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DETERMINING ENVIRONMENTAL DRIVERS OF FISH COMMUNITY STRUCTURE ALONG THE COAST OF MAINE

By

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A THESIS

Submitted in Partial Fulfillment of the

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Thesis Co-Advisors: Dr. Yong Chen
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An Abstract of the Thesis Presented
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The work presented here was conceived to determine whether structure in marine communities could be related to multiple scaled environmental parameters, as seen in lake and stream systems. Four datasets collected from 2001 to 2005 were used. The datasets ranged from local scale tidepool and estuarine surveys, to more regional intertidal/subtidal surveys and conclude using a coast-wide trawl survey. Initially, a bootstrap program for running principal component analysis (PCA) was developed and tested for utility with additional information from Pearson correlation coefficients. The bootstrap-PCA program was capable of determining confidence limits for correlations amongst species. The results from analysis of the survey data suggest that factors influencing tidepool species assemblages were embedded in patterns of vertical zonation horizontal gradients in sediment type (wave energy). Patterns became more structured from spring to late summer and associations amongst tidepool variables shifted from physical-algal associations to invertebrate-fish associations. The analysis of an estuarine dataset suggested estuarine assemblages reflect an interaction between topography and the location of culverts as restrictions to tidal flow, and the resulting differences in the impoundment of water. Patterns of fish assemblages, in a regional survey sampling the intertidal/subtidal zone, was structured and related to potential wave energy at two scales. The first scale was local potential wave energy which related a specific site and the morphology/behavior of species capable of occupying the space. The second scale was regional and related to patterns of immigration and extinction mediated by energy acting as a barrier to certain species. When a coast-wide trawl survey was analyzed, structure in fish populations along the coast correlated to oceanographic differences observed between eastern and western Maine. Temperature, longitude and their interaction were related to patterns in biological structure in the survey data. When seen as a whole, the results demonstrate that structure is present in the distribution of species at all scales. Fisheries management initiatives would do well to understand the scales that are relevant to their mandate.

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This is my second go at acknowledging everyone who impacted my life during the completion of a thesis. This does not guarantee it will be shorter.

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My committee of Yong Chen, David Townsend, James McCleave, Cynthia Loftin and Michele Dionne. I am very pleased with how my committee put me first, and always helped. Yong and Dave were excellent 51% and 49% advisors, respectively. I could not have asked for more supportive and encouraging advisors who at least appeared to trust my judgment. Jim, thank you for the Conover papers during the comprehensives and really a great set of readings. I actually liked all my comprehensive readings, but the behavioral ecology with life history theory and evolution is right up my alley. Cyndy, thanks for spending a lot of time on my thesis… I appreciate it more than I can write here and I know it is not glamorous but I needed it. Michele, thanks for calming my nerves at critical times, I really needed that as well.

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CHAPTER 1

INTRODUCTION

1.1. Project Introduction

The objective of this study is to determine spatial correlations in the abundance of fish and invertebrates, and relate any patterns to physical processes that act as constraints. Survey data from several Maine coastal and nearshore habitats are used to develop statistical techniques for defining organization in ecological systems. Initially, the distribution of tidepool and estuarine fish are discussed in order to develop a foundation from which hypotheses and predictions regarding the organization of fish and invertebrate assemblages can be based (Chapter 2). Then two methods are employed in analyzing the data and determining species correlations and physical constraints. The first tests hypotheses concerning patterns of fish assemblages in relation to physical explanatory variables, or can the variation in fish assemblages be explained by environmental variable X (Chapter 4, 5, 6 and 7)? The second uses re-sampling to evaluate the analyses by developing confidence limits for identifying clusters of species and evaluating statistical significance (Chapters 3, 5, 6). Recommendations for management of fisheries along the coast of Maine and how the information relates to ecological processes are covered in Chapter 8.

The work presented is based on a series of studies, primarily in waters adjacent to Acadia National Park. The manuscript is organized according to scale with a more detailed look at species interactions at small scales to begin, progressing to questions about landscape (coast-wide) differences in the assemblages of fish. An assemblage is defined as a number of species whose abundances are positively correlated with one another and can be designated as a distinct group based on some habitat variable. The finer scale studies include abundance data from tidepools and estuaries. Both were collected in surveys in Frenchman's, Blue Hill and Penobscot Bays. Based on observations made in those studies, sampling of intertidal habitats adjacent to Acadia National Park was completed to determine whether simple physical metrics could be used to identify nearshore fish communities. Communities differ from assemblages in the assumption of interactions among constraining variables and organisms and among organisms are assumed or can be demonstrated. Finally, an inshore trawl survey, collected by the Maine Department of Marine Resources, was analyzed to determine whether fish assemblages can be identified and related to persistent oceanographic features present along the Maine coast.

1.2. Motivation

This project was developed in attempting to enhance knowledge of ecological processes and offer practical management applications. The study is a first step in bridging community ecology and management along the nearshore: determining the structure of, and forcing agents on, assemblages of fish and invertebrates. The failure of many fisheries around the world has shown that traditional single species based fisheries management needs to be changed and that community ecology must be explicitly considered in fisheries management (Frissell & Bayles 1996, Lauck et al. 1998, Mangel and Levin 2005, Pauly et al. 2002). Understanding of ecological processes, and the resulting application to fisheries management, has been constrained by paradigms in ecology (Mangel and Levin 2005, O'Neill 2001, Wu and Loucks 1995). The paradigms change over time, leading to rapid reform of prevailing theories and research directions. The failure of fisheries management and the present-day desire for ecosystem-based management are embedded in the paradigm shifts that mark the past century, and it is therefore important to briefly review the progression of ecology and fisheries to the present day.

1.2.1 Equilibrium Generated Paradigm

Western philosophies, rooted in the belief of divine providence and order, have long embraced the concept of "the balance of nature" (Wu and Loucks 1995). This requires assumptions of stability and equilibria across scales, with destructive and conservative forces antagonistically maintaining the balance (Wu and Loucks 1995). Odum (1969) explains the importance of ecological succession in the management of the human-nature relationship. He describes ecosystem processes (1) as orderly, directional and predictable, (2) with succession that is community-controlled (species-species interactions), although patterns are structured by physical processes (perturbations in particular), and (3) that culminate in a stable "climax" state, with high diversity. At the climax of succession, the net ecosystem production is 0 and internal biological feedbacks among the large numbers of species maintain equilibrium. Species fall on a gradient of r-selected (fast growth) to K-selected (slow growth), inhabiting early colonization and climax communities, respectively (Odum 1964, MacArthur and Wilson 1967). The primary sources of control are top-down (Hairston et al. 1960), where predators control the abundance and distributions of prey, and bottom-up (Lindeman 1942), where the production at lower trophic levels limits the production at higher trophic levels. From these tenants, the argument is made that by controlling key factors in the environment, and taking advantage of perturbations, one can gain maximum benefits and efficiency from the system.

The equilibrium concept has trickled into most disciplines of biology. The model of diversity (see Hubbell 2001) suggests that at equilibrium there is neutral evolution, such that the number of extinctions and mutations giving rise to new species are balanced (Turner and Hawkins 2004). MacArthur and Wilson (1967) suggested that islands reach an equilibrium state based on the distance from source populations and the size of the island. As time has passed, these theories have proven to be heuristically useful, but empirically incorrect (see Conner et al. 2000).

1.2.2. Panarchy, Complexity and Ecosystem Paradigms

Gunderson and Holling (2002) define an ecosystem as biotic and abiotic components that lead to dynamic process and structure that mutually reinforce one-another through feedbacks. Panarchy, the name given to their concept, argues that ecosystems are complex systems driven by slow and fast moving variables. Fast variables are where the focus of management usually lies while slow variables are often overlooked, and the interaction between the two is poorly understood. Interaction between slow and fast moving variables is critical in producing pattern, while variation is also an essential component. Change and unpredictability are inherent properties of complex systems; and change in such systems is described through adaptive cycles of construction and creative destruction (Gunderson and Holling 2002), which are essentially the older view of succession and climax with a new loop allowing for the deconstruction of the system and reinitiation of successional stages. The theory predicts change to be episodic, with periods of slow accumulation followed by rapid change. The cycle is placed within three variables: (1) potential, which determines possible options; (2) connectedness, which demonstrates internal control, and; (3) resilience, which indicates the vulnerability of the system to disturbance or how much perturbation is required to cause rapid change. One can imagine that in early succession connectedness and resilience would be low, and potential high. Still, small sets (2-6 variables) are believed to be sufficient to capture key behavior in a system but operate at different scales and are connected as nested cycles. This results in non-linear causation, between physical processes and ecosystem structure, and multi-stable state behavior, resilience that changes as slow variables change, biotic-structural feedbacks and spatial contagion that reorganizes over time.

Panarchy is not the only theory developed in the post-equilibrium period. Hierarchal patch dynamics explicitly includes non-equilibrial systems (Wu and Loucks 1995 and references therein). Relationship between pattern and process becomes paramount as local systems, embedded in a regional mosaic of patches, result in system dynamics (Wu and Loucks 1995). Identification of patches and tangible boundaries allow understanding of discrete, but interactive, components. Process rates become important as scale is considered such that higher level change (larger scale, more stable) can be considered constant and lower levels (small scale, ephemeral processes) operate so fast they can be averaged (Wu and Loucks 1995). The result is a dynamic mosaic of patches, each at different levels of succession, whose patterns and process are operating at different spatial and temporal scales (Wu and Loucks 1995).

Of course, this discussion would not be complete without including the ecosystem paradigm. Paradigms, by definition, are prior intellectual structure given to complex problems such that they may be distilled to research problems and solutions (O'Neill 2001, Wu and Loucks 1995). As such, the ecosystem concept itself can be viewed as a paradigm (O'Neill 2001). Ecosystems are collections of interacting populations with assumed feedback loops (strong interactions) within some boundary. Averaging of spatial and temporal heterogeneity occurs at every scale. Ecosystems still maintain stability as a property and disturbances are viewed as external forces. By considering ecosystems, often named for the dominant species (cod, coral reefs), managers will initiate a recovery if the system is viewed to have deviated from predetermined optimal conditions (O'Neill 2001). Under these assumptions, the role of subordinate species is ignored and objectivity regarding patterns and processes is lost (O'Neill 2001).

1.2.3. Fisheries, Paradigms and Failure

The equilibrium paradigm fed the ideas resulting in the "traditional stock assessment" where a population of fish is in theory maintained at some stock size that will return a maximum number of new recruits per spawner. The "bloom stage" could be achieved by applying disturbance (fishing pressure) that maintains an intermediate biomass of the population, and the system would respond with higher total community respiration and net production. Past failure lay in lacking incorporation of scale and heterogeneity (Wu and Loucks 1995). Worse, the inability to recognize the roles of uncertainty and uncontrollability in biological systems (Lauck et al. 1988) resulted in unrealistic expectations for management. Although risk is now often incorporated into stock assessments and ecosystem models have begun to be applied to fisheries, interactions among species and issues involving scale are still often inadequately addressed by averaging estimates of natural mortality, trophic levels, respiration, and other important properties of ecosystems. Lauck et al. (1998) argue that by focusing on populations of a single species, the risk of overexploitation cannot be effectively mitigated.

It has been recognized that changes to variables that constrain ecosystem structure occur across scales. Physical variables (sea-level change, temperature, salinity, fishing pressure to name a few) can each change, and the resulting cumulative impacts can precipitate unpredictable shifts in population demographics because of multi-scale interactions (Gunderson and Holling 2002). Gunderson and Holling (2002) attribute past management failures to governing institutions becoming rigid and economic sectors become dependent on the services extracted from an ecosystem, then ecosystem constraining variables change enough to induce rapid change (collapse) leaving the public without faith in the institutions erected to manage the resources. Further, the need for ecosystem complexity to be distilled to simple and understandable properties resulted in disciplinary hubris (Gunderson and Holling 2002).

The result of a panarchial view of ecosystems is a belief in maintaining (1) resilience in ecosystems, (2) flexibility in institutions, and (3) incentives in economies to mediate human-nature interactions, as necessary management priorities (Gunderson and Holling 2002). Hierarchal patch dynamics places emphasis on considering ranges of spatial scales, environmental constraints, dispersal barriers and mechanisms for dispersal (O'Neill 2001, Wu and Loucks 1995). It is particularly important to focus on factors that influence dispersal, including barriers to dispersal, and how humans are influencing the patterns and process. The temporal and spatial coverage offered by management (surveys, etc.) must be scaled to the problem at hand. Interactions and feedbacks can stabilize populations with regards to local conditions (stability is more likely over shorter time scales); however regional heterogeneity is important and must be considered within the design.

Scientists involved in marine resources policy, management and conservation have offered a number of options to address the lack of scale consideration inherent in fisheries. These include ecosystem-based management, adaptive management and the use of marine protected areas, to name a few. Long-term datasets and the quality and quantity of the data are particularly relevant to questions of scale. Many datasets used for management only cover limited temporal and spatial scales. The 30-year trawl survey used for stock assessment by the National Marine Fisheries Service (NMFS) represents a small-scale when considering the time scale of human alteration in the Gulf of Maine (Lotze and Milewski 2004) and overall spatial coverage (Chen et al. 2006). In hindsight, it appears to be erroneous to use 30 years of data to understand populations of fish that reproduce at age 12, resulting in less than 3 generations of population information, and that interact with a large number of other species.

1.3. Conclusions and Project Goals

Placing emphasis on ecosystem-based management without, at minimum, understanding the spatial and temporal dynamics to be included is a risk-filled step. First, an understanding of patterns and process must be developed, the spatial organization and heterogeneity uncovered, and physical constraining forces elucidated. From this, management priorities should be incorporated to address the multi-scale attributes of ecological systems and their interactions with humans. The resulting tools will allow fisheries managers to incorporate appropriately defined marine protected areas, better understand interactions among species, and begin to form the basis for understanding the structure of marine systems required to shift away from reliance on maximum sustainable yield/single-species practices. The work presented in this thesis represents a first step in accomplishing this: identifying analyses that determine patterns and structure in biological communities, and identify statistically significant variables (species and environmental parameters) that drive ecological patterns.

1.4 Approaches to Analysis

A large part of this thesis will be the development and evaluation of techniques to identify key variables that drive patterns in fish assemblages along the Maine coast. The techniques will focus on identifying correlations amongst species and relating these correlations to environmental parameters (the constraints). Principal component analysis (PCA) is used throughout. PCA has a long tradition in ecology and is one of the oldest and most commonly used ordination techniques, and as a result has many years of study and application that have demonstrated its usefulness. With the development of a bootstrap program for PCA that allows for determining confidence limits and simulation of data without relying on distributional assumptions, the application can be tested for utility. The technique lends itself well to data collected from surveys, such as the NMFS trawl survey, and therefore can be used with existing datasets to identify relevant variables. Principal component loadings were used, with Pearson correlation coefficients, to identify groupings of species that are responsible for patterns in assemblage structure. New variables, generated by PCA, that represent the assemblage structure are tested for significance against environmental variables using general linear models. The results are used to determine boundaries, population discontinuities, and the physical constrains on assemblages of fish and invertebrates across a variety of scales along the coast of Maine.

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CHAPTER 2

SEASONAL USE OF THE INTERTIDAL ZONE BY FISH AND INVERTEBRATES IN WATERS ADJACENT TO ACADIA NATIONAL PARK: PATTERNS AND TRENDS IN SPECIES

2.1. Tidepools

2.1.1. Introduction

Tidepools may experience substantial human-induced disturbance when ease of access to the intertidal zone is increased. The National Park Service conservation goals include the expectation that natural habitats will be maintained, while allowing for public access. In order to make sound decisions regarding management along the coastal zone, it is important to determine what species inhabit the intertidal environment, how those species interact with one another and with the available habitats, and, eventually, what the consequences of change to the coast will have on these processes.

Fish entering the intertidal zone are more full on departure, than on arrival (Zander et al. 1999) suggesting that there is a net export of available food resources and, as a result, fish may be important vectors for the movement of energy from the intertidal zone into the oceanic ecosystem. Important stressors of the tidepool environment are temperature and salinity fluctuations, desiccation, low oxygen and wave activity (Horn et al. 1999). The dynamic nature of the tidepool habitat offers potential for unused food sources and for refuge from predators, however the species that are present must balance costs and benefits of food availability, physiological costs, and potential predation from both aquatic and terrestrial (including avian) sources.

Zander et al. (1999) notes the general characteristics of fish species expected in tidepools based on observations of tidepool fish from many habitats and coasts. These predictions are derived from the need for adaptation in the body plan and physiology of species attempting to survive what is considered a fairly stressful environment (Zander et al. 1999). Those species that are found in tidepools on a more permanent basis (resident species) are in contrast to species that move frequently and have more ephemeral use of the tidepool habitat (transient species). There is an expectation that there will be differences in the general body plan and ecology of the two classes of species (Zander et al. 1999). Resident species have some combination of reduced or absent swimbladder, small size (less than 30 cm length), dorso-ventrally compressed body form, dermal calcifications (for increased density and robustness), a clinging organ, and an ability to tolerate low oxygen. Transient species are expected to have a functional swimbladder, more classically compressed body morphology, and effective fins. It should be noted that the classification is based on species not individuals, whose distributions are likely more fluid than a species.

Since there are periods of time during the Maine winter that there are essentially no fish in tidepools (Moring 1990b), it could be said that there are no truly resident tidepool species. During the winter, most of the shoreline is ice covered or scoured and deeper distributions are the norm for intertidal species (Collette and Klein-MacPhee 2002). However, I consider resident and transient species within the context of the seasonal cycle. Resident species are those that occupy tidepools consistently over repeated sampling events, while transients are viewed as regular visitors to the intertidal zone that move from location to location and may be simply trapped in tidepools by ebbing tides. The ability for species to be transient or resident species is related to adaptations required for persistence within the tidepools, and the morphology of the species which dictates swimming and dispersal ability.

A 2001 survey of tidepools around Schoodic and Mount Desert Island on the coast on Maine is used to document the use of tidepool by transient and resident species within the seasonal cycle.

2.1.2 Material and Methods

The coast of Acadia National Park and Schoodic Peninsula is composed of granite platforms and outcrops with occasional large boulders and areas of muddy and sandy substrate. Tidepools are scattered around the island and peninsula in irregular depressions, ranging from centimeters to 10s of meter scale. Moring (1990b) documented that fishes are generally absent from tidepools from about November through April, except for the occasional presence of sculpins (*Myoxocephalus* spp.). Therefore, sampling in tidepools was limited to May through October, 2001. The study was broken into four sampling periods representing (1) late spring (June 6 - June 26); (2) early summer (July 3 - August 2); (3) late summer (August 3 - September 18); and (4) early fall (September 29 - October 21).

Fishes were sampled along the coast of Acadia National Park and Schoodic Peninsula (Figure 2.1). Each tidepool was visited once during each sampling period. There was also limited sampling of tidepools during the summer of 2002; however, the number of species captured did not increase and the results of that work will not be considered. Dates and times of sampling were based on tidal cycles, largely due to the large tides (~ 5m) experienced by waters adjacent to Acadia National Park. Some locations were accessible only during certain tides. Pools were not sampled at night because of safety concerns. Sampling trips were avoided during periods of heavy swells. The sampling window for tidepools exists for about 1.5 hours prior to low tide to 1.5 hours after low tide. Therefore, only one or two sampling locations could be inventoried on each appropriate low tide period.

Sampling was conducted in 39 tidepools. The survey was not stratified but did attempt to sample a diversity of locations and position in the intertidal zone. Two or three people with long handled dip nets and small hand nets thoroughly sampled tidepools. These techniques have been shown to be efficient and productive in previous investigations (Chenoweth 1973, Moring 1990a). Searchers stood on the side and/or in the tidepools while sampling. All moveable cover objects (i.e. rocks, algal growth) were removed to expose as much of the pool as possible without permanently damaging the area. No effects of sampling were noted in subsequent trips. Sampling continued until all fish encountered were captured and the census of species was considered to be a complete account of the fish species. To avoid stress for the fish during capture and handling, MS-222 (tricaine methanesulfonate) was used to anesthetize each captured fish. Handling time was kept to a minimum and each fish was identified, measured for total length, and promptly returned to the tidepool from which they were collected.

Physical variables (depth, surface area, bottom type) were collected once for each tidepool. All locations were recorded using a GPS unit. Data on the more temporary tidepool characteristics, salinity, temperature, the presence of invertebrates, and major types of vegetation were recorded during each sampling.

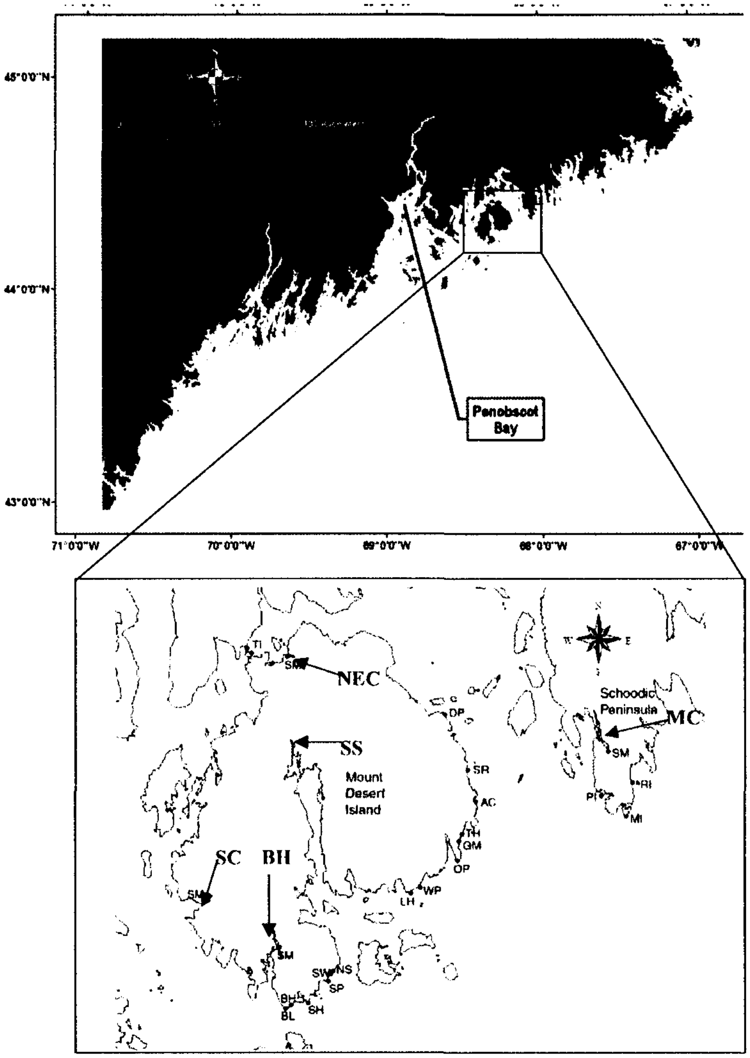


Figure 2.1. Map of sites used in tidepool and estuarine surveys. Circles demark tidepools and arrows demark estuaries. Tidepools: SM = salt marsh pannes. TI = Thompson Island, BL = Bass Harbor Lighthouse, BH = Bass Head, SH = Ship Harbor, SP = Seawall Picnic, SW = Seawall, NS = North Seawall, LH = Little Hunter's Beach, WP = Western Point, OP = Otter Point, GM = Gorham Mountain, TH = Thunder Hole, AC = Anemone Cave, SR = Schooner Rock, DP = Dorr Point, PI = Pond Island, MI = Moose Island, RI = Rolling Island. Estuaries: NEC = Northeast Creek, SS = Somes Sound, SC = Seal Cove, BH = Bass Harbor, MC = Mosquito Cove.

2.1.3. Results

All fish species caught are listed, with taxonomic information and the 4 letter abbreviations used in figures (Table 2.1). Also included is a list of body morphology and other general characteristics (Table 2.1). 628 individuals comprising 12 species of fish were caught over the 2001 season. Most fish were smaller than 5 – 6 cm, and the largest fish caught was a rock gunnel at 18 cm (Table 2.1). Fish caught displayed an array of body morphologies, including those associated with transient and resident species.

I found that 48% (n = 39), 53% (n = 38), 39% (n = 36) and 43% (n = 37) of tidepools contained fish for the four sampling periods, respectively. The average length and the total number of fish are inversely related (Figure 2.2). The average length dropped during the second sample period and increases through the last two. The decrease in average length is countered by an increase in the total numbers of fish captured (Figure 2.2). The increase in numbers and decrease in mean length during the second sample period is a result of the influx young-of-year (YOY = within first year) lumpfish (*Cyclopterus lumpus*; Figure 2.3). Lumpfish were caught in 32% (n = 38) of the tidepools during the second sample period suggesting a widespread occurrence, whereas 25% (n= 36) of tidepools contained lumpfish in the third sample period.

Stickleback YOY were concentrated in the TI sites, representing 5 – 6% of the total number of tidepools sampled, over the second and third sample periods with mean lengths (standard deviation) of 2.23 cm (0.38), 1.70 cm (0.50) and 1.43 cm (0.23) for fourspine, threespine and unidentifiable YOY, respectively. During the second sample period the TI sites contained 208 fourspine, 111 threespine and 2500 unidentifiable stickleback. YOY three, four and nine-spine stickleback (0.7 – 2.2 cm length) and mummichog were also documented to be abundant through the early summer in shallow estuarine mudflat pools and salt pannes.

Initially, the dominant species were pollock (*Pollachius virens*), rock gunnels (*Pholis gunnellus*) and lumpfish (Figure 2.3). Pollock numbers decreased quickly from the 40 individuals caught in the first sample period to 6 during the second and third sample periods and none were seen during the last sample period. Gunnel and sculpin numbers were relatively stable, even though their relative contribution to the catch declined for the second sample period. The total number of gunnels sampled was 30, 35, 37 and 36 for sample period 1, 2, 3 and 4, respectively. Shorthorn sculpin (*Myoxocephalus scorpius*) numbers were 14, 22, 38 and 25 for sample period 1, 2, 3 and 4, respectively. The grubby numbers were also relatively stable, but lower than the shorthorn sculpin at 4, 8, 1 and 6 for sample period 1, 2, 3 and 4, respectively.

The decrease in the relative contribution to the catch of the stable species resulted from the increased number of small lumpfish, and the increases in the third and fourth sample periods were related to the reduced lumpfish numbers (Figure 2.3). Atlantic sea snails (*Liparis atlanticus*) increased in numbers over the course of the season and were most abundant in the last sample period (Figure 2.3). The shorthorn sculpin also became relatively more numerous than the other species, largely due to the declining total number of fish captured. An occasional eel and a number of dead Atlantic silversides were also noted.

Table 2.1. List of species caught during the tidepool survey on Mount Desert Island and Schoodic Peninsula. Fish species listed by common and scientific name, with general taxonomic information and a description of distinctive characteristics included Abbrev = Abbreviation used in figures, T/R = transient/resident, P/B = pelagic/benthic, BF = body from (C = classic compressed, DV = dorso-ventrally flattened, A = anguiliform), ML = maximum length (present study = left column, Gulf of Maine = right column), AO = adhesive organ, SB = swim bladder, AB = air breathing, AF = antifreeze production.

