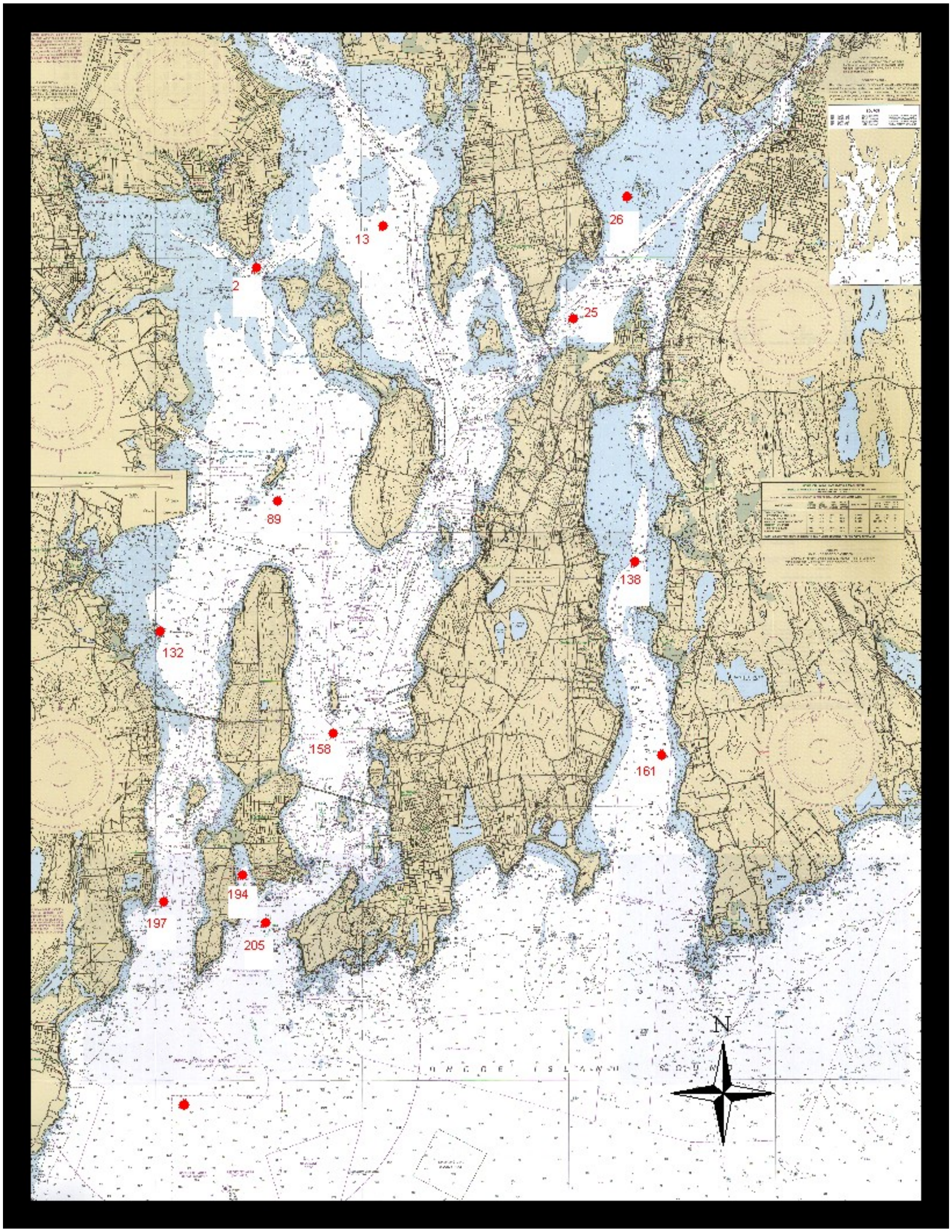


Figure 1: Stations sampled in Narragansett Bay during the 2009-2010 RIDEM otter trawl monthly finfish survey. Numbers indicate assigned station numbers. The red star indicates the station where *Leucoraja erinacea* were caught by rod and reel (#99). Approximate depth range in meters for each station is as follows: 1 = 6-9 m, 2 = 9-21 m, 13 = 9-21 m, 25 = 9-21 m, 26 = 3-6 m, 89 = 6-9 m, 132 = 12-15 m, 138 = 9-18 m, 158 = 21-34 m, 161 = 6-9 m, 194 = 6-12 m, 197 = 9-15 m, and 205 = 27-37 m.