Species	Abbrev	Scientific Name	Order	Family	TR	PB	BF	ML (cm)		AO	SB	AB	AF
Pollock	POVI	*Pollachius virens*	Gadiformes	Gadidae	T	P	C	8.2	105	N	Y	N	N/A
Mummichog	FUHE	*Fundulus heteroclitus*	Cyprinodontiformes	Fundulidae	T	B	C	5.4	10	N	Y	Y	N/A
Threespine stickleback	GAAC	*Gasterosteus aculeatus*	Gasterosteiformes	Gasterosteidae	T	B	C	6.9	8	N	Y	N	N/A
Fourspine stickleback	APQU	*Apeltes quadracus*	Gasterosteiformes	Gasterosteidae	T	B	C	5	6	N	Y	N	N/A
Longhorn sculpin	MYOC	*Myoxocephalus octodesemspinosus*	Scorpaeniformes	Cottidae	R	B	DV	8.9	35	N	Y	N	N/A
Shorthorn sculpin	MYSC	*Myoxocephalus scorpius*	Scorpaeniformes	Cottidae	R	B	DV	12.6	60	N	Y	N	Y
Grubby	MYAE	*Myoxocephalus aenaeus*	Scorpaeniformes	Cottidae	R	B	DV	14.0	20	N	Y	N	N/A
Sea raven	HEAM	*Hemitripterus americanus*	Scorpaeniformes	Hemitripteridae	T	B	DV	16.5	56	N	Y	N	N/A
Rock gunnel	PHGU	*Pholis gunnellus*	Perciformes	Pholidae	R	B	A	18.0	30	N	N	Y	N/A
Lumpfish	CYLU	*Cyclopterus lumpus*	Scorpaeniformes	Cyclopteridae	R	B	C	6.9	40	Y	Y	N	N/A
Atlantic sea snail	LIAT	*Liparus atlanticus*	Scorpaeniformes	Liparidae	R	B	A DV	10.0	13	Y	N	N	N/A
Winter flounder	PLAM	*Pseudopleuronectes americanus*	Pleuronectiformes	Pleuronectidae	T	B	DV	7.9	57	N	N	N	Y

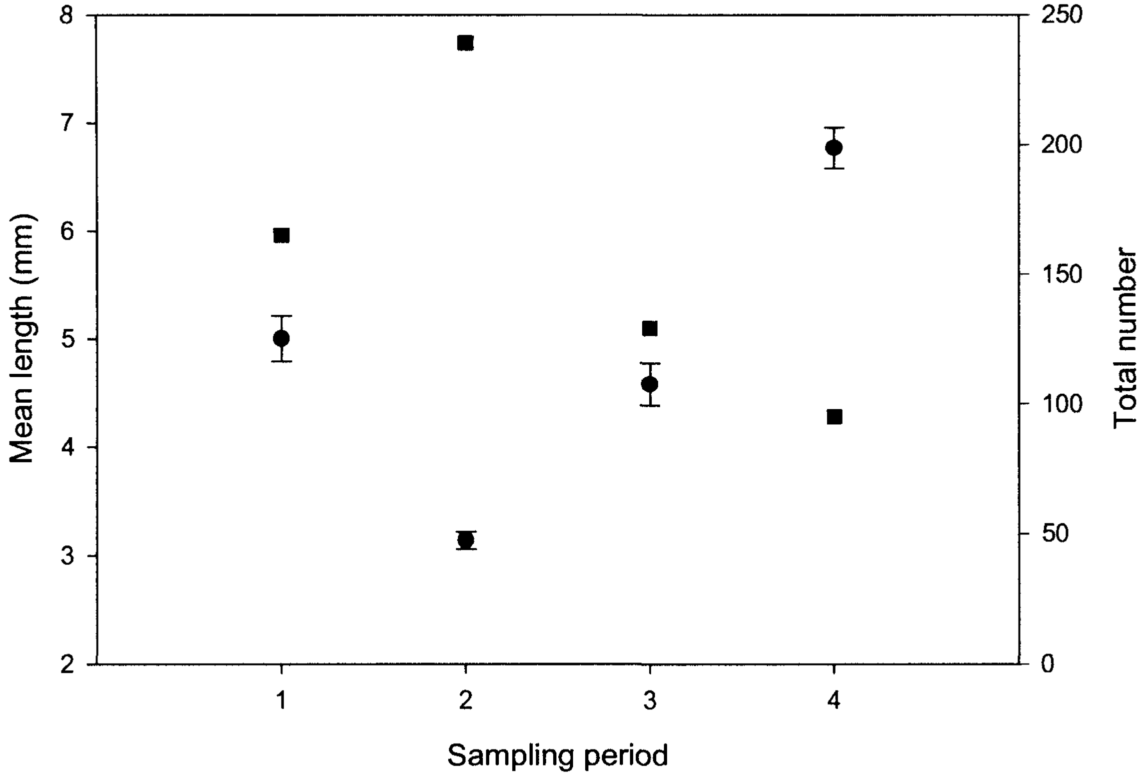


Figure 2.2. Mean length of all fish caught and the total number of fish caught during each sampling period of 2001 tidepool survey. Length = circles; total number = squares. Sampling periods: 1 = June 6 - June 26; 2 = July 3 - August 2; 3 = August 3 - September 18; 4 = September 29 - October 21.

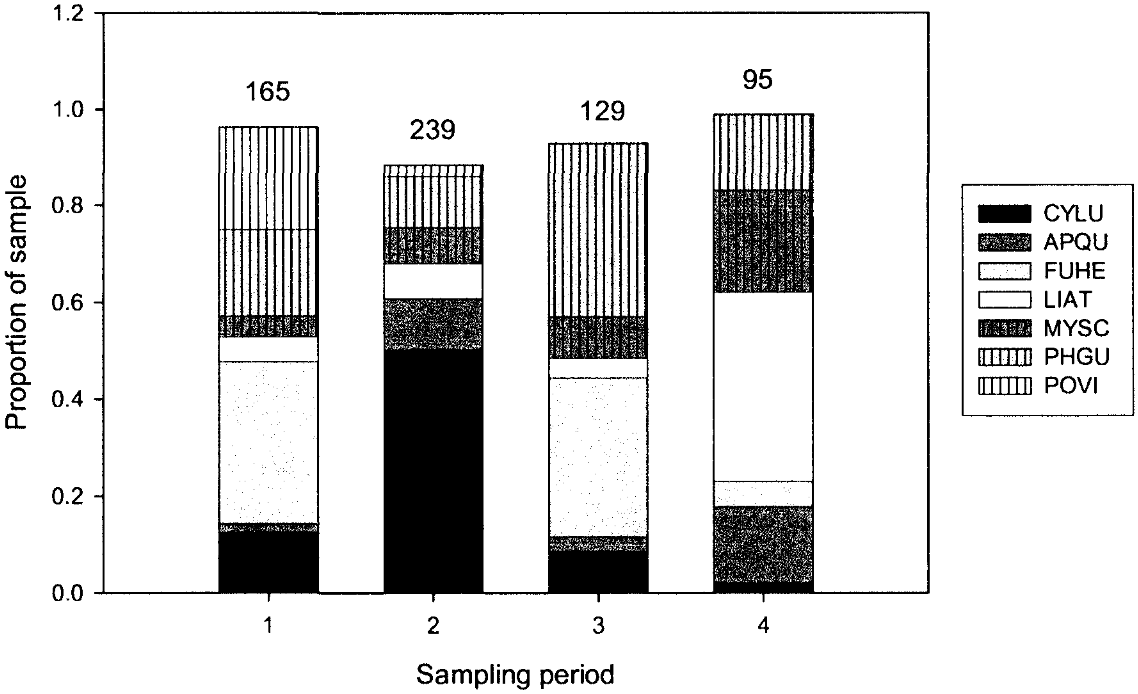


Figure 2.3. Relative proportions of the six most abundant fish caught during the tidepool survey on Mount Desert Island and Schoodic Peninsula during each sampling period. The total number of fish captured were during each sample period are found above each stacked bar. List of species abbreviations used in legend given in Table 2.1.

2.1.4. Discussion

2.1.4.1. Tidepool Use

The most consistent species found in tidepools around Mount Desert Island and the Schoodic peninsula were the shorthorn sculpin, grubby sculpin and the rock gunnel, and both were considered resident tidepool species with adaptations well suited for the tidepool habitat. The species are generally found along the shoreline in New England (Collette and Klein-MacPhee 2002). The grubby is considered a warmer water species and the shorthorn a cold-water species with antifreeze protein capability and limited tidepool occurrence in the winter (Moring 1990b). The shorthorn sculpin is the only species that remains close to the shore during the coldest periods of the year, supporting observations of an increasing proportion of shorthorn sculpin during the last sample period (Collette and Klein-MacPhee 2002). Sculpins alter their color patterns to match the background substrate (Collette and Klein-MacPhee 2002), an adaptation that benefits both predator evasion and feeding on unsuspecting prey as a sit-and-wait predator. All sculpin species are voracious feeders on a large number of invertebrates (Collette and Klein-MacPhee 2002) and for that reason are potentially important predators in tidepools.

The rock gunnel is found in temperate tidepools across the Atlantic basin and into the North Sea (Zander et al. 1999). In a tagging experiment it was found that 13% of tagged gunnels were recaptured under the same rock they were initially captured. A widespread resident of tidepools across the Atlantic, the gunnel uses an anguiliform body form to advantage in hiding in algal fronds or crevasses and under rocks. Rock gunnels can remain out of water in moist areas, such as under algae (Collette and Klein-MacPhee 2002).

Lumpfish and snailfish both have an adhesive organ for grasping algae, rocks and other surfaces within tidepools, although the species differ in behavior and ecology. Snailfish arrived in the tidepools in the late summer and fall, when the lumpfish were beginning to leave. Lumpfish have been found to home to specific tidepools (Moring and Moring 1991). They are not collected in tidepools until the temperature reaches 12.7□C and begin to leave as the temperature drops below 9.3□C, as the algal cover begins to die (Moring 1990b). Lumpfish have been found to associate with floating masses of rockweed (Blacker 1983). In this study, lumpfish were strongly associated with algae and were often initially confused with broken ascophyllum floats and other algal fragments. Furthermore, in one sampling day within the Mosquito cove estuary large rockweed mats were found floating and being stranded along the shores with the receding tide. The floating algae were inundated with large numbers of lumpfish (100s), many of which also became stranded along the shore. This suggests that floating rockweed mats may be a dispersal tool for lumpfish, providing they remain offshore or in rocky intertidal areas. Lumpfish feed on everything possible, and are one of only a few species that have been shown to feed heavily on ctenophores and other jellyfish, however juveniles feed on crustaceans that are abundant in the nearshore (Collette and Klein-MacPhee 2002). Snailfish are found more rarely on vegetation and were often captured under rocks, in crevasses and within periwinkles on tidepool bottoms. They are rarely found in temperatures above 12□C (Detwyler 1963), which may explain their presence later in the year than the lumpfish.

The mummichog feeds on detritus in food-limited systems and displays an exceptional ability to tolerate a large number of stressors. Mummichogs are particularly abundant in salt marsh, mud flat and estuarine habitats, as well as impacted sites (Collette and Klein-MacPhee 2002). The species is capable of breathing air in oxygen-poor environments (Collette and Klein-MacPhee 2002), which along with their eurythermal and euryhaline nature and diet breadth allow them to inhabit environments that would be considered sub-optimal to other species. This includes areas facing eutrophication and solar heating that decrease the oxygen concentrations to levels inadequate for most other species. Mummichog also exhibits a degree of homing ability, although it appears that this behavior has only been observed in tidal marsh habitats (Gibson 1999). As is the case with the fourspine stickleback, the mummichog was found in high numbers in very shallow mud pools on the landward side of MDI. Since mummichogs are common across salt panne pools, fringing marsh and mudflats, and are physiologically equipped for tidepool habitats, they are designated as a resident species restricted to mudflat habitats.

Most transient tidepool species are pelagic and most resident tidepool species are benthic (Zander et al. 1999). The sole “pelagic” species captured in tidepools was the pollock. Pollock are a groundfish, but occupy the water column during early stages. Pollock have been shown to enter into coastal areas during the summer and have been found in tidepools and within the intertidal zone in the Gulf of Maine (Du Buit 1991, Rangley and Kramer 1995a,b). Diet studies from the North Atlantic show the pelagic nature of its food. During the first two years pollock inhabit coastal waters and feed on planktonic invertebrates. Following the inshore life stage, pollock migrate to the open ocean and, although feeding remains on pelagic species, larger euphausiids, fish and cephalopod prey becomes the mainstay of their diet (Du Buit 1991). The pattern of intertidal use described by Rangeley and Kramer (1995a,b) suggests that aggregations of pollock move from subtidal habitats during low tide to occupy rocky intertidal habitat during the flood tide. Rangley and Kramer (1995a,b) observed pollock dispersing into smaller groups or solitary individuals across the intertidal habitat. Algal rich habitats had more pollock than open habitats, likely in response to avian predation risk, and the population declined an order of magnitude over the summer as the distribution shifted to deeper habitats. Our observations are consistent with these, with large schools of pollock aggregating as the tides receded. Although pollock can survive in tidepools, their ecology and tendency to be caught in large tidepools during the ebb tide make this species a true transient species. Presence restricted to early in the year may be due to a combination of lower temperature and higher oxygen conditions during the early year, since pollock have limited tolerance for high temperatures and low oxygen.

The two stickleback species were designated as transient species. Threespine and fourspine sticklebacks display courtship behavior involving a nest territory built and guarded by the male (Collette and Klein-MacPhee 2002). Fourspine sticklebacks are usually confined to brackish water and do not have good dispersal capabilities due to small fins (Collette and Klein-MacPhee 2002). Fourspine sticklebacks in the Thompson Island sites may originate from Northeast Creek and other freshwater sources on the landward side of the island, either through freshwater discharge or due to density dependent habitat choice (Worgan and FitzGerald 1981). The species was abundant, but restricted to the mud flat site, where young fish were trapped in the shallow tidepools exposed at the low tide. Threespine stickleback use open ocean habitats during most of the year and move into the intertidal habitat to spawn and die in the second or third year (Collette and Klein-MacPhee 2002). Young threespine sticklebacks were found in the shallow mudflat tidepools with the fourspine sticklebacks. Threespine sticklebacks were also captured as a mating pair in thick submersed vegetation in a Moose Island tidepool on the Schoodic peninsula. Minnow traps placed in estuarine habitats caught large numbers of mating pairs of fourspine sticklebacks. The results suggest that both species of sticklebacks found in tidepools were generally trapped in mudflat tidepools during ebbing tides, except in the case of threespine mating pairs, which may occasionally use tidepools for nest sites.

Other transient species were the winter flounder (*Pleuronectes americanus*) and sea raven (*Hemitripterus americanus*), which were each only caught once in a tidepool. Although the species is known to inhabit the intertidal zone, in particular as juveniles (Collette and Klein-MacPhee 2002), they were certainly not resident species. Sea raven inhabit depths greater than 2 m but are more common in depths of 37–108 m and temperatures of 6 - 9°C (Collette and Klein-MacPhee 2002). Winter flounder are generally found associated with sandshrimp (*Crangon septemspinosa*) in deeper areas (Chapter 6). No sandshrimp were captured in tidepools.

2.1.4.2 Recruitment

The threespine and fourspine sticklebacks, lumpfish and snailfish, as do many intertidal fish, do not spawn pelagic eggs, rather courtship occurs within nest sites and there is often some form of parental care (DeMartini 1999). Rock gunnels have adhesive eggs that are laid in crevasses and also been shown to have potential biparental care, although this is not certain (Collette and Klein-MacPhee 2002). Mummichogs lay eggs high in the tidal marsh and they are often under periods of exposure to air without any adverse effects. Both adhesive species, lumpfish and snailfish, have male parental care of nest sites after courtship. It is clear that life in the intertidal zone is complex and is accompanied by patterns in reproduction that warrant further research.

The influx of young of year (YOY) lumpfish and mummichogs played an important role in changing the relative abundances of the species caught. Mummichog abundance is solely attributable to tidepools at the Thompson Island site, the only tidepools to ever contain mummichogs. It is not clear why they were completely absent during the second sample period. Mummichogs are the dominant species found in salt pannes, with young fourspine and ninespine sticklebacks. These small and extreme environments often remain beyond any tidal influence for a week or more and are exposed to solar heating. In some cases, water temperatures in pannes and tidal flats were found to exceed 30°C, surely reducing the oxygen levels.

Although both the shorthorn sculpin and the rock gunnel are considered primarily invertebrate feeders, large numbers of young small lumpfish that enter pools could be a food source. Certainly the high abundance of lumpfish decreases quickly from the time they are initially observed. Recruitment of young-of-year fish into, and the large numbers of amphipods and other invertebrates in tidepools offer potential food resources for use by other young fish (pollock, sculpins, etc.). The large numbers of young fish and species capable of ingesting them suggests the tidepool habitat can act as an important trophic transfer of energy from the intertidal zone into the oceanic ecosystem. Pollock are the first species to move offshore after use of the tidepools as juveniles. Sculpins also shift to a deeper distribution during the winter, and the longer residence within the tidepools suggests that they could be an important exporter of energy from the intertidal zone.

2.2. Estuaries

2.2.1. Introduction

On a global scale, the coastal zone is a fraction of the Earth's area, yet it provides a disproportionate amount of primary and secondary productivity on which human society and marine ecosystems depend. Humans have heavily settled coastal regions areas because of plentiful resources and access for trade, and presently approximately 53% of Americans live along the coast (Culliton 1998). Most major cites were built on rivers or locations where rivers and ocean meet, known as estuaries. Estuaries are described as a semi-enclosed coastal body of water having a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage (Cameron and Pritchard 1963). Anthropogenic pressures tend to be exacerbated in estuaries, necessitating studies and inventories of the species present and the environmental constraints involved in shaping their distributions.

Acadia National Park manages 152.32 km^2 in the downeast region of Maine, primarily on Mount Desert Island (MDI) but also including a portion of Schoodic Peninsula and Isle au Haut, 14 outer lying islands along with the authorization by Congress (Boundary Map #123-80, 011; 1986) to acquire and manage conservation easements. The easement authority included parcels and islands between lands adjacent to Schoodic Peninsula to the north and then southward to the Penobscot Shipping Channel. The park's mission of conservation for of all lands within this area justifies the park's interest and involvement in research projects and long-term monitoring efforts.

Few studies have been performed on fish species in Acadia National Park embayments, which include estuaries, bays, coves and harbors, and their relative populations and fish sizes. Brackish water provides habitat for certain species of fish during different parts of their life cycles. Intertidal fish species found in embayments are often euryhaline and are able to occupy varying locations along the salinity gradient.

The goal of this work is to document the relationship between species and environment and discuss the patterns and trends in the abundance and distribution of fish species using species inventories from five estuaries in Acadia National Park.

2.2.2. Methods and Materials

Fish were collected during 2002 and 2003 in five estuaries within Acadia National Park (Figure 2.1, 2.4). Four estuaries are located on Mount Desert Island (MDI), the larger portion of Acadia National Park (ANP), and one of the estuaries is located on adjacent Schoodic Point, the smaller section of ANP on Schoodic Peninsula (see Figure 2.1, 2.4). Estuarine sampling was primarily done during flood tides. Minnow traps, fyke nets and occasional seines were used in 2002 and seines were relied on in 2003.

Minnow traps were set in a grid pattern, with each minnow trap attached to a cinder block to anchor the trap in place. Each trap had a temperature logger (Onset™ StowAway tidbit +23°F to +99°F model) attached, set to record temperature at a frequency of 5 min. The arrangement of traps concentrated effort around the culverts with a few traps placed in the channels towards the freshwater. Typically 9 traps were used in each estuary during each sample period, but Bass Harbor was divided into two sample periods and was sampled with 13 and 18 traps during the early and late summer sampling

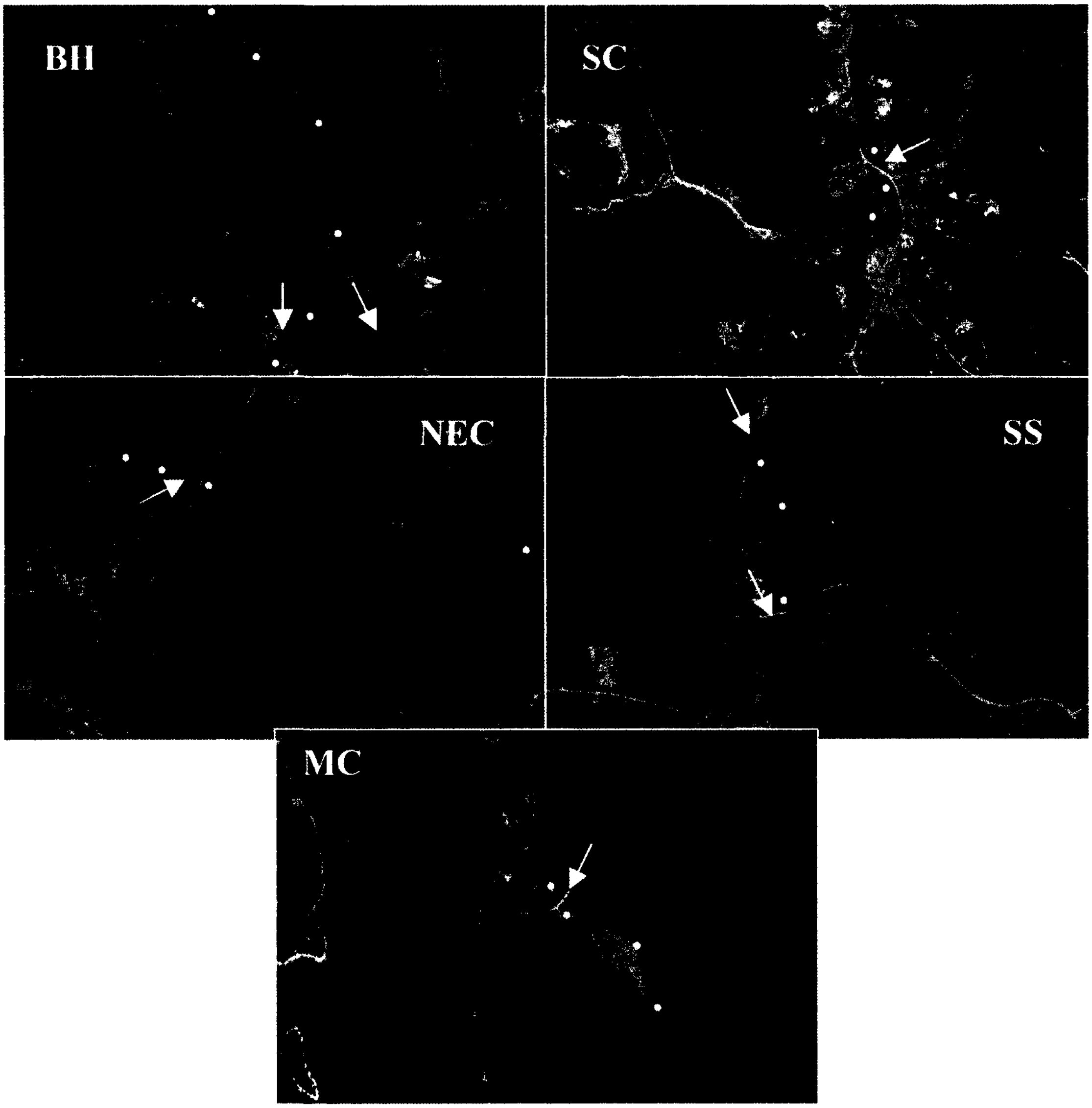


Figure 2.4. Locations of sampling sites during 2003 estuary survey. Sampling sites (circles) are numbered starting at the saltwater endmember proceeding towards the freshwater. Arrows indicate where culverts exist. BH = Bass Harbor, SC = Seal Cove, NEC = Northeast Creek, SS = Somes Sound, MC = Mosquito Cove.

efforts, respectively. While traps were placed in the estuaries, a fyke net was also deployed. The fyke net had two trapping areas with a leader net placed out into the estuary. At the Somes sound site the two traps were placed end-to-end in a channel within the salt marsh. The net was set such that there were two halves that it sampled in the direction of both the freshwater and the saltwater.

The seine was set in the water, with one end attached by line to the beach. The seine was set in the water off the beach in an arcing manner, ending up down the bank from the other end. The net was pulled in slowly pursing the bottom as we came closer into the shore. Fish species, and invertebrates, caught were documented. A subset (n=30) of each species caught was measured for total length and the total number of individuals was recorded. If fewer than 30 fish were caught, all were measured. To avoid stress for the fish during capture and handling, MS-222 (tricaine methanesulfonate) was used to anesthetize each captured fish. Handling time was kept to a minimum and each fish was promptly returned after they had been measured or counted. The stations in each estuary range from high salinity near the estuary mouth and low salinity (~ 100% freshwater) environments near the freshwater source. Physical measurements, such as salinity and temperature, were recorded before each seine was conducted. Either a SBE-19 Seabird self-contained and internally-recording CTD or YSI 85 DO, Conductivity, Salinity, Temperature Instrument from YSI Environmental was used, depending on water depth. Because the estuaries begin as wide open mud flats and constrict towards the freshwater source, two seines were used in 2003. A small seine (4.27 m X 1.2 m, 0.32 cm mesh) was used in sites that were limited in area, while a large seine (30.5 m X 1.2 m, 1.1 cm mesh) was employed when possible.

2.2.3. Results

There were 20 species of fish caught in the survey of estuarine habitats in water adjacent to Acadia National Park (Table 2.2). In the first half of 2002, 3371 individuals representing 12 species were captured (Table 2.3), while 7436 individuals representing 9 species were captured later in the year (Table 2.4). Mummichogs were dominant in both sample periods, although were reduced fro 91% to 81% of the total catch by small changes in the gear types used. Northeast Creek, Bass Harbor and Somes Sound sites were associated with the largest mummichog populations in both sample periods.

The temperature, salinity, and sigma-t (density) values from CTD casts made at each estuary mouth at high tide during a 9-day period (Tables 2.5, 2.6 and 2.7). The results show that Somes Sound sites had the warmest and lightest water. The surface water is influenced by present conditions (solar heating, rain), while the bottom water is more characteristic of processes within Somes Sound proper. Somes Sound sites are provided significant sheltering by Somes Sound and the result is reduced mixing and elevated water temperatures. The Bass Harbor estuary and sampling area was located at the head of Bass Harbor and begins near a culvert located just above the low tide mark. Bass Harbor CTD data during a flood tide demonstrated how water column mixing is influenced by the culvert (Figure 2.5). As the flood tide passes through the restriction in flow at the culvert, the water column becomes mixed such that stratification is nullified and the salinity, temperature and density become intermediate compared to the original surface and bottom values (Figure 2.5). Once the mixed water enters the impoundment on the estuary side of the culvert, solar heating and evaporation begin to play an important role in determining temperature (Figure 2.6) and salinity. The harbor outside of the Bass

Harbor sampling sites is substantially smaller and shallower than the sound outside of the Somes Sound sampling sites. Seal Cove, and to a greater level Mosquito Cove, are short and less protected compared to Bass Harbor and Somes Sound estuaries. This can be seen in the more marine signature in terms of temperature (colder; Table 2.5), salinity (saltier; Table 2.6) and density (heavier; Table 2.7). Northeast Creek was the most protected estuary, with extensive mudflats and a location on the leeward side of Mount Desert Island. The location and morphology of Northeast Creek and surrounding area are responsible for keeping the water temperature high (Table 2.5), and the more significant freshwater input responsible for the lower salinity and density in the bottom sample, which reflects the water being input into the estuary during flooding tides (Table 2.6, 2.7). Mudflats present around Northeast Creek also limit the depth range.

In both sampling periods during 2002, mummichogs were the dominant species captured by a wide margin, in particular in Northeast Creek and upper Bass Harbor (Table 2.3, 2.4). Bass Harbor was kept as two sampling units (upper and lower) to demonstrate the increasing numbers of mummichogs towards the freshwater endmember. The increase in mummichog abundance in the second sampling period (Table 2.7) was due to the addition of a trap, and dipnetting, along a branch of the marsh with limited freshwater input. Other relevant observations were that Mosquito Cove contained more solely marine species in lumpfish, cunners and grubbies (Table 2.3). There was an increased capture of herring, alewives and silversides during the second sample period (Table 2.4) when seine use was used in sampling. Since only a few seines were completed and the bias of minnow traps is well documented, 2002 data is only used to make cursory observations.

Table 2.2. Checklist and taxonomic information of each species caught during estuarine survey of Mount Desert Island and Schoodic Peninsula. Included are abbreviations used in figures.

Common Name	Scientific Name	Abbrev.	Order	Family
American eel	*Anguilla rostrata*	ANRO	Anguilliformes	Anguillidae
Herring	*Clupea harengus*	CLHA	Clupeiformes	Clupeidae
Alewife	*Alosa pseudoharengus*	ALPS	Clupeiformes	Clupeidae
Blueback herring	*Alosa aestivalis*	ALAE	Clupeiformes	Clupeidae
Rainbow smelt	*Osmerus mordax*	OSMO	Osmeriformes	Osmeridae
Atlantic silverside	*Menidia menidia*	MEME	Atheriniformes	Atherinopsidae
Mummichog	*Fundulus heteroclitus*	FUHE	Cyprinodontiformes	Fundulidae
Striped killifish	*Fundulus majalis*	FUMA	Cyprinodontiformes	Fundulidae
Fourspine stickleback	*Apeltes quadracus*	APQU	Gasterosteiformes	Gasterosteidae
Threespine stickleback	*Gasterosteus aculeatus*	GAAC	Gasterosteiformes	Gasterosteidae
Blackspotted stickleback	*Gasterosteus wheatlandi*	GAWH	Gasterosteiformes	Gasterosteidae
Ninespine stickleback	*Pungitius pungitius occidentalis*	PUPU	Gasterosteiformes	Gasterosteidae
Northern pipefish	*Syngnathus fuscus*	SYFU	Gasterosteiformes	Syngnathidae
Cunner	*Tautogolabrus adspersus*	TAAD	Perciformes	Labroidae
Rock gunnel	*Pholis gunnellus*	PHGU	Perciformes	Pholidae
Inshore sandlance	*Ammodytes americanus*	AMAM	Perciformes	Ammodytidae
Atlantic mackerel	*Scomber scombrus*	SCSC	Perciformes	Scombridae
Smooth flounder	*Pleuronectes putnami*	PLPU	Pleuronectiformes	Pleuronectidae
Golden shiner	*Notemigonus crysoleucas*	NOCR	Cypriniformes	Cyprinidae
Pumpkinseed	*Lepomis gibbosus*	LEGI	Perciformes	Centrarchidae

Table 2.3. Numbers of individuals caught during the first sample period in 2002. The list of species was compiled by pooling all gear types.

Species	Seal Cove	Lower Bass Harbor	Upper Bass Harbor	Northeast Creek	Somes Sound	Mosquito Cove	Species Total
Mummichog	310	0	494	904	1232	120	3060
4-Spine Stickleback	21	10	11	3	6	0	51
3-Spine Stickleback	0	46	1	6	26	2	81
9-Spine Stickleback	0	14	15	0	22	2	53
American Eel	0	1	2	18	19	2	42
Marsh Killifish	0	1	5	0	2	0	8
Rock Gunnel	0	0	0	0	2	0	2
Atlantic Silverside	0	0	0	1	1	29	31
Lumpfish	0	0	0	0	0	31	31
Cunner	0	0	0	0	0	6	6
Grubby	0	0	0	0	0	2	2
Mackerel	0	0	0	0	0	3	3
Estuary Total	332	72	528	932	1310	197	3371

Table 2.4. Numbers of individuals caught during the second sample period in 2002. The list of species was compiled by pooling all gear types.

Species	Seal Cove	Lower Bass Harbor	Upper Bass Harbor	Northeast Creek	Somes Sound	Mosquito Cove	Species Total
Mummichog	574	481	1251	2779	920	Not Sampled	6005
4-Spine Stickleback	58	65	33	92	1		249
3-Spine Stickleback	1	325	0	0	0		326
9-Spine Stickleback	0	5	14	65	0		84
Herring	55	0	0	1	0		56
Atlantic Silverside	0	191	72	22	394		679
American Eel	0	5	0	12	0		17
Alewife	5	0	14	0	0		19
Mackerel	1	0	0	0	0		1
Estuary Total	693	1072	1384	2971	1315		7436

Table 2.5: Temperature (°C) on the surface and bottom of water column based on CTD casts at the mouth of each estuary in 2003.

	Bass Harbor	Seal Cove	Northeast Creek	Somes Sound	Mosquito Cove
Date	06/10	06/14	06/12	06/19	06/13
Surface	12.6	8.5	12.2	15.0	9.7
Bottom	9.2	8.3	12.1	13.6	7.5
Depth (m)	4	5	2	1.5	3

Table 2.6: Salinity (‰) on the surface and bottom of water column based on CTD casts at the mouth of each estuary in 2003.

	Bass Harbor	Seal Cove	Northeast Creek	Somes Sound	Mosquito Cove
Date	06/10	06/14	06/12	06/19	06/13
Surface	30.6	31.0	30.6	27.3	32.0
Bottom	32.1	31.6	30.9	31.6	32.8
Depth (m)	4	5	2	1.5	3

Table 2.7: Sigma-t on the surface and bottom of water column based on CTD casts at the mouth of each estuary in 2003.

	Bass Harbor	Seal Cove	Northeast Creek	Somes Sound	Mosquito Cove
Date	06/10	06/14	06/12	06/19	06/13
Surface	23.1	24.1	23.1	20.1	24.6
Bottom	24.8	24.5	23.4	23.6	25.6
Depth (m)	4	5	2	1.5	3

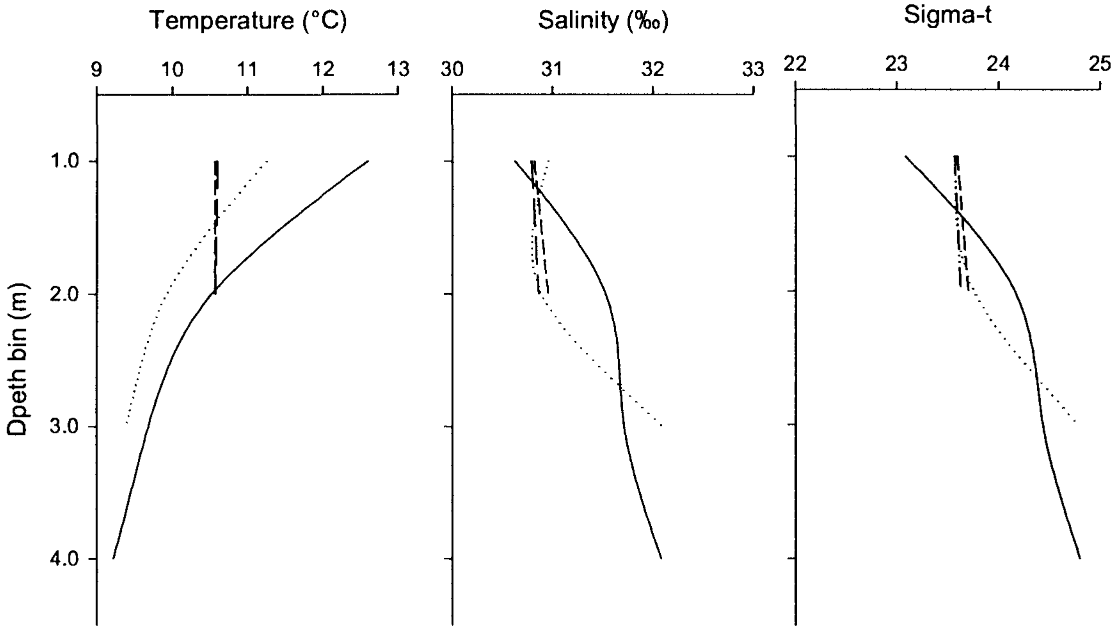


Figure 2.5. Temperature, salinity and sigma-t values against depth in Bass Harbor. Collected by CTD on 06/10/2003. Station 1 (solid line) and 2 (dotted line) were located on the ocean side of a culvert, and station 3 and 5 were on the marsh side (dashed lines). Mixing of water occurs at the culvert, and the depth is reduced quickly as one moves up the estuary towards freshwater.

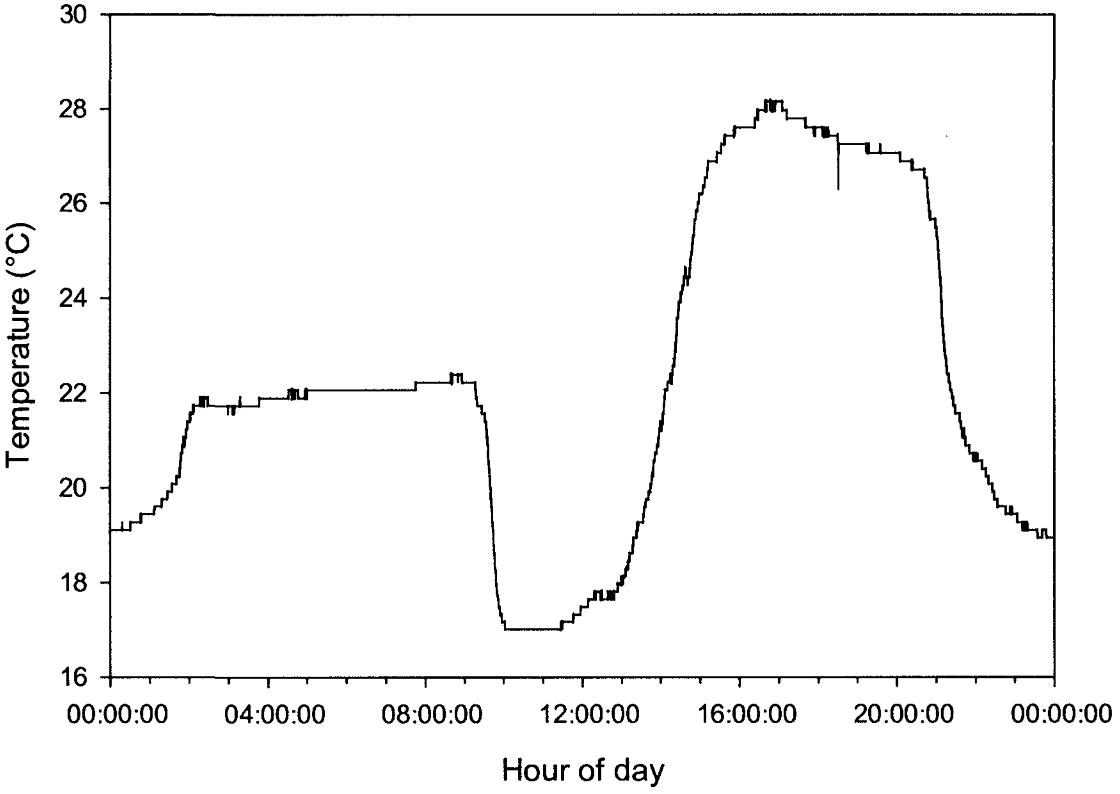


Figure 2.6. Temperature profile from logger placed in Northeast Creek on 07/09/2002. Note the cooler period during midday, when colder ocean water contacts the logger. The temperature during the afternoon ebbing tide increased 6°C, due to solar heating, compared to the nighttime ebbing tide.

Temperature and salinity at the surface and bottom of the water column, for each of the estuaries sampled during 2003, generally showed warming and increasing salinity as the season progressed (Figures 2.7 - 2.11). This is presumably due to reducing input from freshwater and evaporation in the marsh areas. The effect of the spring flooding on salinity can be seen in Figure 2.9, where the freshwater influence is clear at Northeast Creek sampling sites. Salinities are higher in the later part of the summer because of decreasing freshwater input.

The location of sampling within an estuary varied according to the amount of freshwater entering the system, the topography surrounding the estuary and the position of the culvert relative to the mean tide level (Figure 2.7 – 2.11). Seal Cove and Northeast Creek both had much longer distances between the mean low tide and culvert position (over 350 m) compared to the other estuaries (less than 250 m). Furthermore, the end of marine influence above the culvert varied between estuaries with Bass Harbor and Northeast Creek having the longest distances (~ 2000 m) compared to Seal Cove (less than 200 m) and Mosquito Cove and Somes Sound (~ 1000 m). The advance of ocean water was blocked by boundaries in Seal Cove, Somes Sound, Mosquito Cove (sharp rises in topography) and Bass Harbor (beaver dam). Northeast Creek contained no boundary to flow, but the location of the culvert so high in the estuary only permitted spring tides to spill into the impoundment. The presence of the impoundment also allowed the salinity at the bottom to remain above zero, except in the earliest sample period (Figure 2.9).

The fish sampling (Figure 2.7 – 2.11) shows that the location of the estuarine mummichog (*Fundulus heteroclitus*) and fourspine stickleback (*Apeltes quadracus*) was generally restricted to sampling stations that different in relation to the physical landmarks within the estuary (culverts, mean low tide mark, etc.). Fish were absent from the marine stations in Seal Cove, where estuarine conditions were limited to within 200 m above the culvert. For Seal Cove, Somes Sound and Mosquito Cove the freshwater stations were generally the most consistently brackish and contained estuarine species. Exceptions to this existed in Northeast Creek where ninespine sticklebacks (*Pungitius pungitius occidentalis*) and banded killifish (*Fundulus majalis* – not shown), and Bass Harbor where ninespine sticklebacks and Golden Shiners (*Notemigonus Crysoleucas* – not shown), were caught in larger numbers at the freshwater site. Bass Harbor and Northeast Creek had vast brackish water areas inhabited by the estuarine species. Atlantic silversides (*Menidia menidia*) young-of-year were often found with mummichogs at freshwater sites, particularly late in the year.

Sand Shrimp (*Crangon septemspinosa*) were more abundant in the June sampling period and declined to low abundance during the August sampling period, and appeared to retreat from the freshwater sites. Adult blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), Atlantic herring (*Clupea harengus*) and sandlance (*Ammodytes americanus*) were all encountered somewhat randomly and were not included in the analysis. Of note though is the presence of herring in Seal Cove and Mosquito Cove and sandlance in Mosquito Cove. In contrast, the river herring (alewife, blueback) were caught in Bass Harbor, Northeast Creek and Somes Sound sites.

Figure 2.7. Fish species, temperature and salinity encountered during sampling at Seal Cove in 2003. Dates are 6/16/2003 (top), 7/15/2003 (middle) and 8/17/2003 (bottom). The solid line indicates position of culvert in estuary, and dashed line indicates the low tide mark. The most freshwater site effective represents the boundary of freshwater influence.

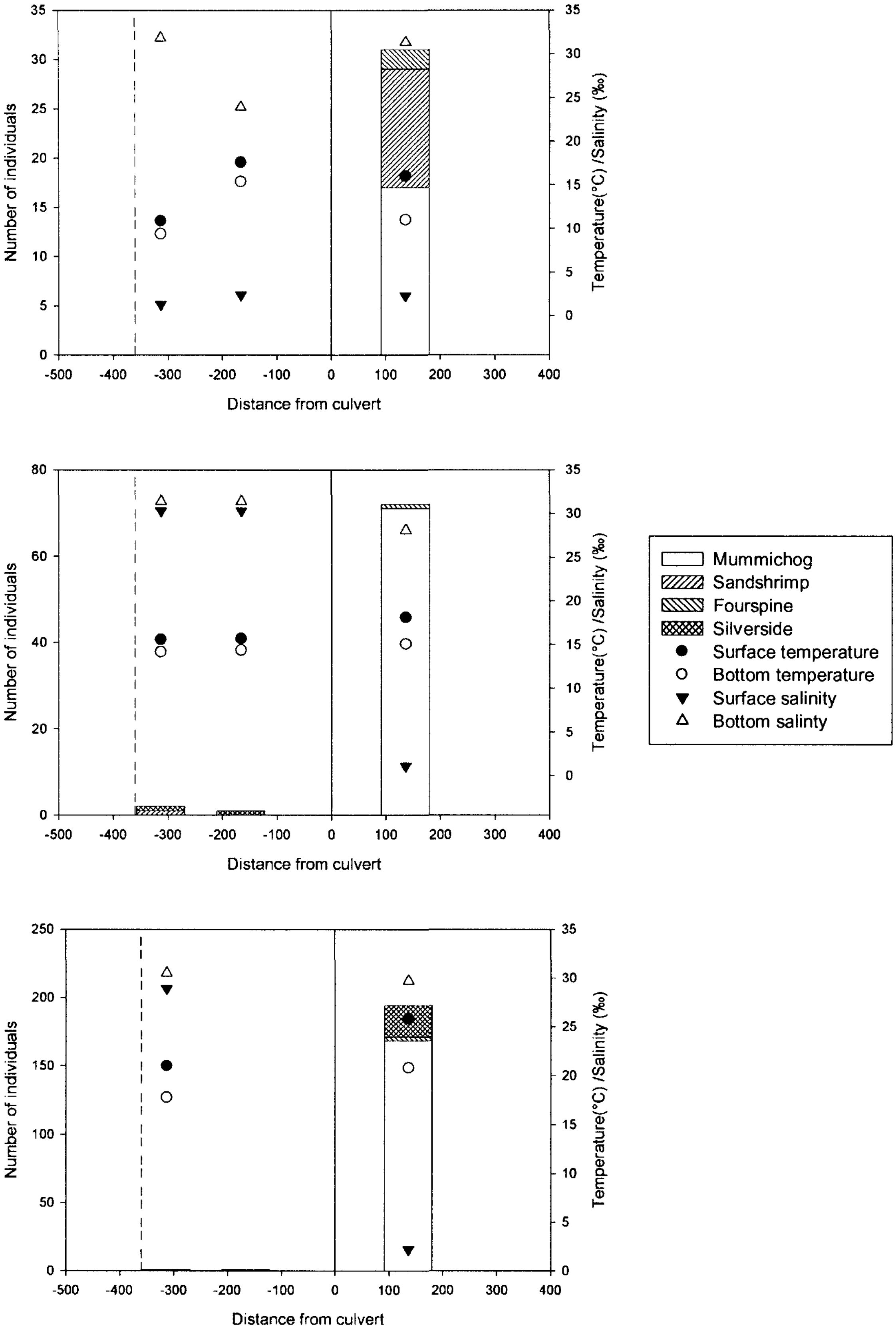

Number of individuals
Temperature(°C) /Salinity (‰)
Distance from culvert
-500
-400
-300
-200
-100
0
100
200
300
400
Mummichog
Sandshrimp
Fourspine
Silverside
Surface temperature
Bottom temperature
Surface salinity
Bottom salinty

Figure 2.8. Fish species, temperature and salinity encountered during sampling at Bass Harbor in 2003. Dates are 6/21/2003- 6/22/2003 (top), 7/21/2003 (middle) and 8/17/2003 (bottom). The solid line indicates position of culvert in estuary, and dashed line indicates the low tide mark. The most freshwater site effective represents the boundary of freshwater influence.

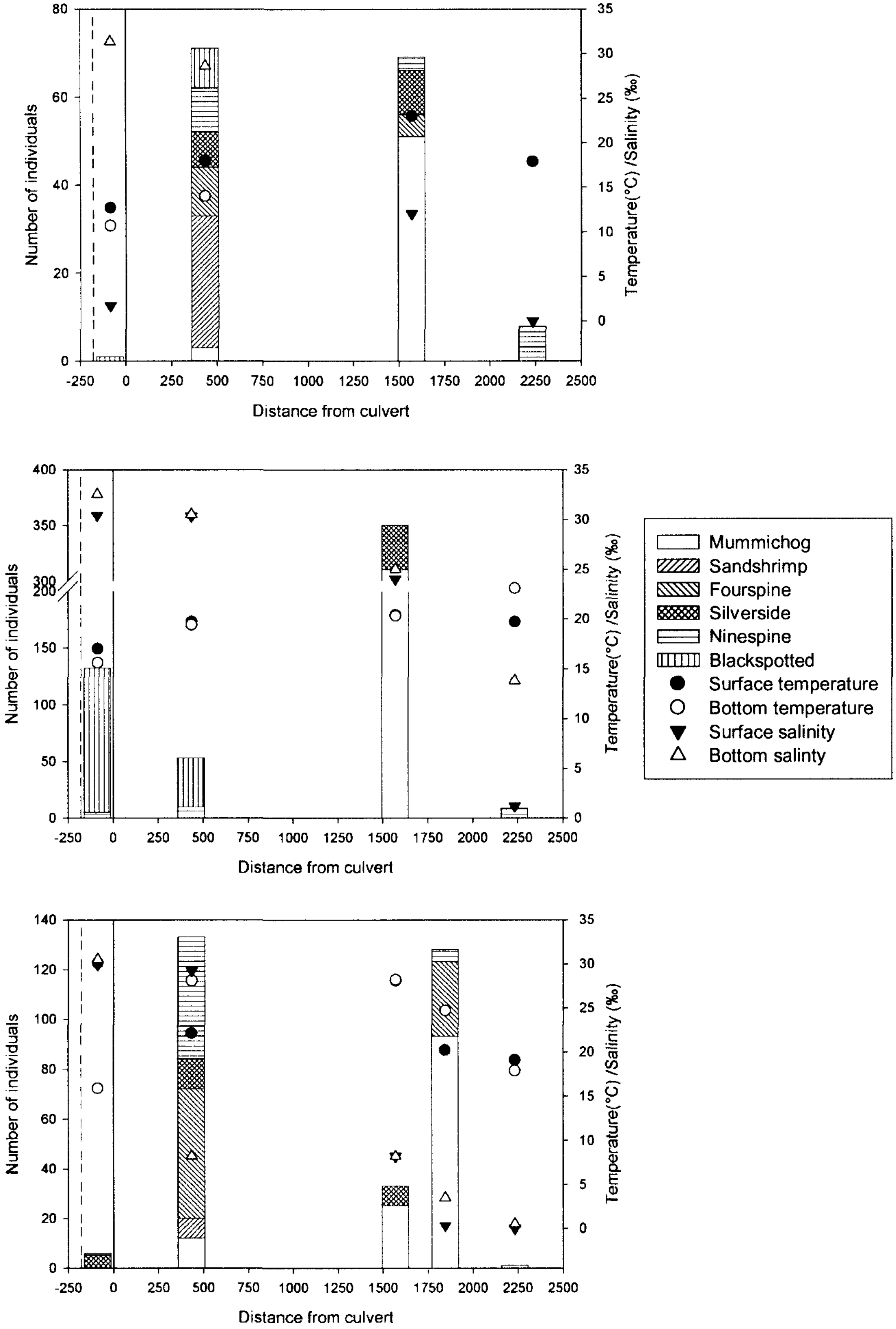
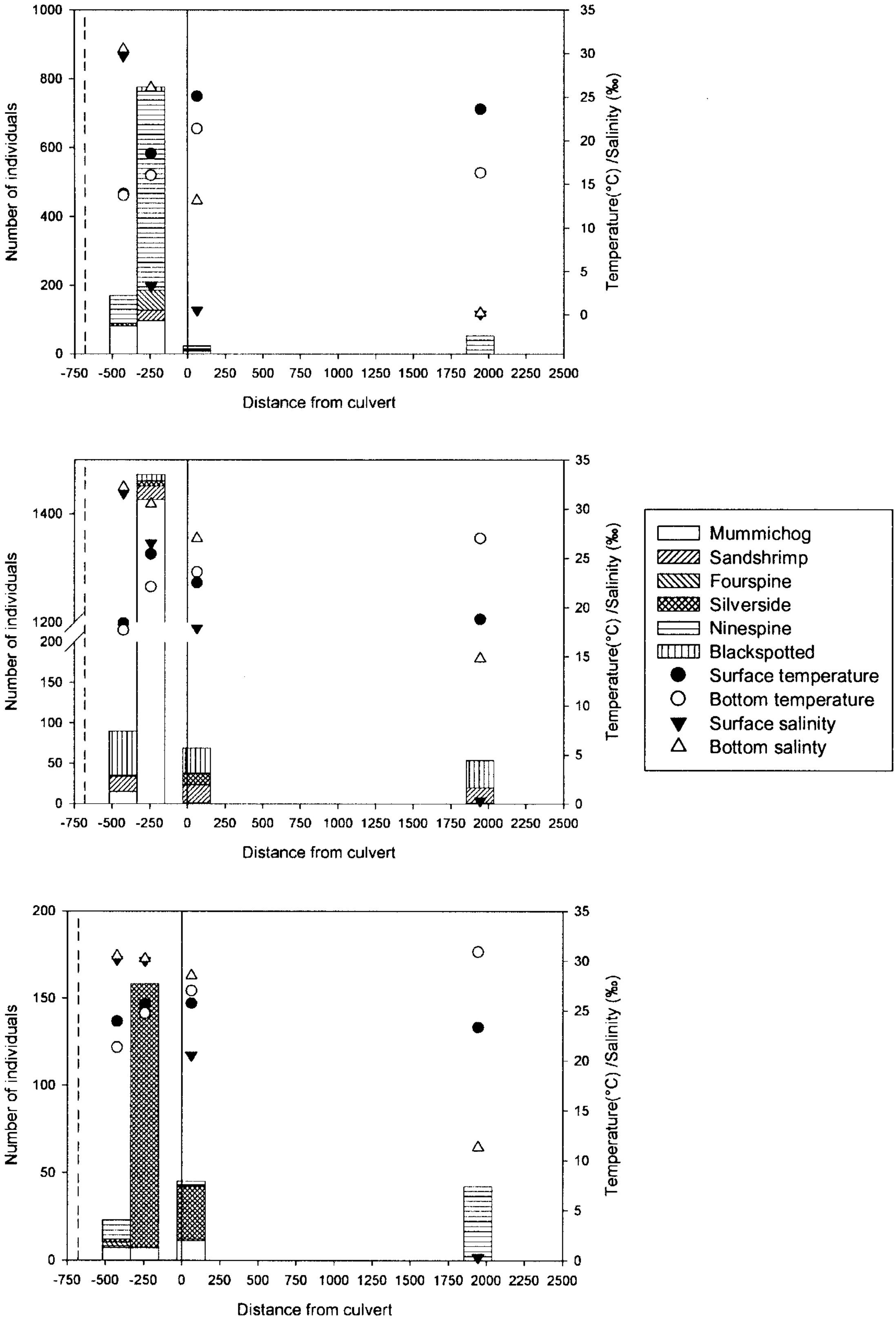
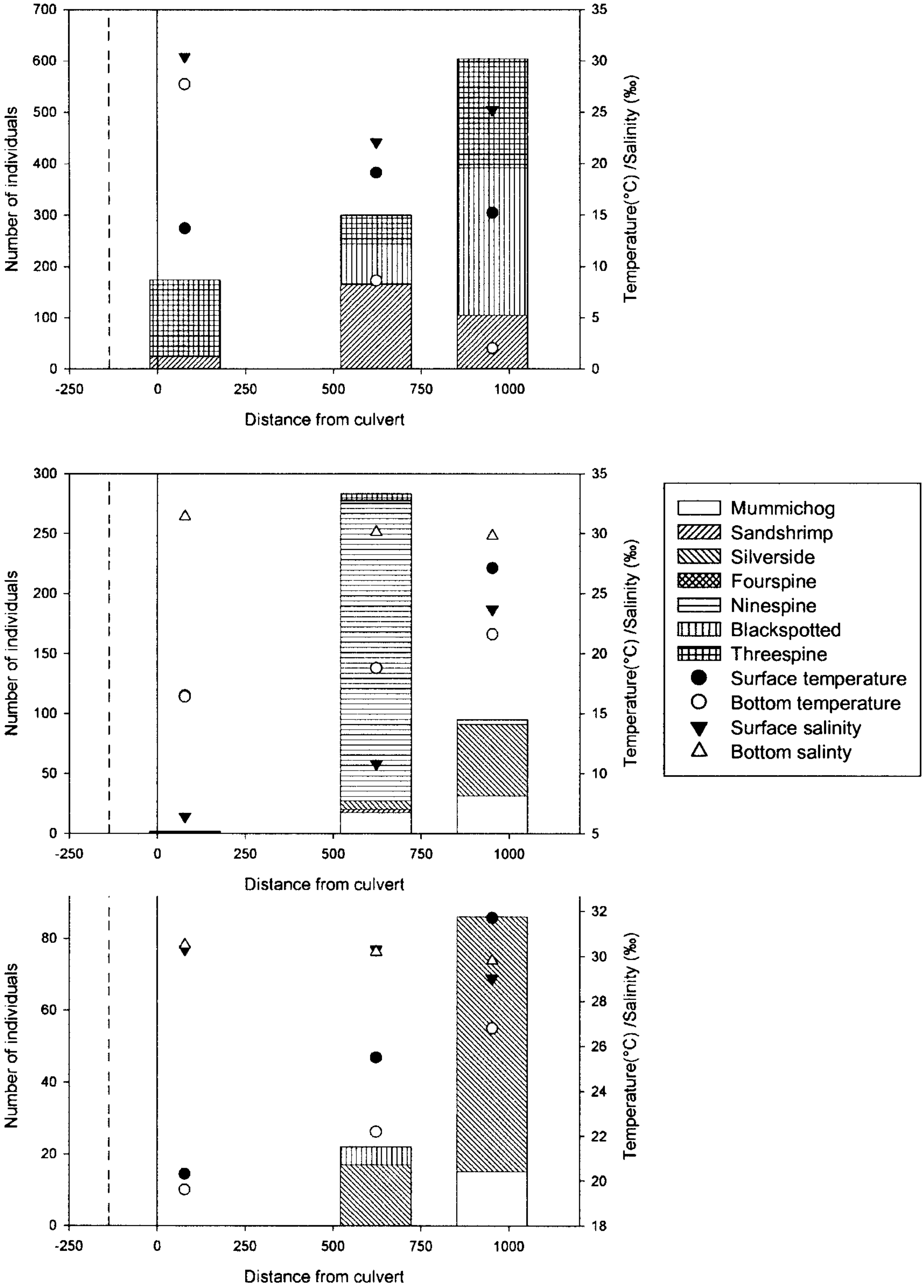

Number of individuals
Temperature(°C) /Salinity (‰)
Distance from culvert
-250
0
250
500
750
1000
1250
1500
1750
2000
2250
2500
80
60
40
20
400
350
300
200
150
100
50
140
120
35
30
25
15
10
5
Mummichog
Sandshrimp
Fourspine
Silverside
Ninespine
Blackspotted
Surface temperature
Bottom temperature
Surface salinity
Bottom salinty

Figure 2.9. Fish species, temperature and salinity encountered during sampling at Northeast Creek in 2003. Dates are 6/24/2003 (top), 7/18/2003 (middle) and 8/19/2003 (bottom). The solid line indicates position of culvert in estuary, and dashed line indicates the low tide mark. The most freshwater site effective represents the boundary of freshwater influence.