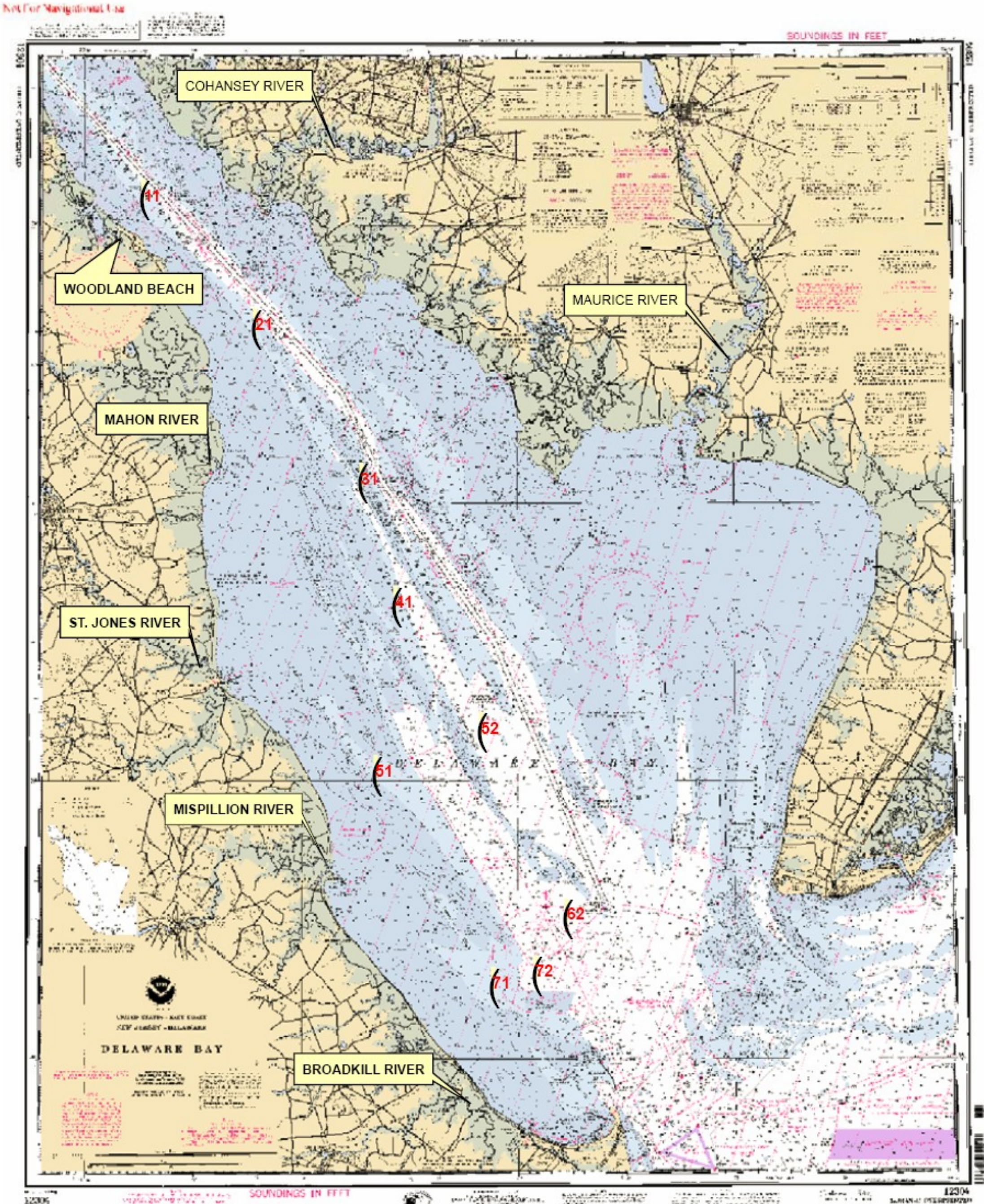


Figure 2: Stations sampled in Delaware Bay during the 2009-2010 DNREC otter trawl monthly finfish survey. Numbers indicate assigned station numbers. Average depths in meters for those stations are as follows: 41=8.1 m, 51=8.6 m, 52=13.6 m, 62=13.9 m, 71=8.4 m, and 72=17.7 m; map adapted from Michels & Greco (2008) with permission from authors.