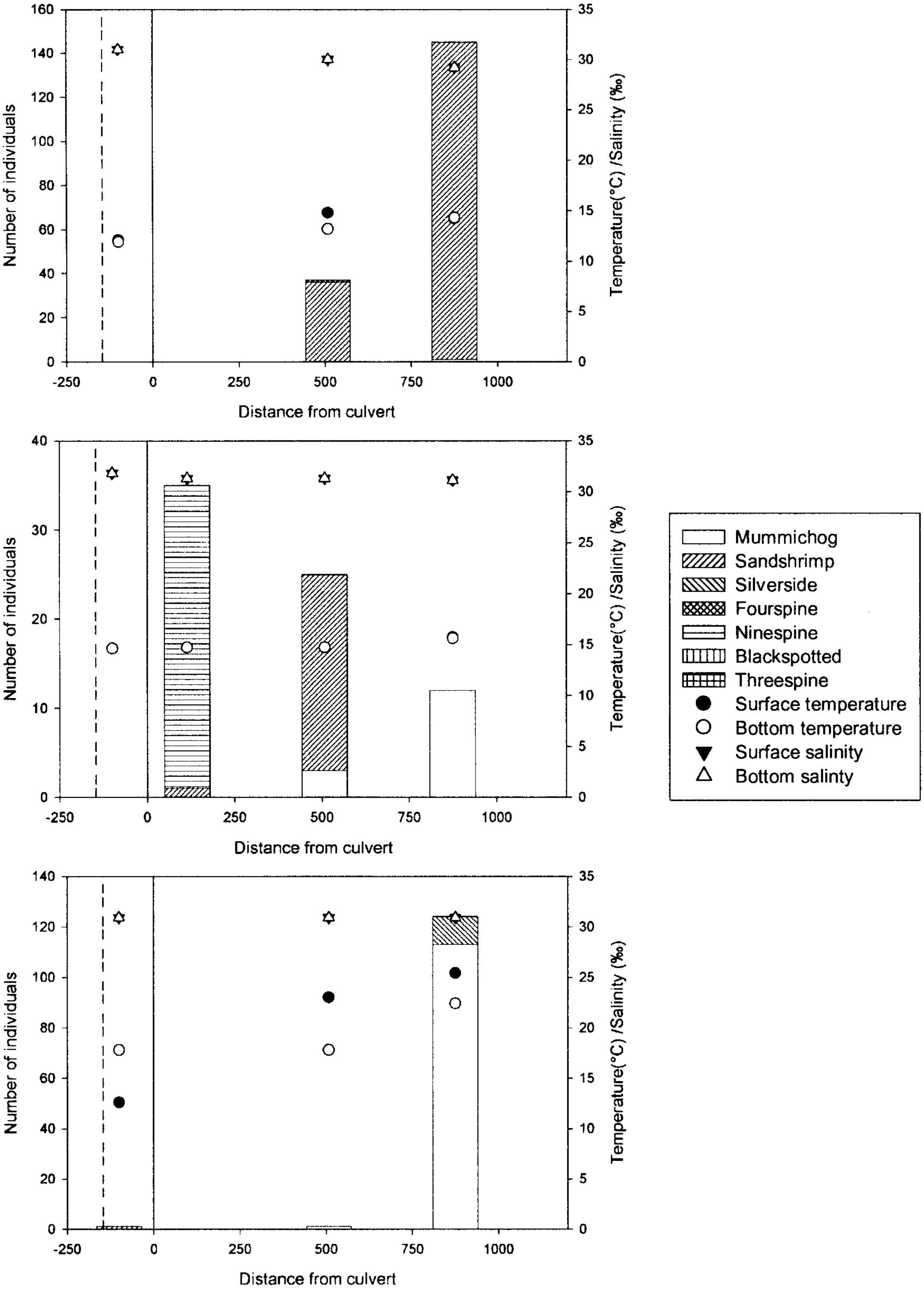
Number of individuals
Temperature(°C) /Salinity (‰)
Distance from culvert
0
200
400
600
800
1000
50
100
150
200
1200
1400
-750
-500
-250
0
250
500
750
1000
1250
1500
1750
2000
2250
2500
0
5
10
15
20
25
30
35
Mummichog
Sandshrimp
Fourspine
Silverside
Ninespine
Blackspotted
Surface temperature
Bottom temperature
Surface salinity
Bottom salinty

Figure 2.10. Fish species, temperature and salinity encountered during sampling at Somes Sound in 2003. Dates are 6/19/2003(top), 7/17/2003 (middle) and 8/16/2003 (bottom). The solid line indicates position of culvert in estuary, and dashed line indicates the low tide mark. The most freshwater site effective represents the boundary of freshwater influence.



Number of individuals
Temperature(°C) /Salinity (‰)
Distance from culvert
700
600
500
400
300
200
100
0
35
30
25
20
15
10
5
-250
250
500
750
1000
300
250
200
150
100
50
80
60
40
20
32
28
26
24
22
18
Mummichog
Sandshrimp
Silverside
Fourspine
Ninespine
Blackspotted
Threespine
Surface temperature
Bottom temperature
Surface salinity
Bottom salinty

Figure 2.11. Fish species, temperature and salinity encountered during sampling at Mosquito Cove in 2003. Dates are 6/25/2003 (top), 7/22/2003 (middle) and 8/20/2003 (bottom). The solid line indicates position of culvert in estuary, and dashed line indicates the low tide mark. The most freshwater site effective represents the boundary of freshwater influence.


Number of individuals
Temperature(°C) /Salinity (‰)
Distance from culvert
160
140
120
100
80
60
40
20
0
35
30
25
20
15
10
5
-250
250
500
750
1000
Mummichog
Sandshrimp
Silverside
Fourspine
Ninespine
Blackspotted
Threespine
Surface temperature
Bottom temperature
Surface salinity
Bottom salinty

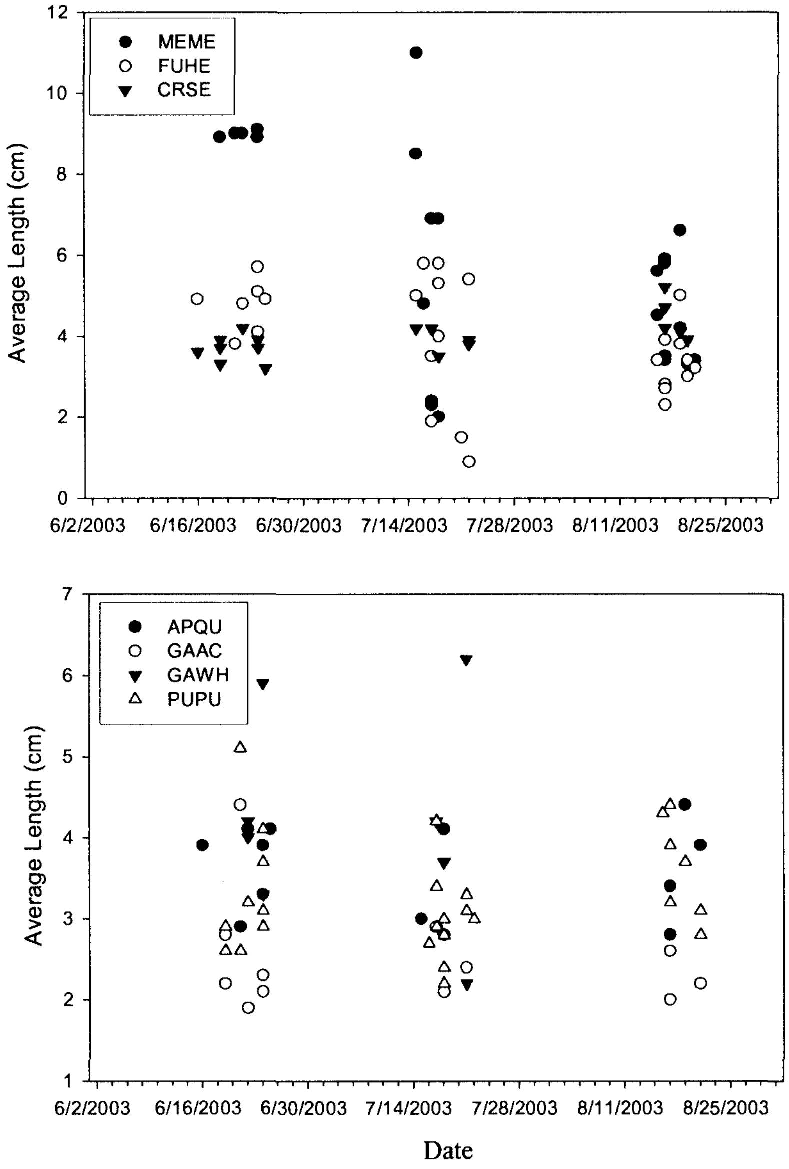


Figure 2.12. Lengths for most abundant estuarine species averaged for each sampling event. Mummichogs = FUHE; silversides = MEME; sandshrimp = CRSE; and fourspine = APQU; threespine sticklebacks = GAAC; blackspotted sticklebacks = GAWH and ninespine sticklebacks = PUPU.

Results show decrease in size for mummichogs and silversides as young recruiting fish begin to be captured by seines (Figure 2.12). Other observations include the absence of blackspotted stickleback during August, and the slight increases in size of sandshrimp at ninespine sticklebacks, with the other species showing little change (Figure 2.12).

2.2.4. Discussion

A large part of changes in fish abundance is related to the seasonal cycle; in particular the reproductive cycle and growth of young fish (Lazzari et al. 1999, Collette and Klein-MacPhee 2002). All the species, except mummichogs, move into the estuaries after over-wintering in the marine environment. Species become susceptible to sampling gear as a function of size and timing of entrance into the estuaries. Young fish are not caught in the seine until they achieve some minimum size (~1 cm), or until the temperature and other physical characteristics of the water matches the requirements for migration into the embayments.

Two species had clear recruitment of young fish occurring, mummichogs and silversides. Mummichogs spend their entire lives in the estuaries, and are the only year-round resident species. They bury themselves in the mud for the winter and reemerge in the spring when conditions permit. They are a shallow water species that is euryhaline and, as a result, occupy a an array of marsh habitats from salt marshes, where they are especially abundant, to eel grass beds, open shores and many altered and impacted habitats where few other species can survive (Collette and Klein-MacPhee 2002). Fundulus are extremely abundant in the brackish water portions of the estuary early in summer when their average population size is largest. They reproduce in early spring or summer and the newly hatched eggs recruit as juveniles later in the summer. Their location further up the estuaries may be to avoid predation, take advantage of available food resources, and coincide with conditions of ideal temperature and salinity, or some combination of these factors. As the 2003 summer wore on the lack of freshwater input and higher temperatures changed the distribution of many species. There is a movement of mummichogs into upper regions of the estuaries as the recruitment of juvenile fish increases. The smaller fish prefer a less open habitat in more constricted areas. Due to this, as one moved towards the sources of freshwater, there were generally smaller fish. Marine species could be seen in greater numbers towards the end of the summer when colder, more saline waters prevailed.

Silversides spawn in the estuaries and young-of-year are often found with mummichogs at freshwater sites, particularly late in the year. Silversides move into estuaries during the summer to spawn, and spawn within the estuary. Sampling found them throughout the estuaries as adults and young juveniles. Silversides lay adhesive eggs that are associated with the marsh grasses (Spartina spp.). They become more abundant in the month of August when young become susceptible to sampling. Even-sized individuals dominate schools of silversides. They can be caught along mud/sand/gravel shoreline, in particular within marsh grasses (Spartina), and are never far from shore. Spartina is common within inner bays and in river mouths. As a result silversides are common in brackish water and are generally restricted in distribution to shallower than a fathom, except in winter to avoid low temperature. Spawning occurs in June and July in the Gulf of Maine with eggs deposited on sandy bottoms, on Spartina up to the high tide mark (Collette and Klein-MacPhee 2002).

Migratory saltwater forage fish can dominate samplings due to their schooling behaviour. Blueback herring and alewives, both anadromous species, use the estuaries for feeding and are required to pass through them to spawn in freshwater and to migrate to the ocean as young (Collette and Klein-MacPhee 2002). These two fish of the family Clupeidae have historically and continue to be of importance to the commercial fishing industry, and are captured in herring fisheries around MDI (Personal Observation). Silversides move into estuaries during the summer to spawn. Sampling found them throughout the estuaries as adults and young juveniles. They became even more abundant in the month of August when the young became susceptible to sampling.

Most marine sticklebacks are restricted to the shoreline and many spend their full life in estuaries. The threespine stickleback are small (less than 9 cm) can occupy full freshwater and full freshwater. They are caught occasionally in the open ocean, often in association with floating seaweeds (Collette and Klein-MacPhee 2002). Threespine sticklebacks enter creeks and estuaries in the spring to spawn, usually in schools (Personal Observation), and are associated with deeper water during the winter (Collette and Klein-MacPhee 2002). Their diet includes copepods, isopods, schizapod shrimps, young squid, young fish and eggs, while some had only fed on diatoms (Collette and Klein-MacPhee 2002).

The range of the ninespine stickleback is much the same as the threespine, spawning in summer along the shore. It is chiefly restricted there to harbors and the creeks in salt marshes, where large numbers can be caught with mummichogs (Personal Observation, Collette and Klein-MacPhee 2002). Fourspine sticklebacks are common to salt marshes, as are other sticklebacks and mummichogs. They are primarily restricted to salt and brackish conditions, although other life history and diet characteristics similar to the threespine stickleback (Collette and Klein-MacPhee 2002).

Once sampling occurs in more freshwater conditions, the ninespine stickleback, banded killifish, Golden Shiner, and other species begin to replace the mummichog as the most abundant species.

The scale of the estuary area in the present study is small compared to more conventional estuarine systems. Bass Harbor Marsh, Northeast Creek and Seal Cove all have measurable freshwater flow throughout the summer. Somes Sounds and Mosquito Cove have substantial flow in the month of June, but freshwater supply decreases significantly over the summer and the only significant flow is after periods of rainfall (Personal Observation). Therefore, the freshwater input has little effect on the salinity within the full embayment. There is argument whether these are in fact estuaries or merely embayments. A measurable dilution of salt water and the presence of estuarine fish species do support the inclusion of the habitats as estuaries. Still, many of the estuaries are dependent on rainfall for the freshwater component of their flow. May and June of 2003 were associated with plentiful rain and cooler temperatures. Tidal flow was more effective later in the summer and saltwater was able to advance further up into the estuary because of lack of freshwater input.

Bass Harbor is a shallow estuary, which constantly receives freshwater through the summer, though freshwater inundation decreases as the watershed becomes dryer due to lack of rain. The station closest to freshwater has low salinity values at the surface and bottom, and is located just below a beaver dam. The freshwater species golden shiner was captured there, although its presence may be due to being flushed over the dam rather than choice. In Northeast Creek, golden shiners were captured, as well as banded killifish, which appears to share some habitat with its close relative the mummichog. Without a barrier to movement, such as the dam in Bass Harbor, the fish appear to be venturing into estuarine conditions by choice. Fish collected in Northeast Creek were generally located in the lower sampling stations closer to the salt water where mainly saltwater species that are physiologically challenged by freshwater were found.

The presence of culverts affected all the estuaries, although the location relative to mean tide level is different in each of them. The primary effect is at the site of the culvert due to a constricted channel where there is high water flow and potential productivity (see Leonard et al. 1998). In particular, the gradient in temperature and salinity can be nullified by turbulent mixing upstream (flood tide) or downstream (ebbing tide) from culverts. The influence of culverts in Acadia National Park estuaries could not be overlooked. They were present in all the estuaries, and due to varying placement and local topography, have different influences on dynamics within the estuary. Seal Cove and Northeast Creek have bridge/culverts that are high relative to mean tide level. Seal Cove has a sharp increase in topography towards Seal Cove Pond, which limits the build up of water on the freshwater side of the culvert. Mummichogs and silversides utilized this area, although in reduced numbers compared to other estuaries, as the summer progressed. On the saltwater side of the culvert in Seal Cove there were few species, and mummichog and silverside numbers were drastically reduced. At Northeast Creek, the relief on the freshwater side of the culvert is dominated by a large marsh with little to no rise in topography. This results in a large pool of brackish water, which from the 2002 sampling is known to contain large numbers of mummichogs. During low tide, the brackish pool of water drains over the mudflat and fringing marsh below the culvert, and with the increased freshwater input compared to Seal Cove enables the use the area by large numbers of mummichogs and silversides, as well as sticklebacks.

The situation in Bass Harbor, Somes Sound and Mosquito Cove is different in that the culvert is found lower in the system, trapping a pool of saline water before the freshwater influences the salinity. Somes Sound did not have any sampling stations on the marine side of the culvert for logistical reasons, but the marine stations at Bass Harbor and Mosquito Cove did not produce many individuals or species of fish, except for a large school of blackspotted sticklebacks during the second sample at Bass harbor. Bass Harbor shares topography like that of Northeast Creek, with a large low salt marsh extending away from the culvert in the freshwater direction. Mummichogs and silversides are again common, but other species are capable of movement into the area due to a stronger saltwater input. All three low-culvert sites had the most anadromous species captured, although it is not possible to give any estimate of the population health or the effect of obstructions to flow on survival and growth. The placement of the culvert relative to the tidal range and the natural topography of the estuary interact to influence the spatial organization of estuarine conditions and, as a result, the distribution of species.

2.3. Conclusions

Patterns of tidepool fish may be best described by the geomorphology of the area, and the resulting sediment composition and algal communities. Patterns will be embedded in the seasonal trend of fish abundance as different species move in and out of the intertidal zone. We are encouraged to report an abundance of marine life inhabiting tidepools across Acadia National Park. For future intertidal work the wave exposure of the site, which is heavily correlated to many of the other important variables, will be tested as a constraining variable is the structure of fish assemblages.

The estuaries of Acadia National Park are like most in the New England region. Road construction and over-exploitation of anadromous fish populations have altered the structure of the systems. It is unfortunately not possible to give many recommendations without more complete studies of interaction among these impacts. Managers will need to understand species/community changes and modifications in the flow regime of estuaries to be able to make informed decisions. It would be worth knowing whether estuarine fish communities could be described on the basis of the presence, absence or position of the culvert in relation to the natural topography.

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CHAPTER 3

DEFINING CLUSTERS AND VARIABLES USING BOOTSTAPPING OF PRINCIPAL COMPONENT ANALYSIS: DEVELOPMENT OF TECHNIQUES FOR ANALYSIS OF ECOLOGICAL DATA

3.1. Introduction

The structure of communities is the result of a number of species-environment and inter- and intra-species interactions. As a result, in order to determine how communities relate to physical variables, there are a number of response variables and predictor variables that need to be tested which require multivariate statistical techniques. The work of Magnuson et al. (1998), Schlosser and Kallemeyn (2000) and Auster et al. (2001) provide a basis for multivariate analysis of marine and aquatic species abundance data.

Principal Component Analysis (PCA) is a well-known tool for reducing data and identifying patterns in ecological studies. In the present case, PCA is applied to species abundance data (response variables) collected at a number of sampling sites (experimental unit). This type of data is commonly collected as fisheries-independent data in trawl surveys. PCA produces new variables that explain variation in the original data, with the first few principal axes accounting for the largest amount of the total variance. The new variables are not correlated and when using normally distributed or standardized original variables, PCA produces normally distributed new variables, an assumption in any parametric tests (Gotelli and Ellison 2004). The new variables can be used in further analyses such as regression, analysis of variance and can include a spatial component if the data permit (Gotelli and Ellison 2004). PCA depends on intercorrelations within the original data to produce the new variables and, as a result, may not produce results and may not be successful when using unstandardized variables (Gotelli and Ellison 2004). Standard PCA suffers from a lack of ability in statistically, and quantifiably, defining groups or clusters within the analysis and is often not accompanied by any account of confidence bounds or description of the variance around scores.

Bootstrapping is a widely used technique where the original data set is resampled, with replacement, allowing for the creation of confidence limits and an understanding of the distribution around estimated parameters (Chernick 1999). There has been a great deal of application of bootstrapping including survival and multivariate analyses (Chernick 1999). A recent ecological application is the estimation of statistical significance and identification of feeding groups based on stomach content analysis of fishes in the Gulf of Maine using dendrograms (Garrison and Link 2000). Diaconis and Efron (1983) were the first to apply the bootstrap procedure to PCA, but the application was primarily to showcase the advantages given by computer-intensive data analysis. Peres-Neto et al. (2003) demonstrated the application of bootstrap techniques to PCA and the value to ecologists in understanding which principal components are important and which represent random "noise in the data". One would like to avoid describing patterns based on randomness. Jackson (1993) uses bootstrap of principal components to establish "stopping rules", when the principal components generated are no longer providing meaningful dissection of the correlations amongst variables. The bootstrap procedure out-performed other techniques in identifying structure in the datasets (Jackson 1993). I have developed a program in SAS for bootstrapping PCA, as to appropriately and statistically define groups of species that cluster with one another, and place confidence limits on the new variables generated in the analysis.

Transformations are commonly applied to datasets prior to a multivariate, or for that matter any, statistical analysis to satisfy the distributional assumptions of normality and constant variance of residuals. Typically, count numbers are transformed to normal distribution with square root transformation, proportion number are transformed to normal distribution with an arcsine squared root transformation, and log-normally distributed data are often log transformed. The choice of data transformation may influence the resulting interpretation of PCA results. Abundance data can be subjected to transformations and standardization. There are a number of recommended transformations of data, including the Z-score (Gotelli and Ellison 2004), natural log and square root. I will compare the results of these transformations to those generated with non-transformed data, and discuss the consequences on interpretation of the PCA results.

This work will utilize a dataset of fish species abundance collected from tidepools along the Maine coast to determine the applicability of a bootstrap-PCA program and what pitfalls may be present. The transformations will be compared to determine the best approach for abundance data.

3.2. Materials and Methods

3.2.1. The Data Set

The dataset is relatively small with limited species and sites, as to make interpretation more straightforward. The dataset was obtained from a survey of tidepool fishes and relevant physical and biological variables around Acadia National Park. A discussion of the dataset can be found in chapters 2 and 4, and is limited to sample periods 3 and 4 is this study.

3.2.2. The Programs

A full text version of the bootstrap-PCA program, written for use in SAS™, can be found in Appendix A. Essentially, the program resamples the dataset until it has generated a new set of data that is equivalent, in the number of sites, to the original. A Pearson correlation matrix, eigenvectors, eigenvalues and factor scores for each principal component/site is generated and held in memory. The process continues for the desired number of iterations and, once completed, the results are written to files. The files were imported into Microsoft© Excel™ for organization. SYSTAT™ v.10.2 was also used for running PCA on the original data, for comparison to the bootstrapped results. Sigmaplot™ v. 9.01 was used for all graphing.

3.2.3. Standardizations

There are a number of standardizations that will be tested in the analysis, for effects on interpretation of clustering, eginvector scores, and identification of outliers. The first standardization to be used is the Z-score, given by Gotelli and Ellison (2004) as

$Z = \frac{\left(Y_i - \bar{Y}\right)}{s}$, where Y_i is the value of a sample, $\bar{y}$ is the mean from all samples, and s is the sample standard deviation.

Two other transformations will also be used, where Z denotes a transformation and the subscript the type. The first is the natural logarithm:

$Z_{i\mathrm{LN}} = \ln(Y_i + 1)$

and the second is the square root:

$Z_{i\mathrm{SQRT}}$ = Sqrt(Y_i).

The use of Euclidean distance was used to describe distances between principal components generated from different analyses. The Euclidean distance ($d_{i,j}$), is defined as:

$$d_{i,j} = \sqrt{\sum_{k=1}^{n} \left(y_{i,k} - y_{j,k}\right)^2}$$

In addition, a difference calculation was used, where the square root and power components of the Euclidean distance are not applied and only the subtraction is used.

To compare to the results of transformations the untransformed data will also be employed in the PCA-Bootstrap procedure. The optimal number of Bootstrap iterations will also be tested at n=100, 500, 1000 and 10000 and evaluated for stability of scores.

3.3. Results

Initially, the results of the bootstrap and PCA for sample 4 suggest that the fish species sampled are not distinguishable as communities (Figure 3.1). However, once the loadings from the 100 runs are divided into those where rock runnels received a positive score (25 out of 100 runs) and those where they received a negative score (75 out of 100 runs), it becomes clear that there is a division between the species (Figure 3.2). The tendency for scores to vary between positive and negative values, as seen in Figures 3.2 and 3.3, is referred to as flip-flopping.

When the square root transformation was applied to the same data used to generate Figures 3.1 and 3.2, the results were encouraging with the amount of flip-flopping decreasing (Figure 3.4) and a much clearer separation between the fish species occurred when plotting the loading for the first and second principal components (Figure 3.5). The effect of transformations was then determined using data from the third sampling period as well. The number of iterations during the bootstrap process was increased, for the third sample period, to n=200 to produce more opportunities for the flip-flopping to occur.

The effect of the transformation types for the two sampling periods was first attempted by comparing only component loadings (Figure 3.6 and 3.7 for sample periods 3 and 4, respectively). The results show agreement that characterize mudflat species *Fundulus heteroclitus, Apeltes quadracus* and *Gasterosteus aculeatus* as a different group than the rocky intertidal *Pholis gunnelus, Pollachius virens*, *Myoxocephalus scorpius*, *Myoxocephalus aenaeus*, *Cyclopterus lumpus* and *Liparus atlanticus*. The results further suggest that *Pollachius virens* and *Myoxocephalus aenaeus* are not completely associated with the other rocky intertidal species as they did not overlap with other species.

The Euclidean distance was used to compare eigenvector scores. Rock gunnel was chosen because it was the most common species, and never received an eigenvector

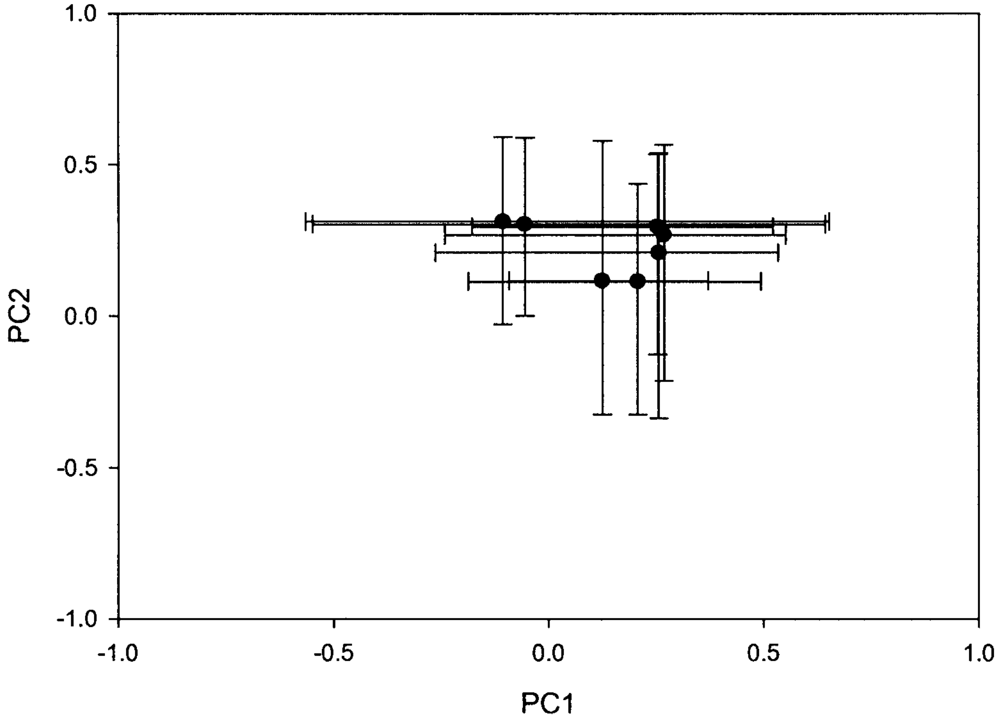

Figure 3.1. Results of PCA with bootstrap created 95% confidence intervals displaying the loadings for tidepool fish species calculated for principal component 1 (PC1) and 2 (PC2).

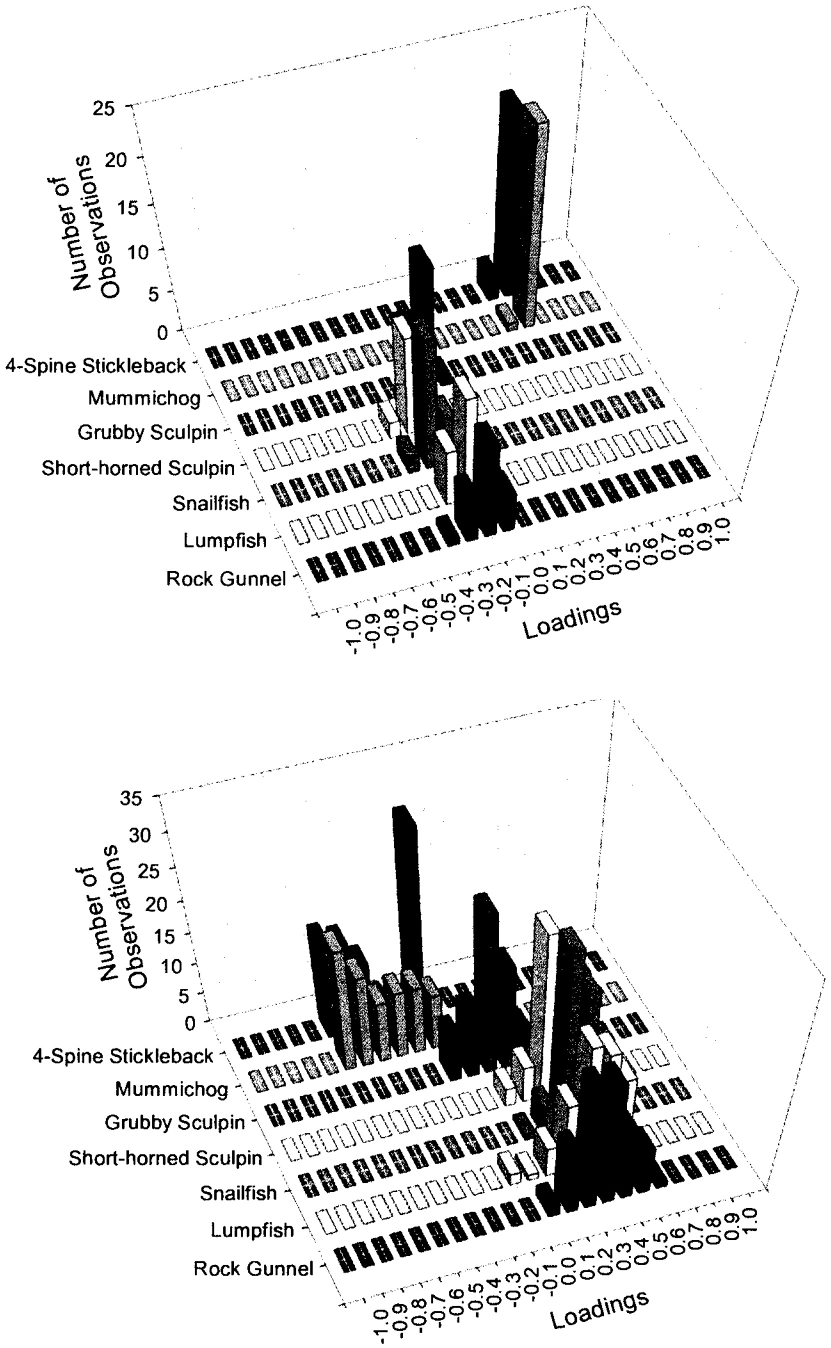

Figure 3.2. Frequency distribution for loading scores from bootstrapped principal component analysis divided into when rock gunnels scored negative values (top, n=25) and positive scores (bottom, n=75).

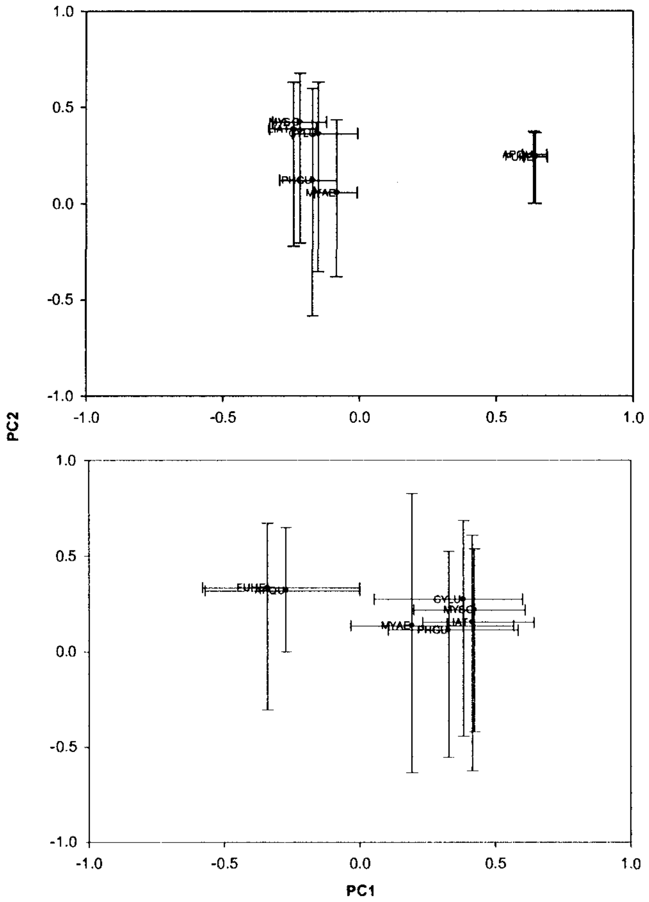

Figure 3.3. Principal component loadings for each of the species when rock gunnels scored negative values (top, n=25) and positive scores (bottom, n=75). PHGU = *Pholis gunnelus,* FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus* Means and 95% confidence limits calculated from component loadings generated from bootstrapping of principal component analysis.

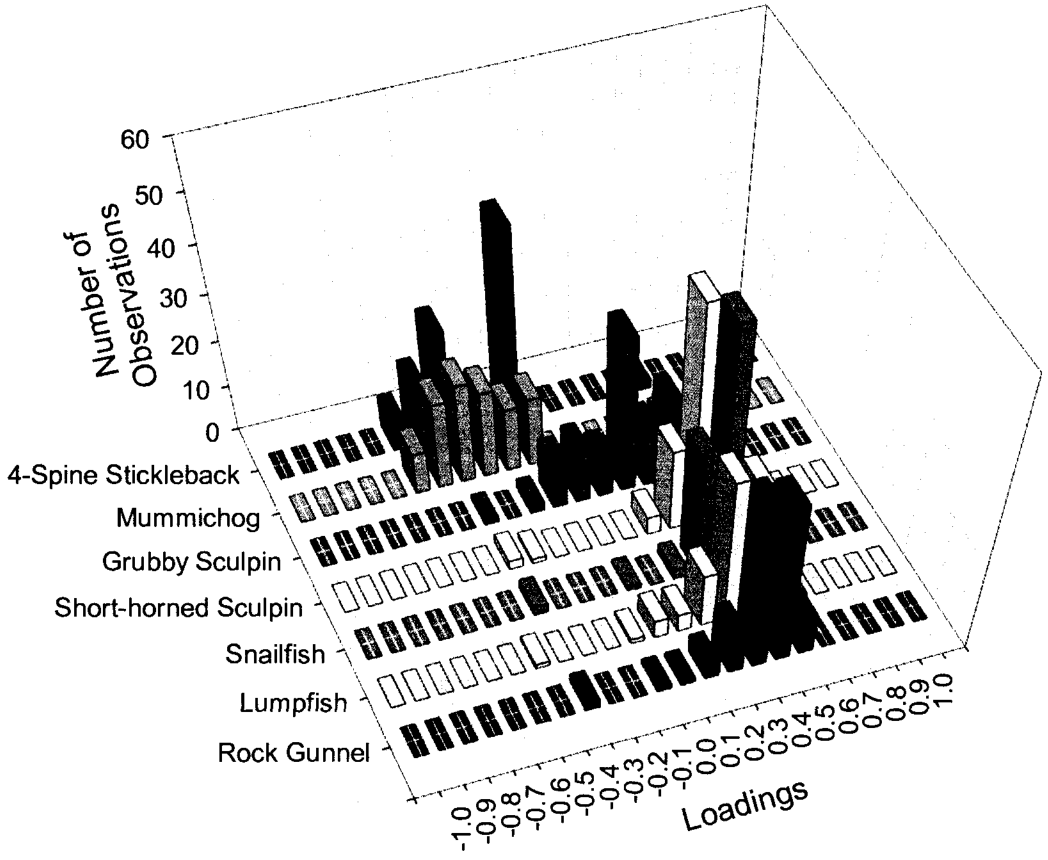

Figure 3.4. Frequency distribution for loading scores from bootstrapped principal component analysis for square root transformed tidepool data from sample 4. Note that the number of negative loading scores has been significantly reduced compared to other runs (Figure 3.2).

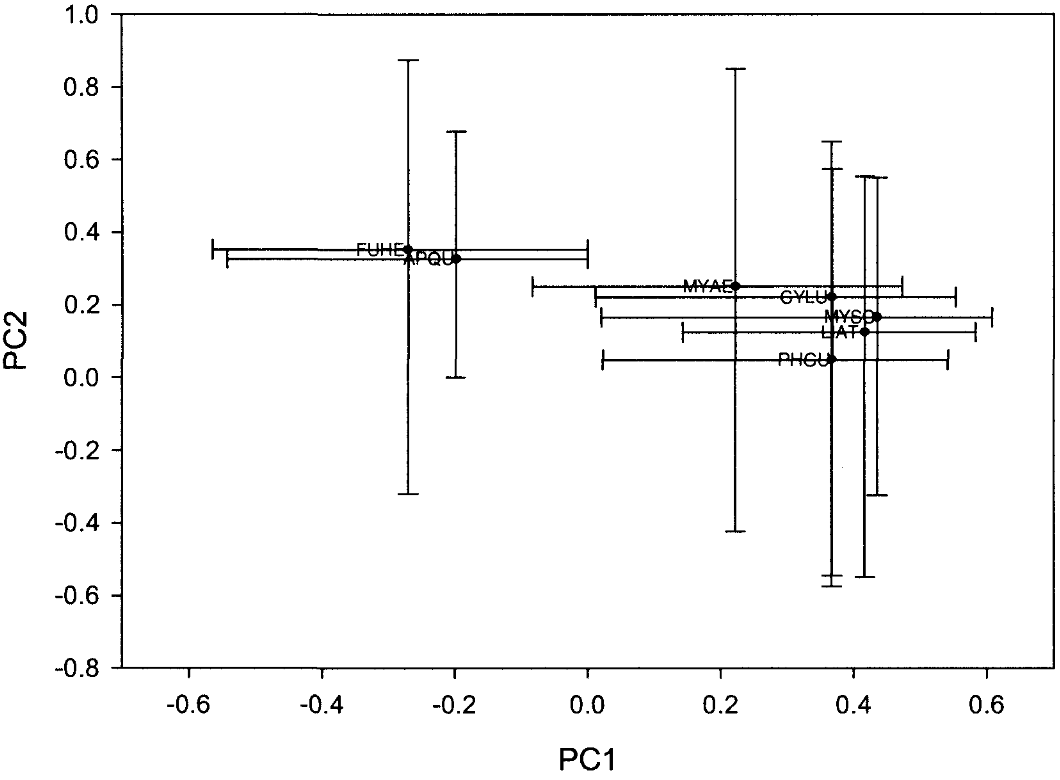

Figure 3.5. Results of PCA with bootstrap created 95% confidence intervals displaying the loadings for tidepool fish species calculated for principal component 1 (PC1) and 2 (PC2) using square root transformed data. Both means and confidence limits calculated from component loadings generated from bootstrapping of principal component analysis. FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*

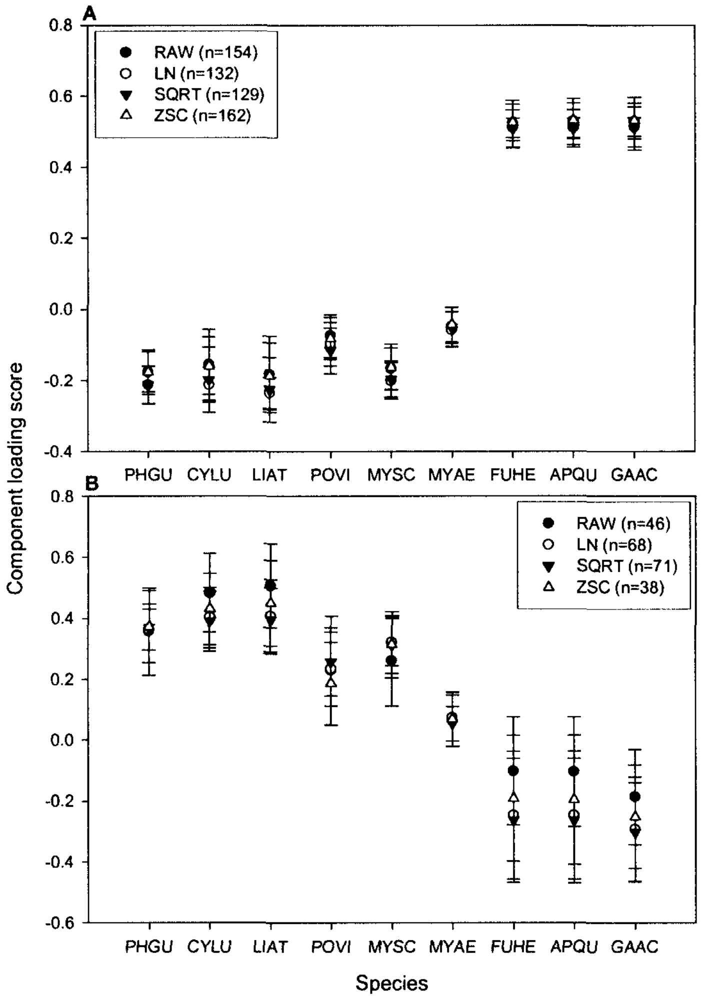

Figure 3.6. Component loading scores for all species in sample period 3. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: PHGU = *Pholis gunnelus,* POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

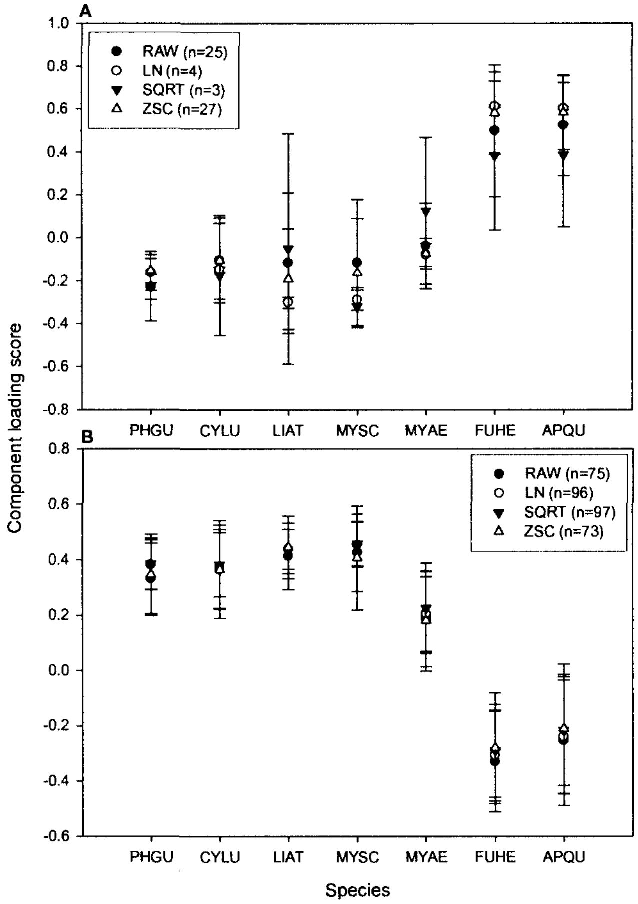

Figure 3.7. Component loading scores for all species in sample period 4. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: PHGU = *Pholis gunnelus,* POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

score of 0 in any bootstrap runs. This is in contrast to many of the other species, which were missed during bootstrapping due to low presence across sampled tidepools.

In sample period 3, both the distance (Figure 3.8) and Euclidean distance (Figure 3.9) measures agreed with the characterization of 3 distinct groups: rocky intertidal (*Pholis gunnelus, Myoxocephalus scorpius*, *Cyclopterus lumpus* and *Liparus atlanticus*), secondary rocky intertidal (*Pollachius virens* and *Myoxocephalus aenaeus*) and mudflat (*Fundulus heteroclitus, Apeltes quadracus* and *Gasterosteus aculeatus*). The results of the analysis of sample period 4 for both the distance (Figure 3.10) and Euclidean distance (Figure 3.11) measures also agree with the characterizations, although with fewer species since the *Pollachius virens* and *Gasterosteus aculeatus* were not captured.

Of perhaps more important implications is the effect of transformation played on the calculation of the loading and eigenvalue scores. The cause of the different results in Figures 3.1 and 3.5 is the number of iterations associated with positive and negative gunnel scores (Figure 3.7, see legends). Lower numbers of iterations with either positive or negative results, as a result more skewed towards one direction, resulted in better component loading scores. The square root and natural logarithm results had the least flip-flopping of scores. This difference also caused the eigenvalue scores to be affected (Figures 3.12 and 3.13). When the first principal component eigenvalue scores were subjected to one factor analysis of variance, testing for differences amongst transformations, the eigenvalue scores and percent of explained variance for natural logarithm and square root transformations were

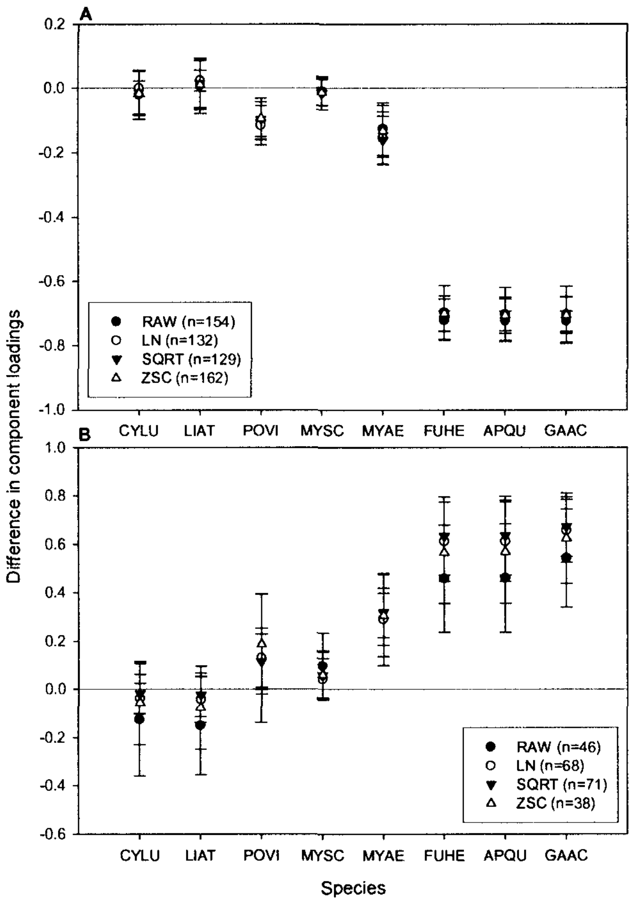

Figure 3.8. Distances for all species relative to the rock gunnel (*Pholis gunnelus*), calculated for species in sample period 3. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. The reference line indicates a score of zero, which would indicate a complete correlation with rock gunnel abundance. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

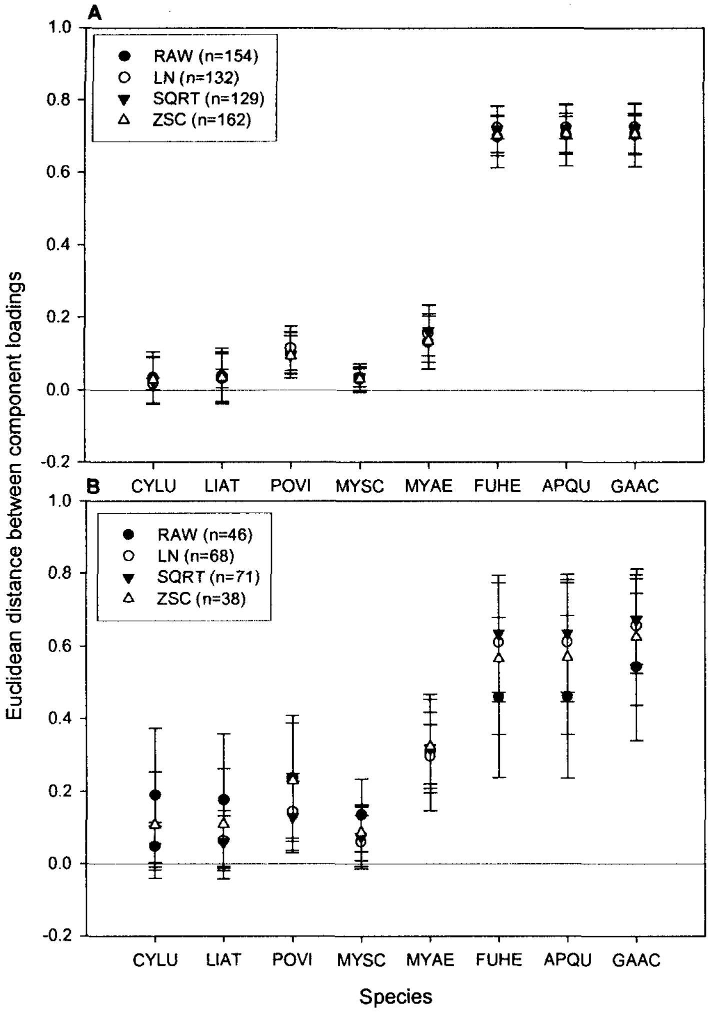

Figure 3.9. Euclidean distances for all species relative to the rock gunnel (*Pholis gunnelus*), calculated for species in sample period 3. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. The reference line indicates a score of zero, which would indicate a complete correlation with rock gunnel abundance. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