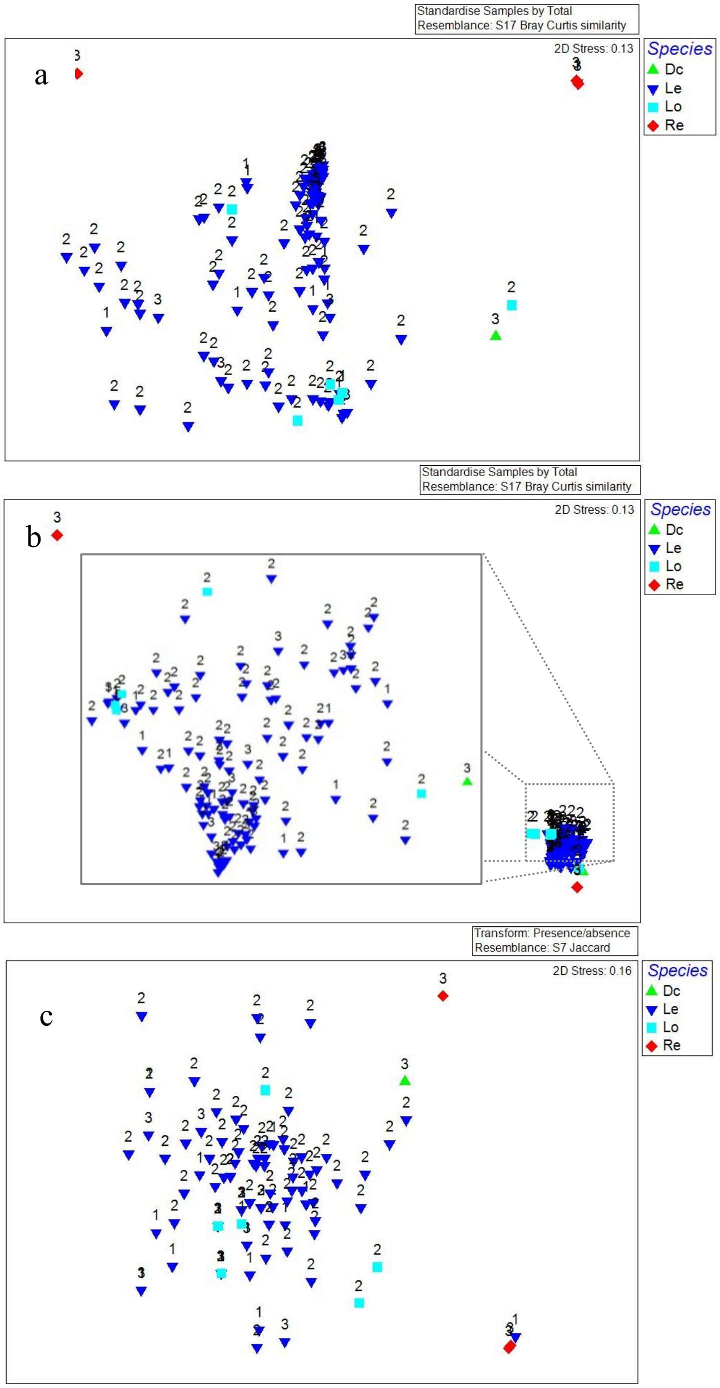


Figure 3: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Narragansett Bay, RI. Prey groups (see Szczepanski ms 3 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. To more closely examine the relationship of the dense cluster of points in the nMDS of %W (denoted by the dashed box), an nMDS subset was configured and superimposed. Symbols represent species abbreviations and numbers represent size classes (1=YOY, 2=JUV, and 3=ADU).