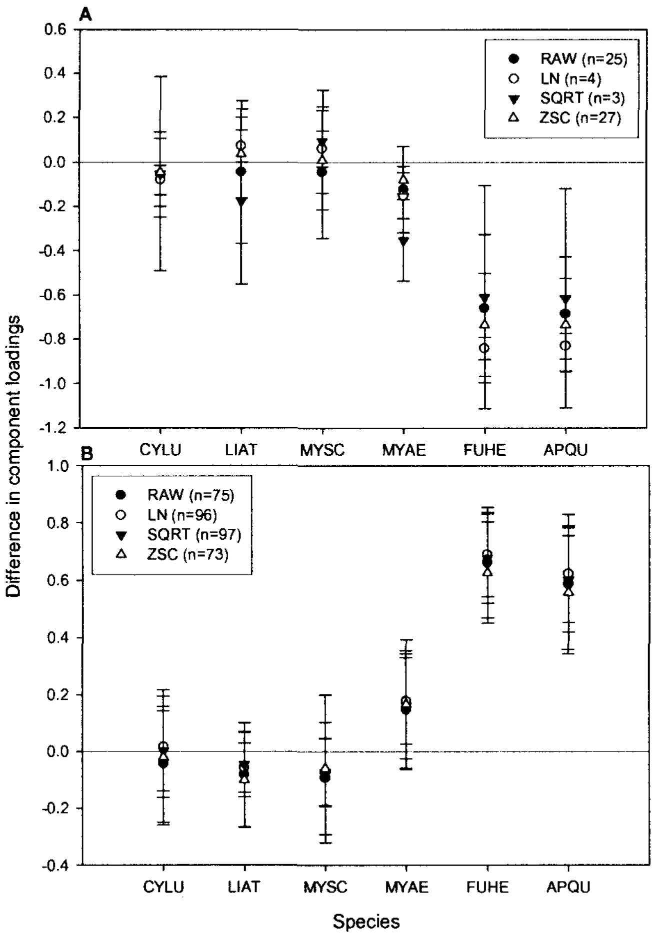

Figure 3.10. Distances for all species relative to the rock gunnel (*Pholis gunnelus*), calculated for species in sample period 4. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. The reference line indicates a score of zero, which would indicate a complete correlation with rock gunnel abundance. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

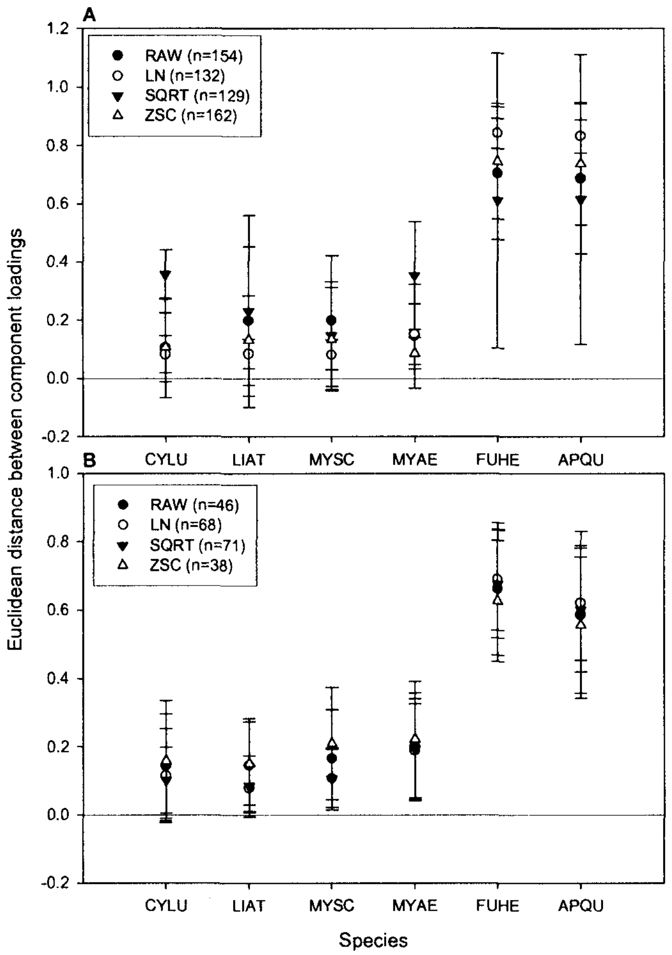

Figure 3.11. Euclidean distances for all species relative to the rock gunnel (*Pholis gunnelus*), calculated for species in sample period 4. Results are divided into occasions where rock gunnels were scored with negative (A, above) or positive (B, below) values (see Figure 3.2), for the various transformations (see legend). Numbers of bootstrap runs used to calculate means and standard deviation also shown in legend. The reference line indicates a score of zero, which would indicate a complete correlation with rock gunnel abundance. Transformations: RAW = no transformation, LN = natural logarithm, SQRT = square root, ZSC = z-score. Species: POVI = Pollachius virens, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, MYSC = *Myoxocephalus scorpius*, MYAE = *Myoxocephalus aenaeus*, CYLU = *Cyclopterus lumpus*, LIAT = *Liparus atlanticus*, GAAC = *Gasterosteus aculeatus*.

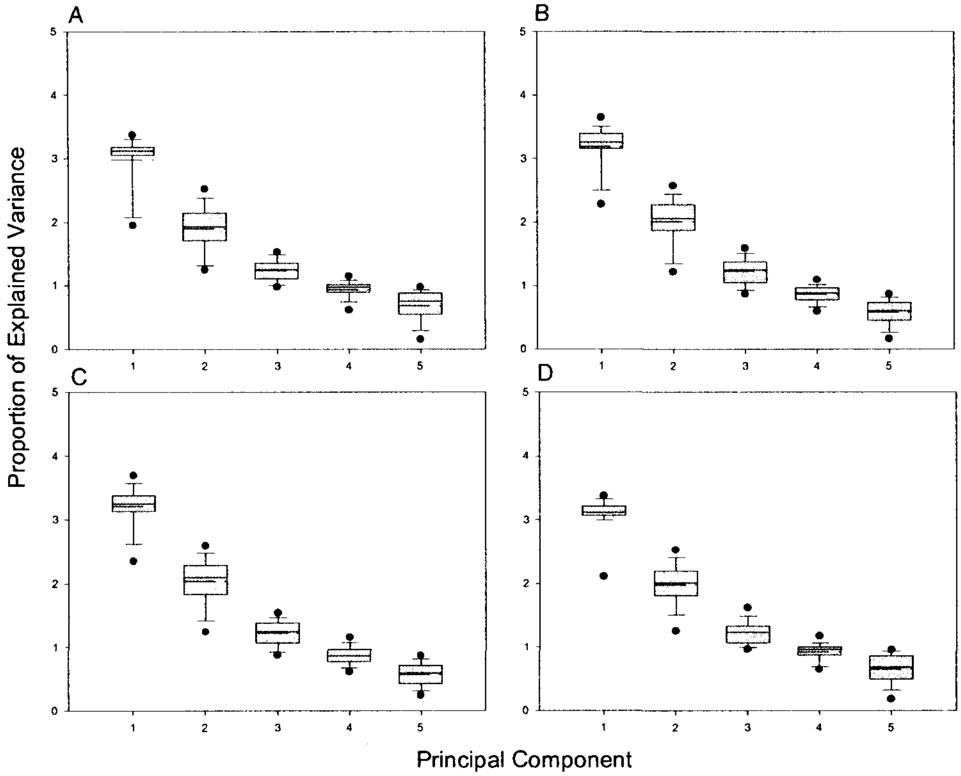

Figure 3.12. Box plots of the proportion of explained variance for first 5 principal components of sample 3 generated from bootstrap (n=200). Mean (dashed line within box), median (solid line within box), 25th and 75th percentile (boundary of box), 10th and 90th percentile (whiskers) and scores beyond 5th and 95th percentile (circles) are shown. Each graph gives results using different data transformation (A = raw data, B = natural logarithm, C = square root, D = z-score).

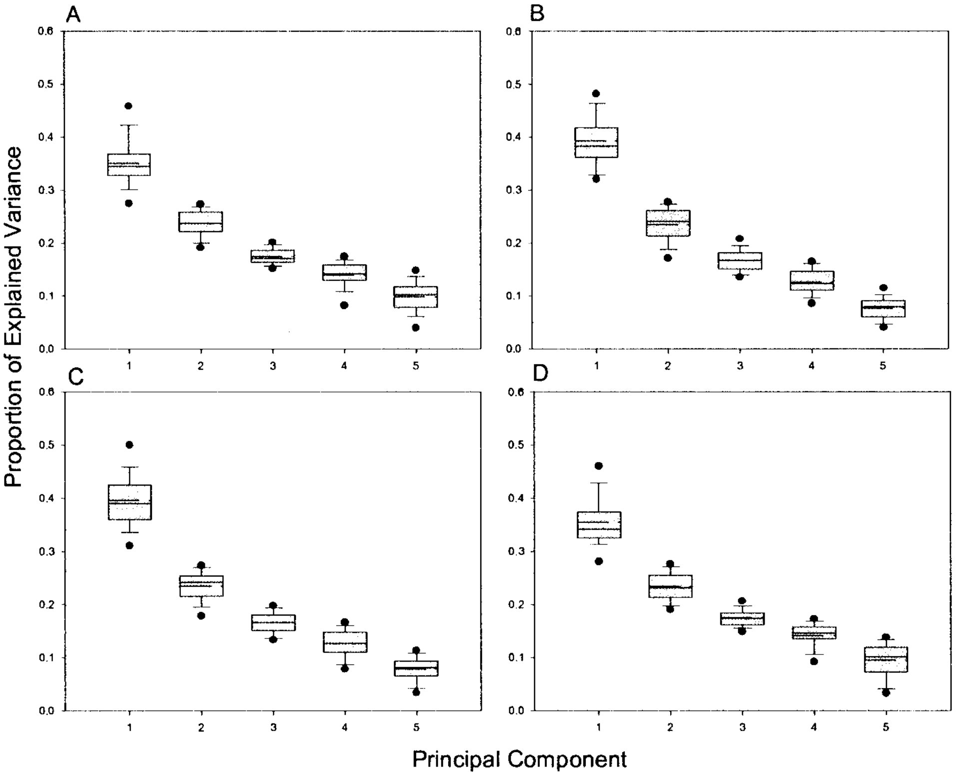

Figure 3.13. Box plots of the proportion of explained variance for first 5 principal components of sample 4 generated from bootstrap (n=100). Mean (dashed line within box), median (solid line within box), 25th and 75th percentile (boundary of box), 10th and 90th percentile (whiskers) and 5th and 95th percentile (circles) are shown. Each graph gives results using different data transformation (A = raw data, B = natural logarithm, C = square root, D = z-score).

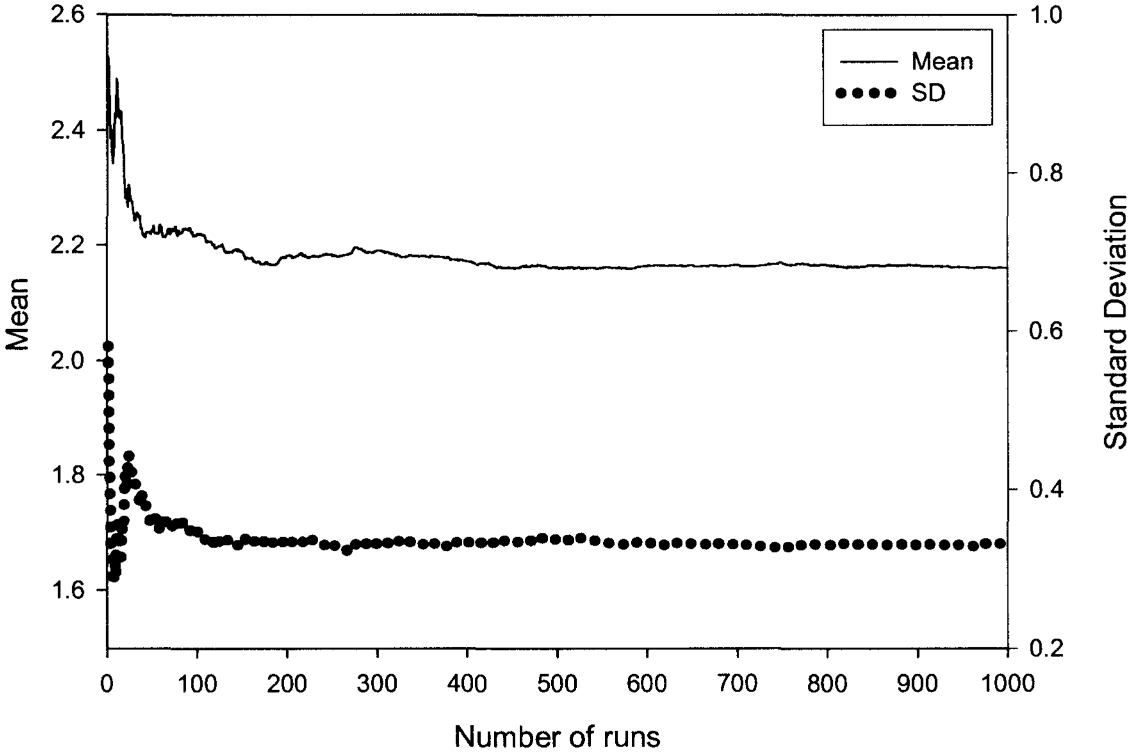

Figure 3.14. The mean eigenvalue score and associated standard deviation calculated on 2-1000 bootstrap iterations.

significantly higher (Bonferroni post hoc test, p<0.00001) than the z-score transformed and non-transformed data in Sample 4. The same result was seen in sample 3, but with reduced differences (Bonferroni post hoc test, p<0.01).

If only the results associated with negative gunnel scores in sample three or positive gunnel scores in sample four were considered, the differences among species increased, error estimates were reduced and there was more coherence among the transformation types. The consequence of this is that one may have to consider both the negative and positive values in elucidating the results of the bootstrapped PCA. When one considers the influence of the number of runs in determining the mean eigenvalue scores (Figure 3.14), it is clear that at least 200 runs of each scenario should be employed to make conclusions.

3.4. Discussion

Correlations amongst fish species were strong despite more sporadic and rare detection of some species, and as a result, use of the bootstrap-PCA results requires careful examination of outputs. If used in conjunction with the stopping rules outlined by Jackson (1993) and robust PCA techniques developed by Jackson and Chen (2004), the determination of confidence bounds and associations among species is a powerful tool. Jackson (1993) advocates using the bootstrap-created 95% confidence limits for eigenvalues and eigenvectors in determining stopping rules and relevant variables. The present results suggest that bootstrapped PCAs may produce variable results that will have to be checked for flip-flopping in order to avoid dismissing variables (species) as unimportant. The concern is that wide confidence limits may be an artifact of the analysis, and not reflect the true structure of the dataset.

"Flip-flopping" could result from relatively low sample size (numbers of tidepools) or that 0 scores were common for some species (fourspine stickleback). In regards to sample size, as a thumb of rule PCA often require that the number of sites is at least equal to 2.5 – 3 times the number of variables being tested (Jackson 1993). That is, the sample size required is relative to the number of variables. Since this requirement is achieved in the analysis, the sample size will be discounted as a cause. It is known that ordination analyses are sensitive to zeros (Sharma 1996). Although many zeros were given to species suggesting that some species may be rare, I do not believe they should be removed from the analysis. The reason is two-fold. First, zeros are common in ecological studies where processes that determine abundance operate on many scales. For example, rare species may become common over time, and excluding the species at a given time may result in biases in the assemblage structure as species are chosen for the analysis. Second, species not being present is information that may be important. The problem of flip-flopping of scores should be dealt within the analysis. The flip-flopping is not believed to be an artifact of the bootstrap procedure. Slight differences in the original data matrix and sites are responsible for the differing scores given to each species, and it is important to note that the relative score of one species compared to the others does not change. A good example of the sensitivity of PCA and component loadings to the data set is seen in Chapter 7 (Tables 7.5, 7.8) where the SYSTAT generated loadings changes direction (positive to negative) for the monkfish (*Lophius americanus*) between the spring and fall sample periods. However, the change in direction did not suggest a different grouping of species. To the contrary, the group of species positively and negatively associated with monkfish was remarkable similar between the two sample periods, and also received loadings with different directions relative to zero. Therefore, it is the magnitude of the component loadings and the correlations with other species that is important, not the direction of the component loading score given alone. The result of calculating the Euclidean distances and distances from rock gunnel to the other species demonstrates its usefulness in determining differences among species loadings.

The test of the effect of transformations distilled down to two characteristics that showed a difference amongst the type of transformation. First, the eigenvalue scores demonstrate that the natural logarithm and square root transformations had higher eigenvalues and contributed more to the total explained variance for the first two principal components. Because the square root transformation more consistently kept mean and median values equal and reduced the spread of outliers compared to the natural logarithm transformed data, we suggest using square root transformations in the case of abundance data. The conclusion from this is that the effects of numerous zeros can be mitigated by appropriate transformation of raw data, and observing the results.

Ultimately the questions that are of importance are whether specific species are associated with one another, and what factors are responsible in shaping those associations. The relevance to management is that the methodology will allow identification of strong species-species interactions and determine the limits of biotic communities that depend on specific physical characteristics. Eventually, this can be applied to protect threatened species and communities, minimize the ecological impacts of fishing and bycatch of non-target fish species, through identification of potential marine protected area (MPA) boundaries and determining how one should best monitor the system for change. O'Neill (2001) argues that ecosystems, by definition, include biases regarding spatial coverage by assuming a closed system. The analyses presented here constitute a methodology for determining structure in populations of organisms. By doing so, biases imposed by prior assumptions of ecosystem boundaries are removed in favor of designating structure based on environmental variables. Ecologically speaking, the results demonstrate that there are specific assemblages of fish that are related to the physical environment, and that the structure can be measured over time.

In conclusion, use of the bootstrap-PCA technique demonstrated that structure in the biological systems can be identified across differing habitats. Furthermore, the component loadings given by the analysis are important compared to other species, not taken alone, since they may flip-flop depending of the dataset used. Square-root transformations outperformed other transformation and standardization types for fish abundance data. The PCA-bootstrap technique appears to have potential uses that will contribute to understanding the structure of assemblages of fish determined from surveys. The structure and ecological significance of the analysis will be covered in Chapter 4.

3.5. References

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CHAPTER 4

PRINCIPAL COMPONENT ANAYLSIS AND INTERTIDAL ECOLOGY: LINKING PHYSICAL AND BIOLOGICAL PROPERTIES.

4.1. Introduction

Tidepool fishes are those that inhabit tidepools at low tide and for that reason are isolated in an area that may experience frequent disturbances. These fish include those that inhabit tidepools for much of their entire life cycle, those who use tidepools as refugia during juvenile stages and those that are accidentally stranded in tidepools during low tide. Intertidal areas are also particularly susceptible to oil spills, sewage and chemical pollutants released into coastal areas, and coastal development (Moring 1983). Strong associations between fish species and invertebrates and algae, many of which are sessile, that utilize tidepool habitats means that moving out during disturbances may be insufficient to reduce the effect of disturbances.

A first step in conservation and protection of natural resources is describing the distribution of organisms and their associated habitats. Moring (1993a) described the tidepool fishes that are found along the coast of Maine. I am interested in the characteristics of tidepools that makes them suitable for fish to use. Microhabitats are considered to be subsections or finer subdivisions of a habitat, in this case tidepools, in which an animal lives (Kramer et al. 1997). This begs the question: are characteristics or microhabitat variables quantitatively related to tidepool fish communities along the coast of Maine. This will be necessary information to predict the consequences of shoreline disturbances that alter the physical characteristics of near shore habitats. The microhabitat variables can be broken into biological (algal and invertebrate abundance) and physical (substrate, temperature, etc.) characteristics.

Acadia National Park (ANP) receives nearly 3 million visitors annually, largely during the months of July-September. There are competing interests in the pressures of tourism and development in and around the park combined with the National Park priority of protecting ecosystem health. Recently there have been changes in management policy at the park designed to protect particular habitats that are susceptible to destruction by human activities. Organisms that inhabit the intertidal zone may be put at risk to exposure from human activities necessitating monitoring and development of assessment techniques that can be integrated into management decisions.

In this chapter, principal component analysis will be used to reveal relationships among environmental parameters and the fish community structure.

4.2 Statistical Methods

Principal component analysis (PCA) is a multivariate statistical technique that reduces the number of variables (species, physical variables) to new variables that explain the correlations in the original dataset while not losing essential information. PCA is one of the most common data-exploratory multivariate ordination techniques used in ecological studies (Rao 1964, Jackson 1993, Chen and Harvey 1995). Principal component analyses were used in this study to derive a set of new variables (principal components or PCs) that could explain variation in tidepool fish abundance. For location of sites, refer to Figure 2.1. Multiple PCs are derived for each of the groups of variables (F = fish abundance, A = algal abundance, P = physical variables, and I = invertebrate abundance) equal to the number of original variables within each group. However, the first principal component derived for each group (F1, A1, P1 and I1) explains the greatest amount of variance within the group, with each additional principal component explaining lesser and lesser amounts of the variance. Typically, only the first few principal components are considered since they explain the majority of the variance; the remainders of the derived PCs are of little value and are thus not reported.

The physical and biological variables collected during the tidepool inventory are given in Tables 4.1 and Table 4.2, respectfully. Fish counts for each tidepool were transforming by taking the square root (Chapter 3). The relative abundance of algal and hard and soft invertebrate species or group of species was described for each tidepool by assigning an abundance score from 0-5 with 0 indicating absence, 3 indicating average abundance and 5 indicating dominance in the tidepool. The relative abundance score had 1 added to them and was natural-log transformed and standardized. Temperature and salinity were measured with an YSI 85 DO, Conductivity, Salinity, Temperature Instrument from YSI Environmental. The area was assumed a rectangular shape and used the maximum length and width. Mean depth was calculated from transects across the maximum length and width of the tidepool. To account for irregular shape and complex cover a physical complexity score was calculated for each tidepool, using information collected in surveys regarding the shape, and amount of cover afforded by rocks and algae. For each additional source of complexity (irregular edge, overhanging ledge, large boulder, crevasses, algal cover, each additional substrate type) a value of one was added. The scores were summed and a scale from 1 to 9 resulted (mean = 4.7, median = 4). Relative tidal position was assigned to each tidepool as a value from 1 to 3 with a score of 1 given to a tidepool below the low tide mark on an average tide, 2 for a

Table 4.1: Physical variables collected for each tidepool.

Variable	Units
Pool Length	cm
Pool Depth	cm
Substrate type	(rock, mud, etc)
Physical complexity	Combined measure
Vertical Height	Relative position
GPS	UTM
Algae Cover	Estimated %
Bottom Cover	Estimated %
Temperature	ºC
Salinity	‰
Tidal Height	m
Rain	Relative scale
Wind	Relative scale
Lighting	Relative scale

Table 4.2: Biological variables collected for each tidepool. Each of listed species, or groups of species, was given a relative abundance score from 1 – 5.

Algae

- Eel Grass
- Spartina type
- Ascophyllum
- Rockweed Fucus
- Brown fuzzy algae
- Enteromorpha
- Brown thread like
- Irish Moss
- Sugar kelp
- Horse kelp
- Edible kelp
- Sea Lettuce
- Green Fuzzy
- Purple laver
- Dulse
- Coralline crust
- Coralline 3-D

Hard Invertebrates

- Barnacle
- Mussel
- Periwinkle
- Whelk
- Limpet
- Sponge
- Crab
- Hermit Crab
- Sea star
- Urchin

Soft Invertebrates

- Amphipod
- Isopod
- Nudibranch
- Scaleworm
- Worm-like
- Anemone
- Cucumber
- Eggs
- Shrimp

tidepool was below low tide mark on a spring tide, and 3 for a tidepool that below low tide mark on any tide.

To evaluate the patterns or relationships among the fish, invertebrate, algal and physical principal components, the data sets were subjected to Pearson multiple pairwise comparison tests with Bonferroni corrected alpha levels. Bartlett Chi-square statistic was used to test the global hypothesis concerning the significance of all of the Pearson pair wise correlations. The data were grouped into four sampling periods representing (1) late spring (June 6-June26); (2) early summer (July 3-August 2); (3) late summer (August 3-September 18); and (4) early fall (September 29-October 21) to determine seasonal patterns in fish species abundance relative to the changes in microhabitat over the sampling periods.

4.3. Results

The first four principal components explain a greater amount of the variance in fish over each successive sample period except the last, Period 4 (Figure 4.1). The Bartlett Chi-square statistic for testing the global hypothesis concerning the significance of all correlations in the variable X site data matrix was 133.2 (df = 105, $P = 0.033$), 113.5 (df = 55, $P < 0.001$) and 115.6 (df = 66, $P < 0.001$) for sampling periods 2, 3 and 4, respectively. Sample period 1 found to not have a significant Bartlett test and will not be considered further. A matrix of correlation coefficients (Tables 4.3, 4.4, 4.6) and p-values for each of the principal components was generated. The tables present the results of the first 2-4 derived principal components only as the remainder did not offer additional information. To show the relative importance of the original individual variables in each of the derived principal components, eigenvectors scores were tabulated for sampling periods 2 (Table 4.7), 3 (Table 4.8) and 4 (Table 4.9). In the second sampling period, the Pearson pairwise comparisons demonstrated a significant positive relationship between the algal (A1) and invertebrate (I1) first principal components, and a negative relationship between both A1 and I1 and the first physical (P1) principal component (Table 4.3). For the third sampling period, there were significant positive relationships between the first fish principal component (F1) and the first invertebrate principal component (I1). There was also a significant relationship between A1 and I1, and a significant negative correlation between A1 and P1 (Table 4.4). In the fourth sampling period, the only significant relationships were between F1 and A1, and F1 and I1 (Tables 4.5).

From the eigenvector scores it can be seen that in Period 2 the kelp, fucoid and Irish moss algae dominate A1, the limpet, crab and a number of other species dominate I1 and P2 is largely influenced by temperature, physical complexity and area (Table 4.6). In sampling period 3 and 4, the negative scores of sticklebacks and mummichogs and the positive scores of the remainder of the fish species dominate F1 (Figure 4.2). Principal components A1 and P1 remained much the same as in period 2, although relative position had a greater influence in P1 (Table 4.7). There is no change in the important contributors to the principal components generated for the fourth sampling period, compared to the third sample period (Table 4.8). Important trends in the eigenvectors for Period 4 are (1) that pollock (not present) and grubbies had lesser impacts on the F1 scores, (2) the A1 eigenvectors are lowest for the mudflat species *Spartina* and *Enteromorpha*, and (3) generally eigenvectors for I1 were all positive, except the periwinkle was negative and among the lowest scoring invertebrate species.

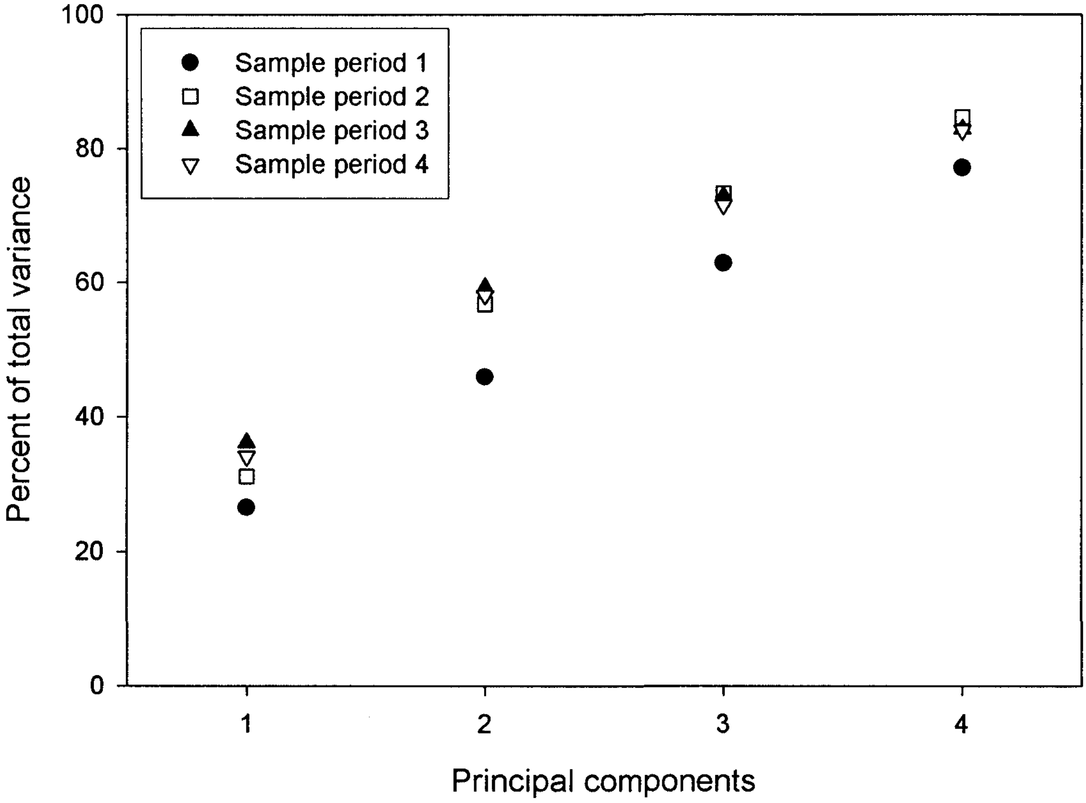

Figure 4.1. Cumulative total explained variance for the first four principal components calculated for each of the four sample periods.

Table 4.3. Correlation coefficients from Pearson pairwise comparisons between principal component scores for Period 2. Principal components listed are from analysis of fish species (F1-4), algal abundance (A1-A3), invertebrate abundance (I1-I4) and physical parameters (P1-P4) for . Bolded values represent significant values ($p < 0.02$).

	F1	F2	F3	F4	A1	A2	A3	I1	I2	I3	I4	P1	P2	P3	P4
F1	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F2	0.00	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.
F3	0.00	0.00	1.00	.	.	.	.	.	.	.	.	.	.	.	.
F4	0.00	0.00	0.00	1.00	.	.	.	.	.	.	.	.	.	.	.
A1	0.27	-0.29	0.27	0.37	1.00	.	.	.	.	.	.	.	.	.	.
A2	0.22	0.04	0.07	0.04	0.00	1.00	.	.	.	.	.	.	.	.	.
A3	0.18	0.04	-0.13	-0.28	0.00	0.00	1.00	.	.	.	.	.	.	.	.
I1	0.50	0.01	0.29	0.34	**0.66**	0.22	0.10	1.00	.	.	.	.	.	.	.
I2	-0.18	-0.24	-0.14	-0.12	-0.03	-0.11	0.19	0.00	1.00	.	.	.	.	.	.
I3	-0.04	0.16	0.01	-0.06	-0.30	0.00	0.21	0.00	0.00	1.00	.	.	.	.	.
I4	0.20	0.20	0.14	0.04	-0.27	0.27	0.04	0.00	0.00	0.00	1.00	.	.	.	.
P1	-0.21	0.29	0.21	0.13	-0.05	0.03	0.02	0.07	-0.07	0.08	-0.05	1.00	.	.	.
P2	-0.37	0.12	-0.30	-0.32	**-0.63**	-0.09	0.20	**-0.57**	0.05	0.23	0.21	0.00	1.00	.	.
P3	-0.10	0.07	-0.05	-0.03	0.13	0.13	0.24	0.05	0.01	0.12	-0.25	0.00	0.00	1.00	.
P4	-0.01	-0.13	0.05	-0.24	-0.02	0.15	0.16	-0.01	0.29	0.11	0.08	0.00	0.00	0.00	1.00

Table 4.4. Correlation coefficients from Pearson pairwise comparisons between principal component scores for Period 3. Principal components listed are from analysis of fish species (F1-3), algal abundance (A1-A2), invertebrate abundance (I1-I3) and physical parameters (P1-P3) for Period 3. Bolded values represent significant values ($p < 0.01$).

	F1	F2	F3	A1	A2	I1	I2	I3	P1	P2	P3
F1	1.00	.	.	.	.	.	.	.	.	.	.
F2	0.00	1.00	.	.	.	.	.	.	.	.	.
F3	0.00	0.00	1.00	.	.	.	.	.	.	.	.
A1	0.52	0.09	0.16	1.00	.	.	.	.	.	.	.
A2	0.05	0.39	-0.16	0.00	1.00	.	.	.	.	.	.
I1	**0.60**	0.38	-0.02	**0.60**	0.44	1.00	.	.	.	.	.
I2	0.01	0.19	-0.14	0.05	0.21	0.00	1.00	.	.	.	.
I3	-0.14	0.14	0.05	0.11	0.11	0.00	0.00	1.00	.	.	.
P1	-0.51	0.11	-0.15	**-0.59**	-0.06	-0.32	-0.29	0.19	1.00	.	.
P2	-0.02	0.41	0.15	0.28	-0.00	0.19	0.03	0.27	0.00	1.00	.
P3	-0.04	0.25	0.00	0.03	0.05	0.05	-0.38	0.15	0.00	0.00	1.00

Table 4.5. Correlation coefficients from Pearson pairwise comparisons between principal component scores for Period 4. Principal components listed are from analysis of fish species (F1-2), algal abundance (A1-A3), invertebrate abundance (I1-I3) and physical parameters (P1-P4) for Period 4. Bolded values represent significant values ($p < 0.01$).

	F1	F2	A1	A2	A3	I1	I2	I3	P1	P2	P3	P4
F1	1.00	.	.	.	.	.	.	.	.	.	.	.
F2	0.00	1.00	.	.	.	.	.	.	.	.	.	.
A1	**0.59**	0.12	1.00	.	.	.	.	.	.	.	.	.
A2	-0.14	-0.35	0.04	1.00	.	.	.	.	.	.	.	.
A3	-0.16	-0.20	-0.07	0.07	1.00	.	.	.	.	.	.	.
I1	**0.59**	0.28	0.48	-0.20	-0.41	1.00	.	.	.	.	.	.
I2	-0.17	0.06	-0.27	-0.36	-0.35	0.00	1.00	.	.	.	.	.
I3	-0.18	0.24	-0.28	-0.26	0.17	0.00	0.00	1.00	.	.	.	.
P1	0.01	0.30	-0.08	-0.06	0.16	0.22	-0.36	0.38	1.00	.	.	.
P2	0.22	0.22	0.49	0.01	0.16	0.21	-0.14	-0.10	0.01	1.00	.	.
P3	-0.13	0.46	-0.09	-0.14	-0.03	-0.06	0.04	0.03	0.01	-0.00	1.00	.
P4	0.22	-0.17	0.10	0.04	0.09	-0.08	-0.28	0.01	-0.02	-0.01	-0.00	1.00

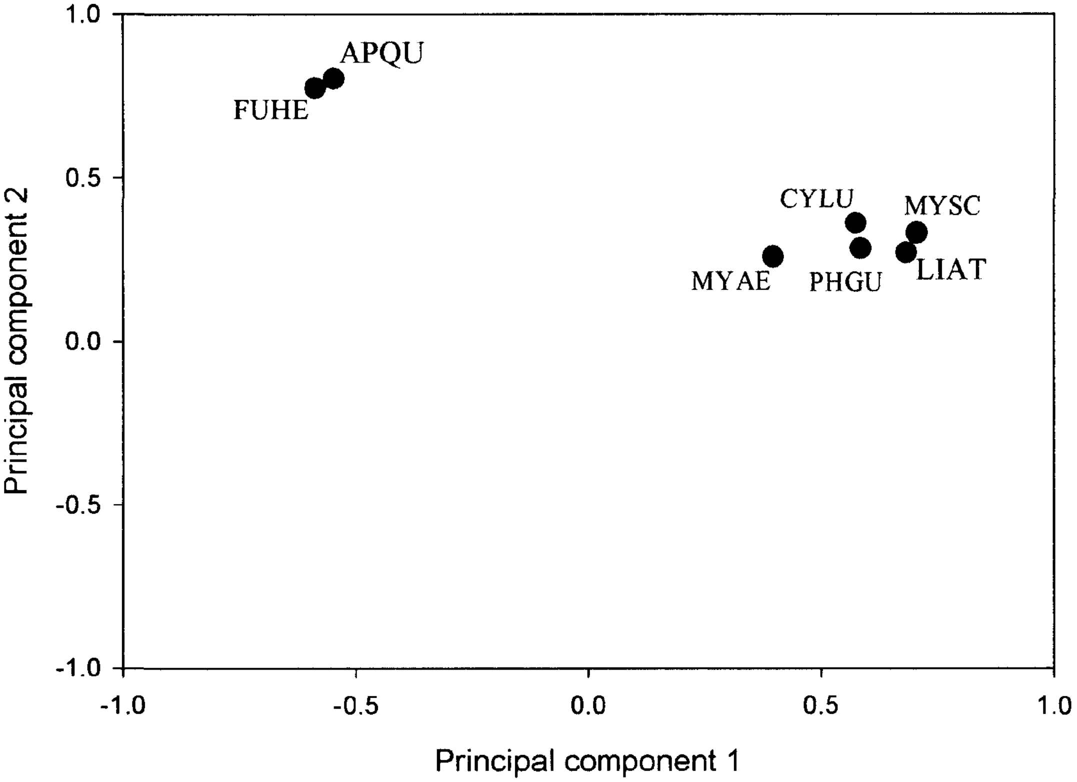

Figure 4.2. Loadings from first two principal components from analysis of the fish data for the fourth sample period. CYCL = lumpfish, LIAT = snailfish, MYAE = grubby, MYSC = shorthorn sculpin, PHGU = rock gunnel, FUHE = mummichog, APQU = fourspine stickleback

Table 4.6. Eginvector scores for principal components that demonstrated significant relationships for Period 2.

A1		I1		P2	
Sugar kelp	0.369	Limpet	0.414	Time of day	-0.060
Irish moss	0.313	Crab (*Carcinius*)	0.384	Substrate	0.072
Horsetail kelp	0.313	Nudibranch	0.317	Salinity	0.133
Dulse	0.306	Isopod	0.309	Tide height	0.198
Fucus	0.303	Seastar	0.301	Temperature	0.467
Brown fuzzy	0.300	Whelk	0.287	Complexity	-0.614
Ascophyllum	0.286	Shrimp	0.272	Area	-0.499
Sea lettuce	0.274	Barnacles	0.055	Depth	-0.130
Green algae misc.	0.270	Anemone	-0.078	Position	0.271
Coralline 3D	0.245	Hermit crab	0.260		
Kelp	0.221	Mussel	0.003		
Eelgrass	0.077	Periwinkle	-0.025		
Spartina	0.077	Brittlestar	0.014		
Brown stranded	0.019	Urchin	0.120		
Purple laver	-0.008	Amphipod	0.175		
Coralline crust	0.181	Egg misc.	0.077		
Enteromorpha	-0.090	Sea cucumber	-0.054		
		Worms misc.	0.151		
		Scaleworm	0.216		
		Sponge	0.191		

Table 4.7. Eginvector scores for principal components that demonstrated significant relationships for Period 3.

F1		A1		I1		P1	
GAAC	-0.509	Sugar kelp	0.319	Whelk	0.382	Tide height	0.545
APQU	-0.507	Fucus	0.316	Limpet	0.362	Temperature	0.471
FUHE	-0.504	Brown fuzzy	0.313	Crab (*Carcinius*)	0.360	Time of day	0.393
LIAT	0.248	Irish moss	0.298	Seastar	0.282	Salinity	-0.342
CYLU	0.222	Coralline crust	0.288	Scaleworm	0.280	Position	0.326
PHGU	0.233	Brown threads	0.282	Hermit crab	0.245	Area	0.040
MYAE	0.061	Horsetail kelp	0.281	Shrimp	0.235	Complexity	-0.243
MYSC	0.211	Coralline 3D	0.265	Barnacle	0.231	Depth	-0.116
POVI	0.128	Dulse	0.257	Isopod	0.125	Substrate	0.173
		Green misc.	0.243	Urchin	0.225		
		Ascophyllum	0.222	Brittlestar	0.003		
		Kelp	0.212	Worms misc.	0.063		
		Enteromorpha	-0.133	Eggs misc.	-0.029		
		Purple laver	0.087	Nudibranch	0.208		
		Spartina	-0.131	Amphipod	0.138		
		Sea lettuce	0.195	Sponge	0.178		
				Anemone	0.209		
				Periwinkle	0.128		
				Mussel	0.205		

Table 4.8. Eginvector scores for principal components that demonstrated significant relationships for Period 4.

F1		A1		I1	
MYSC	0.452	Sugar kelp	0.343	Sea cucumber	0.366
LIAT	0.412	Brown fuzzy	0.340	Brittlestar	0.360
FUHE	-0.406	Fucus	0.328	Hermit crab	0.331
APQU	-0.380	Sea lettuce	0.318	Isopod	0.323
CYLU	0.359	Coralline 3D	0.318	Limpet	0.316
PHGU	0.355	Brown threads	0.315	Crab (*Carcinius*)	0.307
MYAE	0.249	Horsetail kelp	0.305	Nudibranch	0.304
		Kelp	0.228	Seastar	0.294
		Irish moss	0.106	Urchin	0.102
		Coralline crust	0.190	Mussels	0.023
		Purple laver	0.112	Barnacles	0.081
		Dulse	0.227	Periwinkle	-0.126
		Green misc.	0.203	Amphipod	0.136
		Enteromorpha	0.116	Scaleworm	0.113
		Ascophyllum	0.217	Whelk	0.200
				Anemone	0.078
				Sponge	0.169
				Shrimp	0.100

4.4. Discussion

There was no inflection in the Period 1 variance as additional principal components were added, indicating an unstructured dataset (Jackson 1993). The results of the other sample periods suggest that the first and second principal components are the only important contributors to variance. Fish presence became more predictable over the course of the study, starting from randomly distributed species and progressing to increasingly structured correlations among species. Presumably this is related to the seasonal cycle, with deconstruction of patterns during the winter and renewal of patterns in the following year during the warmer growth period. The increase in the structure through the remainder of the sampling periods relates to patterns in recruitment and mortality/behavior of young fish. The influx of young-of-year fish is acted upon by selective predation or individuals engage in habitat choice. The initial more random distribution of young fish then becomes more structured and, as a result, more related to the microhabitat present in the tidepools with increasing date in the year.

The fish principal components showed that there were three primary types of tidepools, those where: (1) fish are absent, (2) mummichogs and fourspine sticklebacks are present, and (3) all other fish are present. This separation is largely controlled by the presence of the two different tidepool habitats around Acadia National Park: rocky ledges and mudflats. The two grouping of fish were clearly separated across this gradient and there appears to be little overlap. The groupings of fish species where mummichogs (*Fundulus heteroclitus*: FUHE) and fourspine sticklebacks (*Apeltes quadracus*: APQU) with threespine stickleback (*Gasterosteus aculeatus*: GAAC) separated from the other species of tidepool fish, particularly in the first component (Figure 4.3, Table 4.7, 4.8).

Furthermore, the rock gunnel (*Pholis gunnellus*: PHGU), Atlantic seasnail (*Liparis atlanticus*: LIAT), lumpfish (*Cyclopterus lumpus*: CYLU), and shorthorn sculpin (*Myoxocephalus scorpius*: MYSC) were separated from the grubby (*Myoxocephalus aenaeus*: MYAE) and pollock (*Pollachius virens*: POVI). Pollock and threespine sticklebacks were only part of the trend in the third sample period, and were not captured in the fourth sample period, although the remaining fish abided by the pattern detailed above.

Detailing finer scale associations will require studies over transition zones between the two primary habitat types. Within the cluster of tidepools with the majority of fish species (positive values in the A1 eigenvectors), the pollock and grubby were grouped to lesser degree than the lumpfish, snailfish and shorthorn sculpins. For the grubby this result is believed to originate from a lesser dependence on algal cover due to camouflage abilities shared with the shorthorn sculpin, and smaller size and presence in warmer water than the shorthorn sculpin which allows use of relatively shallow tidepools with reduced complexity. Pollock have been identified as a part-time transient species of tidepools (Chapter 2). A more unpredictable occurrence is due to reduced probability of capture in tidepools during the ebbing tide, the reducing numbers of pollock along the shoreline later in the year and schooling behavior which contribute to an uncertain relationship with the other species. Pollock use of the intertidal zone (Rangley and Kramer 1995) is confined to rocky shorelines in this study, but they have been captured in marsh habitats in Southern Maine (Michele Dionne, Wells National Estuarine Research Reserve, Personal Communication) suggesting distributional differences along the coast of Maine.

The important physical parameters were always associated with vertical position relative to tide height. Generally relative position of the tidepool influences the physical principal component in the same direction as temperature and tidal height and in the opposite direction as salinity. This relationship amongst variables suggested that as relative position increases, the temperature increases and salinity decreases. This relationship was modified by the tidal height, which were entered as the distance below mean tide level (a negative number), where higher low tides resulted in reduced temperatures and decreased salinities. The interaction between the marine environment (lower temperatures and higher salinities) and the terrestrial environment (higher temperatures, lower salinities) is clearly influencing the distribution of organisms.

Vertical zonation of species in the intertidal zone has been shown on the coasts of most continents (Zander et al. 1999). This pattern was clearly evident in the early sampling periods where A1 and I1 were both strongly correlated with the physical parameters. As the year progresses, strong biological associations slowly replace the initial physical-biological coupling restricted to lower trophic levels. That is, the associations amongst the invertebrate and fish species replace those amongst physical variables and algal species as the significant correlations in tidepools.

From the algal and invertebrate component loadings, the presence of macroalgae (and sea grasses) for the algae and the presence of whelks, crab (*Carcinius*), limpets, seastars, isopods and nudibranchs of the invertebrates were related. It has been shown that there are trait-mediated effects between crabs, periwinkles (*Littorina littorea*) and fucoid algal communities (Trussell et al. 2002). The green crab (*Carcinus maenus*) has been described as a eurytopic voracious generalist predator (Lafferty and Kuris 1996) whose prey consists of most predominant macrobenthic invertebrates (Ropes 1968). The presence of the crab reduces periwinkle grazing on fucoid algae by either direct predation or through water-born cues that influence grazing activity in the periwinkles (Trussell et al. 2002). These studies demonstrate that the relationships amongst these groups play important roles in structuring tidepool communities. The presence of crabs (and to some degree the absence of periwinkles) and other predators (seastars, whelks) is correlated with the presence of the macroalgae, particularly early in the season. Trussell et al. (2002) suggest that the grazing of periwinkles on fucoid algae is most important early in the season while the algal fronds start to grow and that interactions between the two appear to strongly influence the algal community in terms of structure and succession.

Sea cucumbers and brittle stars contribute a strong loading to the first invertebrate principal component in the fourth sampling period, but are not important in any other sample period. During Period 4, a relationship between A1 and I1 was still present but no longer significant. The strong relationship among these variables and F1 suggest an important role of biological characteristics of the tidepool early in the year, and physical conditions such as relative height of the tidepool to the sea level, in structuring the eventual fish community. A strong wind event on August 7, 2001 (wind gusts of 50 mph, NOAA) during sample Period 4 (Figure 4.4) surely contributed to changes in the distribution of all species in the intertidal zone because large swells physically alter the intertidal by removing species and the mixing of the water column caused falling ocean temperatures along the surface. Lower water temperatures coincide with the departure of many species, and are likely a cue for movement to deeper water (Collette and Klein-MacPhee 2002).

Disturbances play a major role in determining intertidal species composition (Underwood 1999). Disturbance occurs over a range of temporal and spatial scales. At the smallest scale there is human physical disturbance of tidepools around Acadia. This effect has been noted at the Anemone cave site, where long-term visitation and direct disturbance of the tidepools has occurred (Petraitis et al. 2002). Direct effects of visitation on intertidal organisms should be studied further, and if an area is considered ecologically important, visitation should be managed appropriately. Still, many tidepools are located along inaccessible coastline and remain beyond the range of most direct human disturbance. This would suggest that not all tidepools are equally susceptible to the effects of visitation and that there may be a good opportunity to study the impacts of visitation in a comprehensive manner. Strong associations between flora and fauna of tidepools and the habitat type present suggest that changes to the coastal geomorphology and to the balance of sedimentation and erosion along the coast could have dramatic influences on the overall community assemblages. If coastal construction allows either higher than expected sedimentation rates along rocky coastal regions or higher than expected erosion in mudflat habitats, then changes in the assemblages of species and the ecological functioning of the system would be expected. The presence of fish species will be affected by alterations to the tidepool by physical (e.g. storm events) and anthropogenic (e.g. oil spills) disturbances during the entire year because of the strong links between physical disturbance and biological properties.

It is important to note that both the periwinkle and the European green crab (*Carcinus maenas*; DeGraaf and Tyrrell 2004) are invasive species. The presence of these two species as part of the composition of tidepools, and the interactions demonstrated with other organisms (Leonard et al. 1998, Trussell et al. 2002) is a sign that invasive species can have a dramatic influence on ecology of ecosystems. Interactions between community members will likely be again altered by the imminent invasion of the Japanese shore crab (*Hemigrapsus sanguineus*; DeGraaf and Tyrrell 2004), which has been spreading northward and is now present in Penobscot Bay.

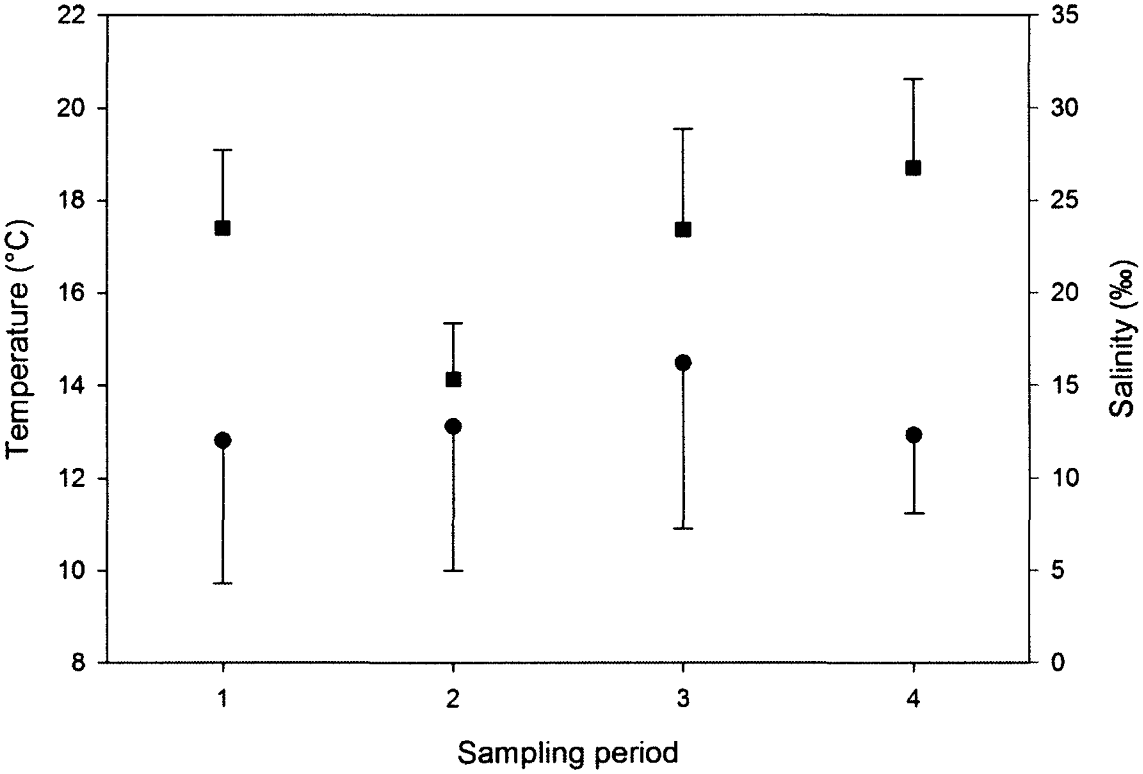

Figure 4.3. Average temperature (circles, left axis) and salinity (squares, right axis) over the four sampling periods. Error bars = standard deviation.

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CHAPTER 5

PRINCIPAL COMPONENT ANALYSIS AND INTERTIDAL ESTUARINE ECOLOGY: WHAT ARE THE LIMITS OF ANALYSIS?

5.1 Introduction

Estuaries are among most productive ecosystems on the earth. Human population growth, and the accompanying development of commercial, industrial, recreational and residential facilities, will place increasing demands on coastal environment (Porter et al. 1997). The estuarine environment in Acadia National Park is used by herons, kingfishers, ospreys, bald eagles, otters, and oceanic predators such as mackerel, striped bass and squid (Kling and Jordaan In Prep). The pressure of visitation and development in and around the park and the National Park mandate to protect ecosystems require species monitoring. This includes understanding the sources of anthropogenic effects on the environment and how these interact with natural variations in physical and biological factors.

Coasts and estuaries can be susceptible to a large number of anthropogenic factors, such as air pollution, water pollution, climate change, sea-level rise and habitat destruction and alteration. The northeast coast of the United States finds itself in the flow of polluted air masses generated by the industrialized northeastern corridor and as a result is exposed to higher than normal levels of mercury deposition, ozone and other pollutants (Bank et al. 2005, Bartholomay et al. 1997, Haines et al. 2000). The sources of pollution that Acadia National Park region is exposed to are related to degradation of coastal waters (Driscoll et al. 2003; Haines et al. 2000). Dionne et al. (1999) also discuss salt marsh loss and habitat alteration though changes in the natural flow. The effects of pollution from afar and land-use along the coast may have effects on the fauna in the region. Visitors to Acadia National Park, and the coast of Maine in general, see the fauna as a part of the National Park experience. But the visible species (herons, eagles, kingfishers, and striped bass for anglers) prey on estuarine neckton, and understanding the ecology of the often overlooked group of prey species is an important part of appropriately managing human activities in estuaries. The patterns and trends in fish populations within Acadia National Park estuaries were discussed in Chapter 2.

In Chapter 3 and 4, the results show a convincing trend in community structure based on differences between two disparate habitats (mudflat and rocky tidepools) and due to strong gradients evident along the vertical zonation pattern. Here I will examine the structure of the estuarine species and how their distributions are related.

5.2. Materials and Methods

5.2.1 Field Collections

Fish were collected during 2003 in 5 estuaries within the Bagaduce watershed, four estuaries on Mount Desert Island (MDI), and one on adjacent Schoodic Point (see Figure 5.1). Estuaries were sampled during flood tides.