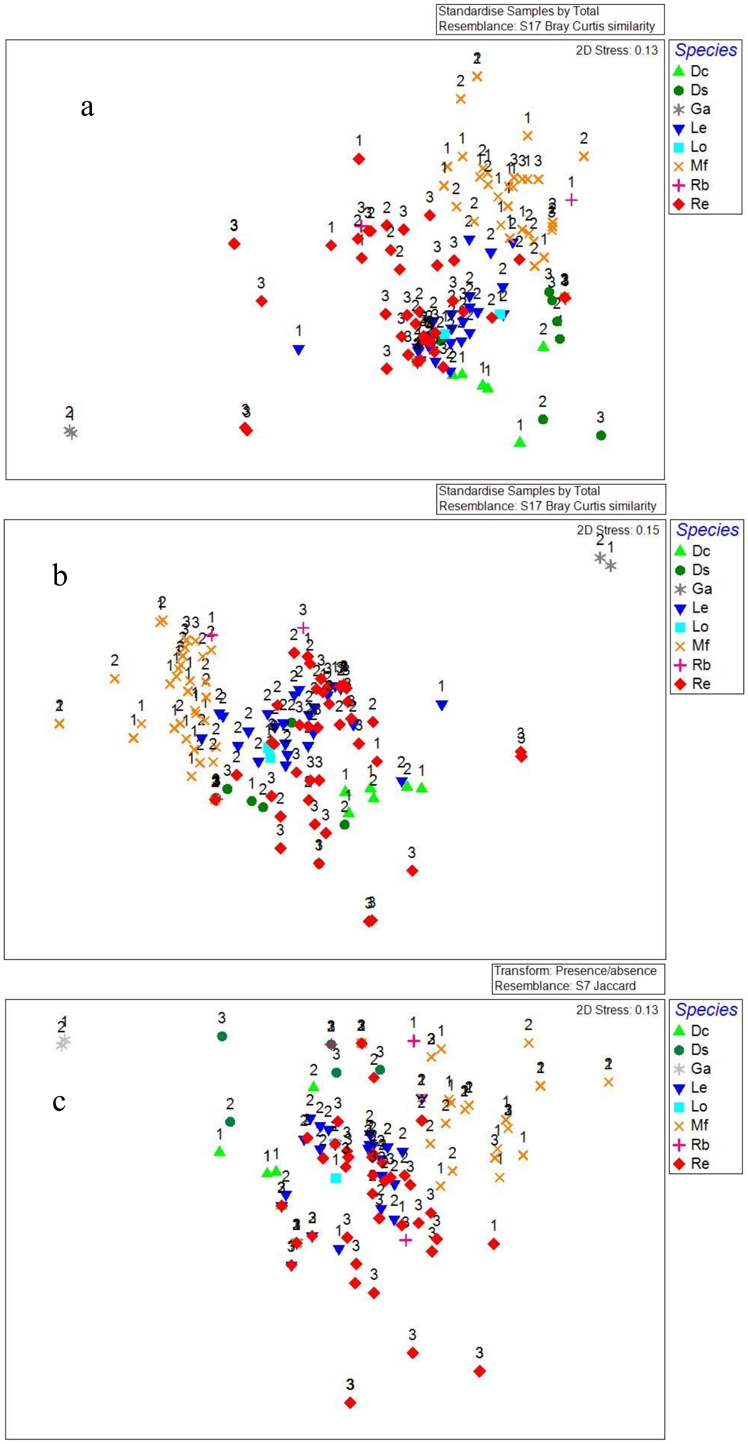


Figure 4: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Delaware Bay, DE. Prey groups (see Szczepanski ms1 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. Symbols represent species abbreviations and numbers represent size classes (1=YOY, 2=JUV, and 3=ADU).

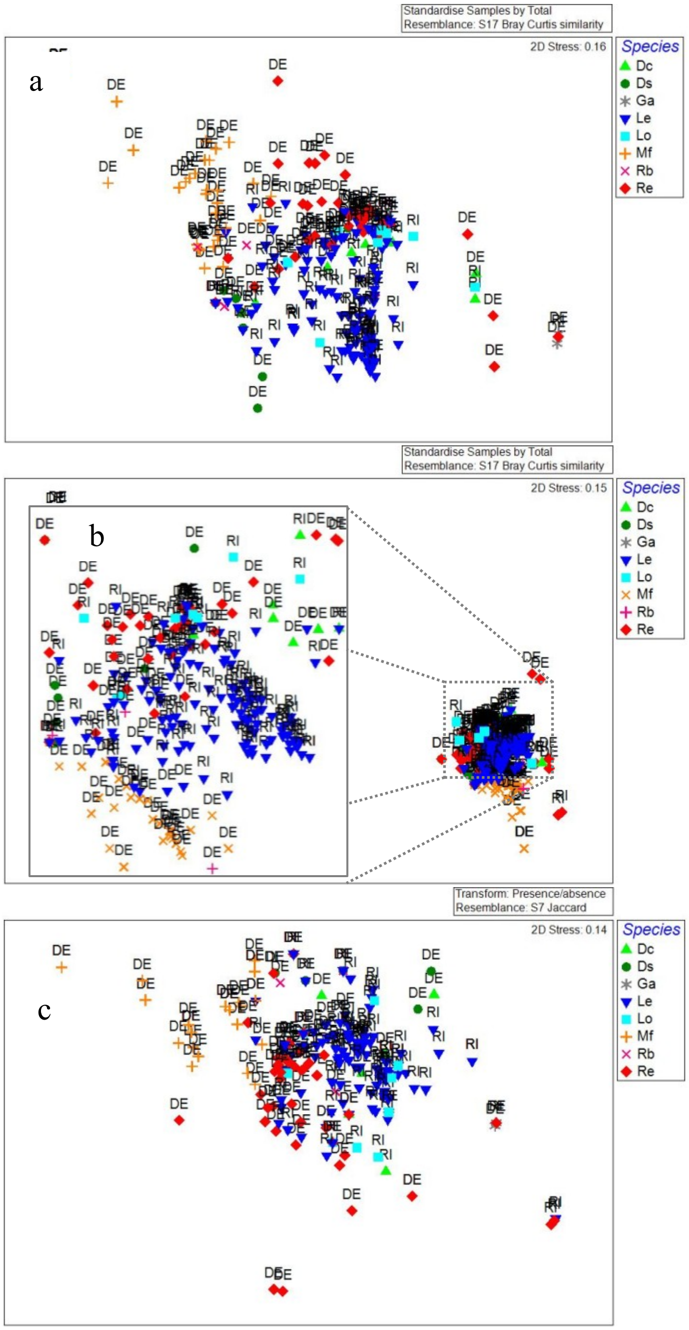


Figure 5: Non-metric multidimensional scaling plots for stomach contents from separate batoid elasmobranch species collected March 2009-December 2010 in Narragansett Bay (RI) and Delaware Bay (DE). Prey groups (see Szczepanski ms.1 for 'Prey Categories') analyzed for proportion of diet within size class by a) prey number, %N, b)wet weight,%W, and c)frequency of occurrence, %FO. To more closely examine the relationship of the dense cluster of points in the nMDS of %W (denoted by the dashed box), an nMDS subset was configured and superimposed. Symbols represent species abbreviations and labels denote geoghraphic location.

CONCLUSION

My research has revealed some vital information about batoid elasmobranch feeding ecology. I have been able to more fully characterize the diets of not only the bullnose ray species, but also the diet of young-of-the-year. Though more clear and detailed abundance and movement data would be required to classify Delaware Bay as a nursery area for these batoids, the patterns of abundance during collection of these samples indicate that it is an important habitat for very young rays. The clearnose skate is another prevalent species in Delaware Bay and was discovered to have different diets between males and females, a phenomenon previously not recorded. Little skates in Narragansett Bay showed differences in diet by site and by month, two factors that are known to also affect prey abundance elsewhere. Since the differences in diet correspond with known abundances of prey for either site or month, I suspect that they feed based on availability. That has been suggested for other regions, and little skates are generalists with a very broad diet. It does not seem unreasonable for this to be the case; however, no concurrent data on all prey abundances were available or able to be collected in order to confirm this hypothesis.

As a whole community, each estuary exhibited a different collection of batoid diets. Narragansett Bay had fewer species than Delaware Bay, with seemingly less specialization and no ontogenetic differences in diet. Delaware Bay had more species with a broader range of feeding strategies (determined from my data and literature); the species here also exhibited different diets by size class. I suspect that a higher degree of interspecific competition influences resource partitioning not just between species but also within species. This is speculative since it is not known if the resources were truly limiting. Differences were expected between diets of batoids from different bays; however, diets of fish varied as much within an estuary as between them. Since prey species were consolidated for comparison, taxonomic resolution decreased; benthic organisms will only be able to eat certain types of prey that can be readily accessed from or near the bottom. On the whole, this study has filled in gaps in batoid feeding ecology and has illuminated areas that need more study. More data for more species are needed, as is corresponding prey abundance data (benthic organisms as well as that of many fish).

An area that could benefit and supplement trophic ecology would be migration studies. Many batoids in Delaware Bay exhibit seasonal movements and understanding where they go or where they come from could give insight into what role they play in the ecosystem, as transient contributions to prey removal or a consistent ones. As climate change becomes more evident and experienced in various ways, knowing if and how batoid ranges may shift would be useful in managing their stocks or their prey.

APPENDIX A

"The 62-foot (19-m) deep-'V' semi-displacement hulled research vessel, "First State", is equipped with an 'A'-frame stern trawling rig. Tow durations in the present survey were 20 minutes. Tows less than 20-minutes were rarely made (due to gear conflicts, etc.); however, in such cases, a 10- minute minimum tow time was required for the tow to be considered valid. Expansion of CPUE (Catch-per-unit- effort) calculations was not necessary for the purposes of this report, since the unit effort was expressed as distance towed. Sampling was conducted from March through December.

The net used in the survey consisted of 3-inch (7.6-cm) stretch mesh in the wings and body, and 2-inch (5.1-cm) stretch mesh in the cod end. The trawl had a 30-foot 6-inch (9.3-m) x 1/2-inch (1.2-cm) headrope and a 39-foot 6-inch (12.0-m) x 1/2-inch footrope with 40-foot (12.2-m) leglines. The 54-inch x 28-inch (1.37-m x 0.71-m) doors were constructed of ¾-inch (1.9-cm) virgin pine lumber, bolted to a 2 inch x 4 inch (5.1cm x 10.2cm) strong back. The doors had a 2-inch x ¾-inch (5.1-cm x 1.9-cm) milled steel bottom shoe runner and ¼-inch (0.64-cm) galvanized chain bridles attached to ½-inch (1.3-cm) galvanized swivels at the head. The lack of towable bottom required a fixed sampling scheme. Station locations from the previous surveys were used (Figure 1-1). There was some randomization in the selection of tow starting sites within each quadrant due to weather, currents and inaccuracy inherent with electronic positioning equipment. Station 51 was permanently relocated in 1998 to approximately 0.5 NM south of the original station location due to repeated gear fouling on a fixed obstruction.

A global positioning system (GPS) was used to determine exact vessel position at the start and conclusion of each tow. Odometer readings from the GPS unit were used to determine distance towed (nautical miles). Mean water depth was determined from fathometer readings taken at five minute intervals including the start and finish points of each tow. A line-out to depth ratio of 6:1 was maintained.

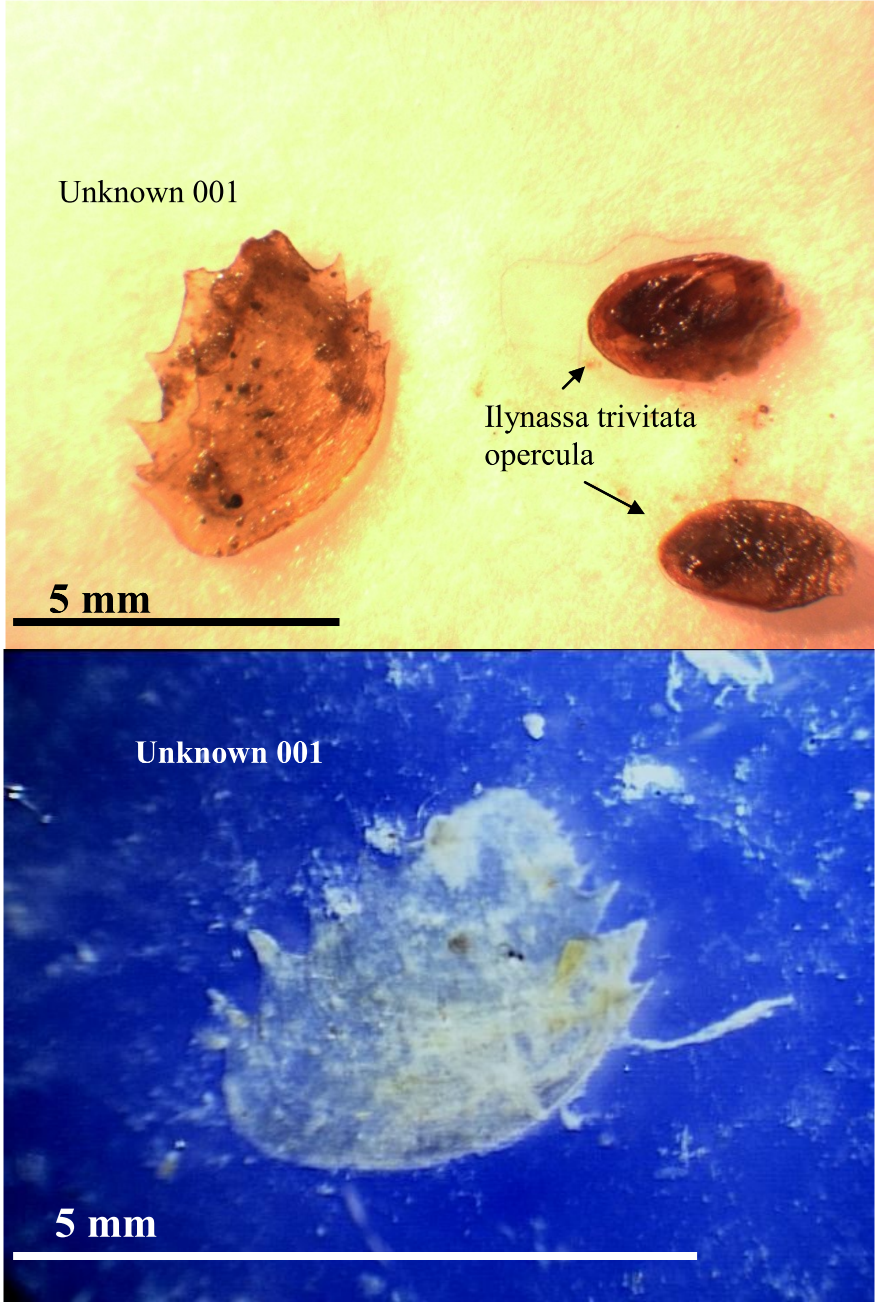
A Yellow Springs Instrument Co. Model 85 oxygen, conductivity, salinity and temperature meter was used to measure surface and bottom temperature (°C), dissolved oxygen (ppm) and salinity (ppt) at the conclusion of each tow. Upon completion of each tow, the sample was emptied on the deck and sorted by species. Aggregate weights were taken for each species. Species represented by less than 50 individuals were measured for fork length to the nearest half-centimeter.

Species with more than fifty individuals were randomly sub-sampled (50 measurements) for length with the remainder being enumerated. Horseshoe crabs (*Limulus polyphemus*) were sexed and measured for prosomal width. Blue crabs (*Callinectes sapidus*) were sexed and measured for carapace width. Certain elasmobranchs were not measured due to difficulty in handling"

Excerpt from:

Michels S.F. and M.J. Greco. (2008). *Coastal Finfish Assessment Survey. Project: F-42-R-1.* Delaware: Dept. Natural Resource and Environmental Control Apr.1, 2007-Mar. 31, 2008.

APPENDIX B



Appendix B: Reference photos of unidentifiable “Unknown 001”. Scale bars represent 5 mm, images recorded using a dissecting microscope using a) direct illumination and b) phase contrast illumination.

APPENDIX C

“5.3.1Coastal Fishery Resource Assessment Trawl Survey

The year 2007 marked the twenty-ninth year of RIDFW's seasonal trawl survey. The survey was initiated in 1979 to monitor recreationally important finfish stocks in Narragansett Bay, Rhode Island Sound, and Block Island Sound. The survey employs a stratified random design and records aggregate weight by species, frequency, individual length measurements, and various physical data. In 1990, a monthly component was added to the survey, which includes 13 fixed stations in Narragansett Bay. Together, both components of the survey aim to monitor trends in abundance and distribution, to determine population size/age composition, and to evaluate the biology and ecology of estuarine and marine finfish and invertebrate species occurring in RI waters. Over the years this survey has become an important component of fisheries resource assessment and management at the state and regional levels.

In 2005, the Division replaced the research vessel and survey gear that has been utilized by the survey since its inception. The R/V Thomas J. Wright was replaced with a 50’ research vessel, the R/V John H. Chafee. During the spring and summer of 2005, a series of paired tow trials were conducted using modern acoustic equipment and new nets designed to match the trawl net used by the National Marine Fisheries Service. The results of this experiment were used to calibrate the old and new vessels in order to maintain the continuity of the survey time series. Unfortunately, the new net design was too large for the new research vessel and could not be successfully towed in many of the areas required by the trawl survey. Because of this a new net was designed in the same dimensions as the net previously used for the survey and is used for the trawl survey. By using a similar net design to the previous survey net, the continuity of the survey is able to be maintained.”

Excerpt from:

Rhode Island Dept. of Environmental Management. (2008). *Rhode Island Marine Fisheries Stock Status and Management.* Jamestown: RI DEM, Div. of Fish and Wildlife. Print.

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