Two seines were used because the estuaries begin as wide open mud flats and constrict towards the freshwater source. A small seine (4.27 m X 1.2 m, 0.32 cm mesh) was used in sites that were limited in area, while a large seine (30.5 m X 1.2 m, 1.1 cm mesh) was employed when possible. The seines were set in the water, with one end attached by line to the beach. The seine was set in the water off the beach in an arcing manner, ending up down the bank from the other end. The net was pulled in slowly pursing the bottom as it came closer into the shore. Fish species and invertebrates caught

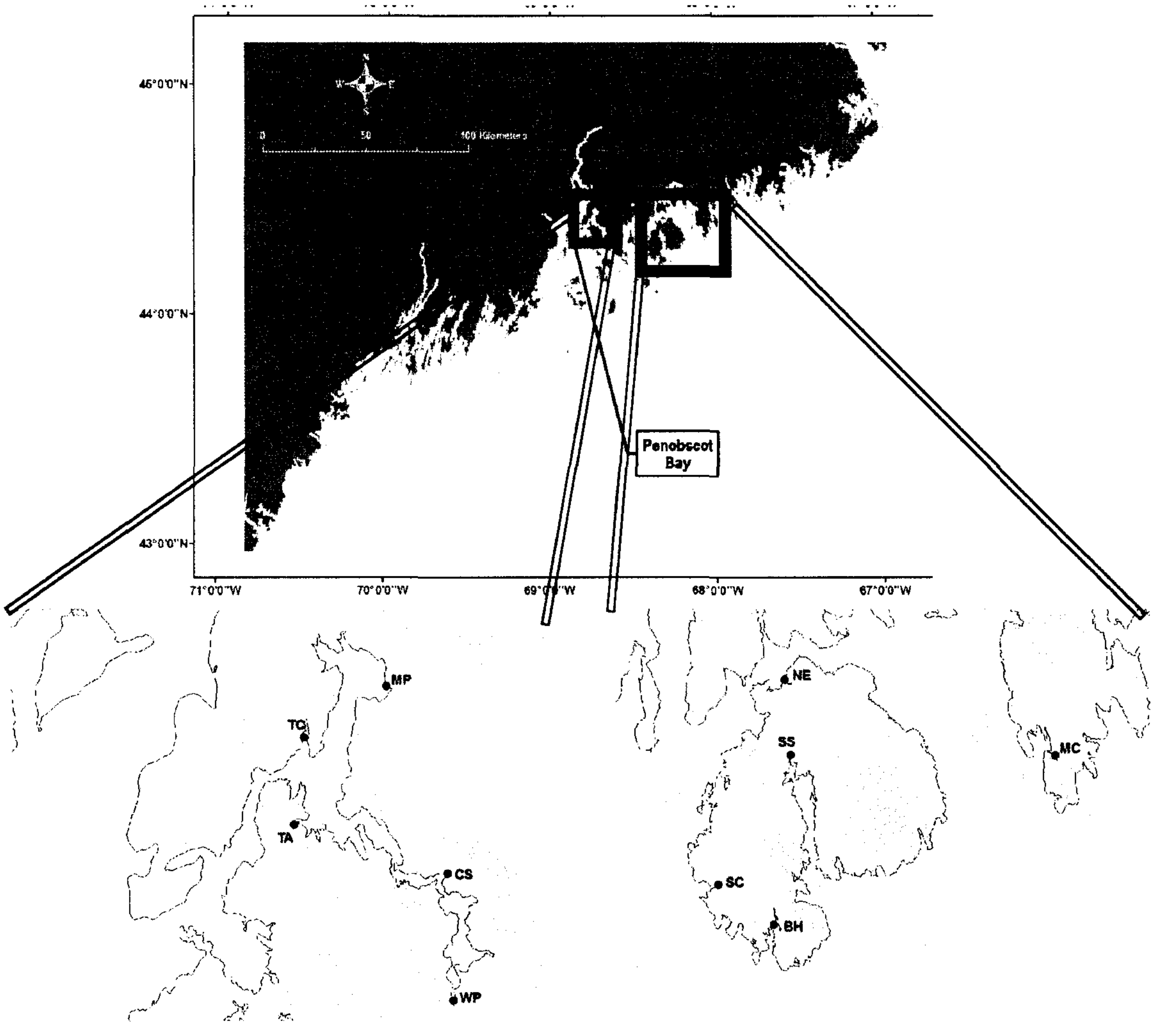

Figure 5.1. Location of 10 Acadia National Park and Bagaduce system estuaries discussed in text. : Bagaduce (left) sites: TC = Tills Cove, MP = Maggie's Place, CS = camp stream, WP = Walker Pond, TA = Tapley's Cove. Acadia National Park (right) sites: BH = Bass Harbor, SC = Seal Cove, SS = Somes Sound, NE = Northeast Creek, MC = Mosquito Cove.

in the net were documented. A subset (n=30) of each species caught was measured for total length, and the total number of individuals was recorded. If fewer than 30 individuals were caught, all were measured. To avoid stress for the fish during capture and handling, MS-222 (tricaine methanesulfonate, 500 mg/L) was used to anesthetize each captured fish. Handling time was kept to a minimum and each fish or invertebrate was promptly returned after it was measured or counted. The stations in each estuary range from high salinity near the estuary mouth and low salinity (~ 100% freshwater) environments near the freshwater source (see Chapter 2). Temperature and salinity values are not included in this chapter as the focus is the relationship among species and the limitations of the data. Only one seine was competed per site each visit.

5.2.2. Data Analysis

For each data period and gear type, the number of species corresponding to the "2.5 rule" was calculated. The "2.5 rule" is that the number of sites (seines) must be 2.5 times the number of variables (species). The reason for this is related to power, as increasing the number of sites relative to variables (species) allows for the analysis to be based on multiple sites (2.5) rather than one site per variable. The species were removed from least common to most common until the required number of species remained. This assumes that the most abundant species are those important in determining community structure.

A full text version of the bootstrap-PCA program, written for use in SAS^{TM}, can be found in Appendix A. The program resamples the dataset until it has generated a new set of data that is equivalent, in the number of sites, to the original. As each PCA is completed, a Pearson correlation matrix, eigenvectors, eigenvalues and factor scores for each principal component and site generated are held in memory. The process continues for the desired number of iterations and, once completed, the results are written to files.

The Pearson correlations were examined to determine which species were correlated with one another. Bootstrap-PCA techniques were used to identify species that were driving the PCA results by examining the distribution of component loadings, and identifying correlations in the loadings amongst species. Sigmaplot^{TM} v. 9.01 was used for all graphing.

5.3 Results

The mummichog (*Fundulus heteroclitus*) was the most consistent species caught during sampling, which results in few negative correlations with the other species (Figure 5.2). Inconsistent relationships occur with some schooling fish (Figure 5.2). Since the anadromous species are captured in open water (less mummichogs) sites and in the more constricted sites (more mummichogs), the result will be negative or positive correlations depending on the distribution of the pelagic species. In the inner sites, the mummichog was negatively correlated to *Menidia menidia* and *Apeltes quadracus* in the second sample period, but had no relationship to any other species. In the outer sites, the mummichog was positively correlated with *Pugitius pungitus* in the first sample period, and negatively correlated with *Apeltes quadracus* and *Menidia menidia* in second sample period (Figure 5.2).

For the silverside (*Menidia menidia*), negative correlations were seen with *Fundulus heteroclitus*, *Pugitius pungitus* and *Fundulus majalis* in the inner sites (Figure

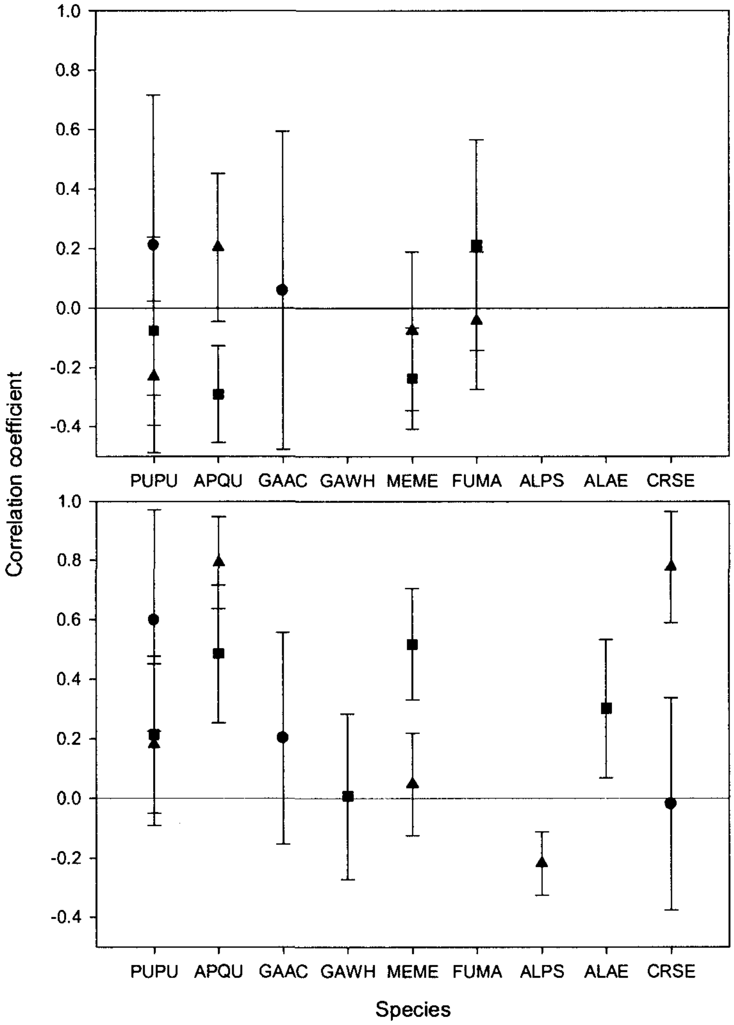

Figure 5.2. Pearson correlation coefficients for *Fundulus heteroclitus* collected by small (top) and large (bottom) nets collected during the first (circles), second (squares) and third (triangles) samples periods.

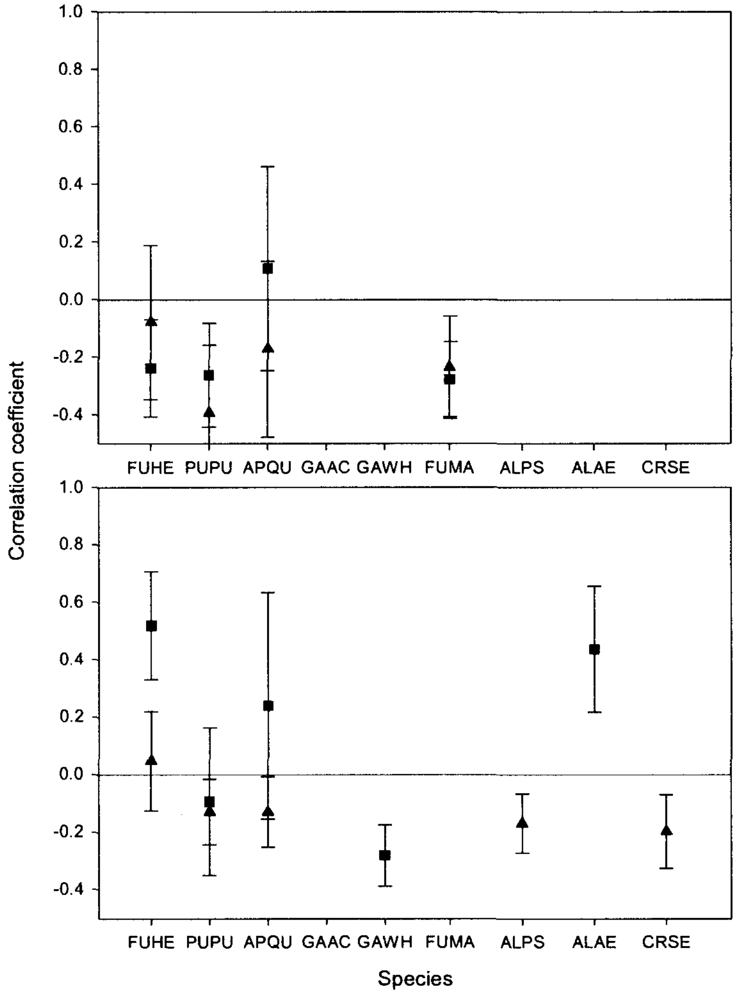

Figure 5.3. Pearson correlation coefficients for *Menidia menidia* collected by small (top) and large (bottom) nets collected during the first (circles), second (squares) and third (triangles) samples periods.

5.3). Using the outer sites, there were negative correlations with *Pugitius pungitus*, *Apeltes quadracus*, *Gasterosteus wheatlandi*, *Alosa pseudoharengus* and *Crangon septemspinosa*, and positive correlations with *Fundulus heteroclitus* and *Alosa aestivalis*. The correlation with *Fundulus heteroclitus* in both the inner sites (negative correlation) and the outer sites (positive correlation) only occurred during the second sample period, and the relationship was negligible for the third sample period.

The ninespine stickleback (*Pugitius pungitus*) had a negative correlation with *Menidia menidia* and a positive correlation with *Gasterosteus aculeatus* in the analysis of inner sites (Figure 5.4). For the outer sites there was a positive relationship to *Fundulus heteroclitus*, *Apeltes quadracus*, *Gasterosteus aculeatus*, *Alosa aestivalis* and *Crangon septemspinosa* abundance, and a negative relationship to *Menidia menidia* (Figure 5.4).

Alosa pseudoharengus, *Alosa aestivalis*, *Crangon septemspinosa* and *Gasterosteus wheatlandi* were not captured at the smaller seine/freshwater sites (Figure 5.2, 5.3, 5.4), and showed a inconsistent trend with other species.

When the frequencies of component loading scores were plotted the distributions that were similar in many cases agreed with the correlation analyses (Figures 5.5 – 5.10). For the inner site during the first sample period, the two correlated species *Menidia menidia* and *Gasterosteus aculeatus* had almost overlapping distributions (Figure 5.5). *Fundulus heteroclitus* had a clearly different loading distribution. For the second sample period, an abundance of negative scores resulted. Again the distributions of negatively correlated species were clearly opposite from one another (Figure 5.6). Still, the "like" distributions were not a guarantee of a positive correlation. In the third sample period

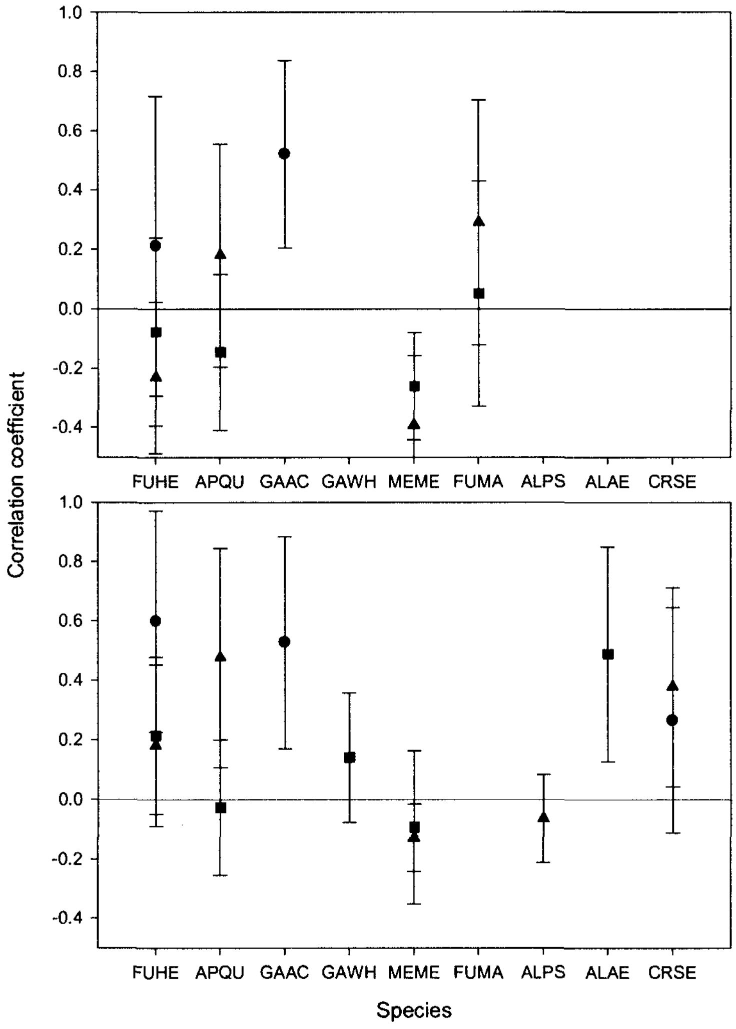

Figure 5.4. Pearson correlation coefficients for *Pugitius pugitius* collected by small (top) and large (bottom) nets collected during the first (circles), second (squares) and third (triangles) samples periods.

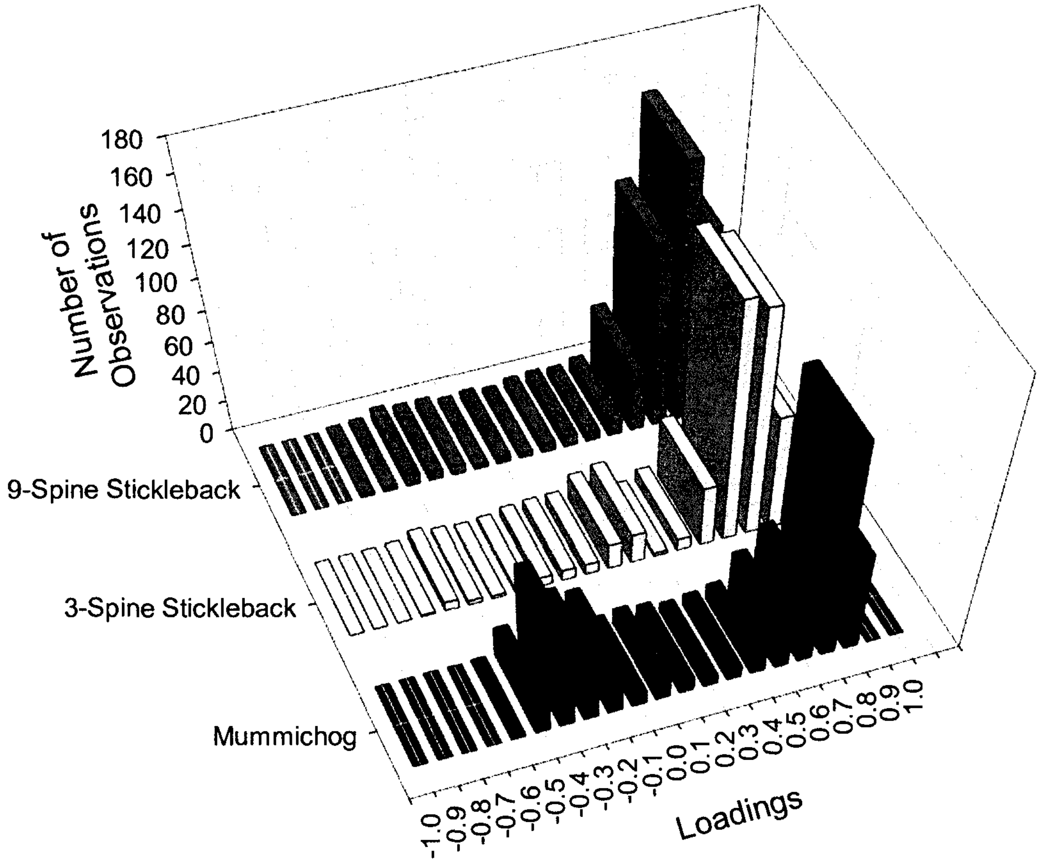

Figure 5.5. Frequency distribution for loading scores from bootstrapped principal component analysis for the inner small seine sites during the first sample period.

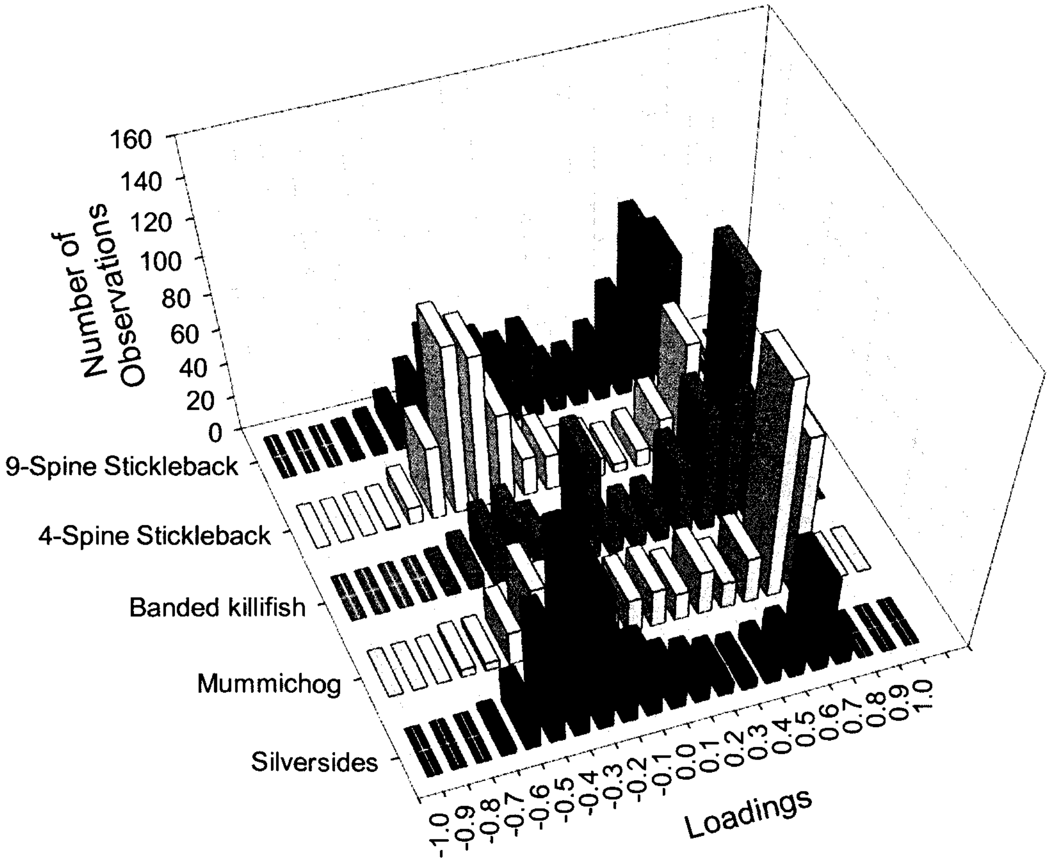

Figure 5.6. Frequency distribution for loading scores from bootstrapped principal component analysis for the inner small seine sites during the second sample period.

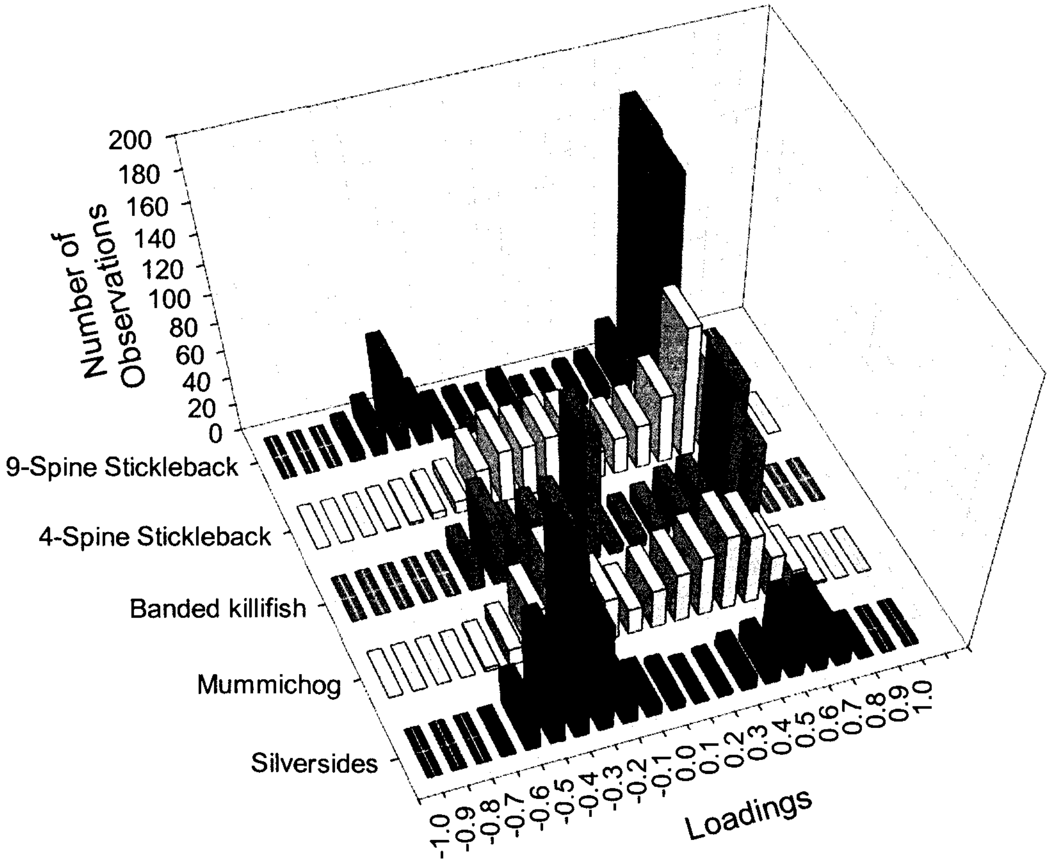

Figure 5.7. Frequency distribution for loading scores from bootstrapped principal component analysis for the inner small seine sites during the third sample period.

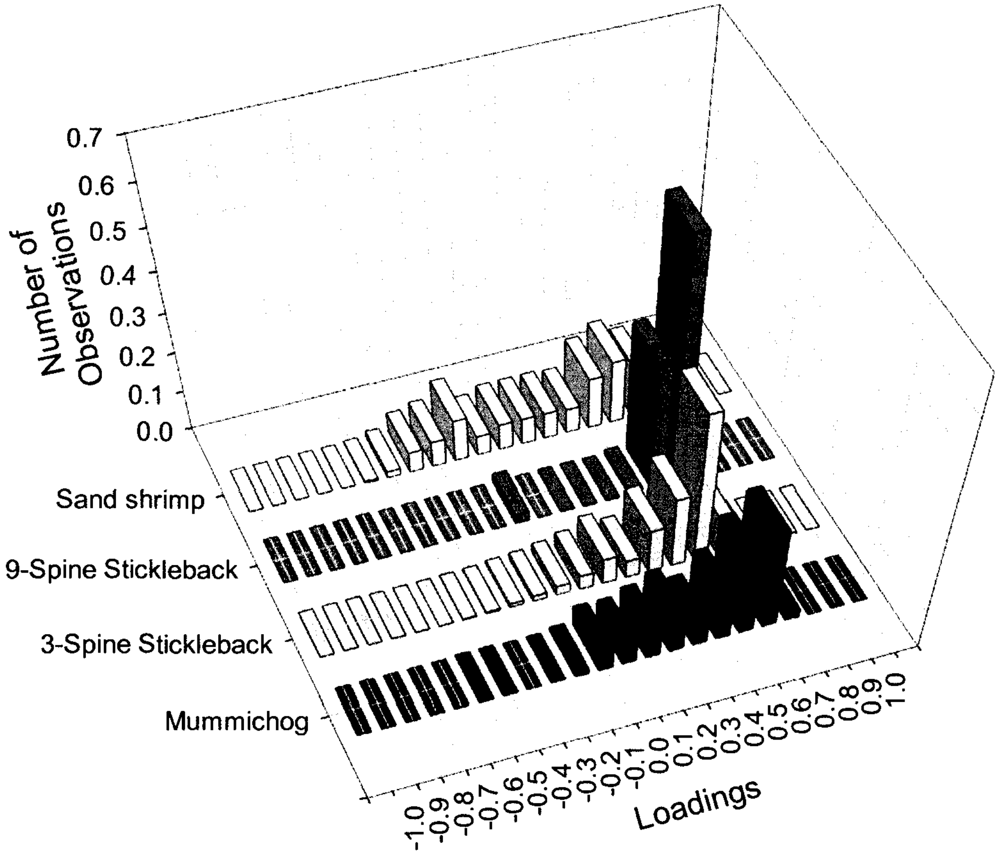

Figure 5.8. Frequency distribution for loading scores from bootstrapped principal component analysis for the outer large seine sites during the first sample period.

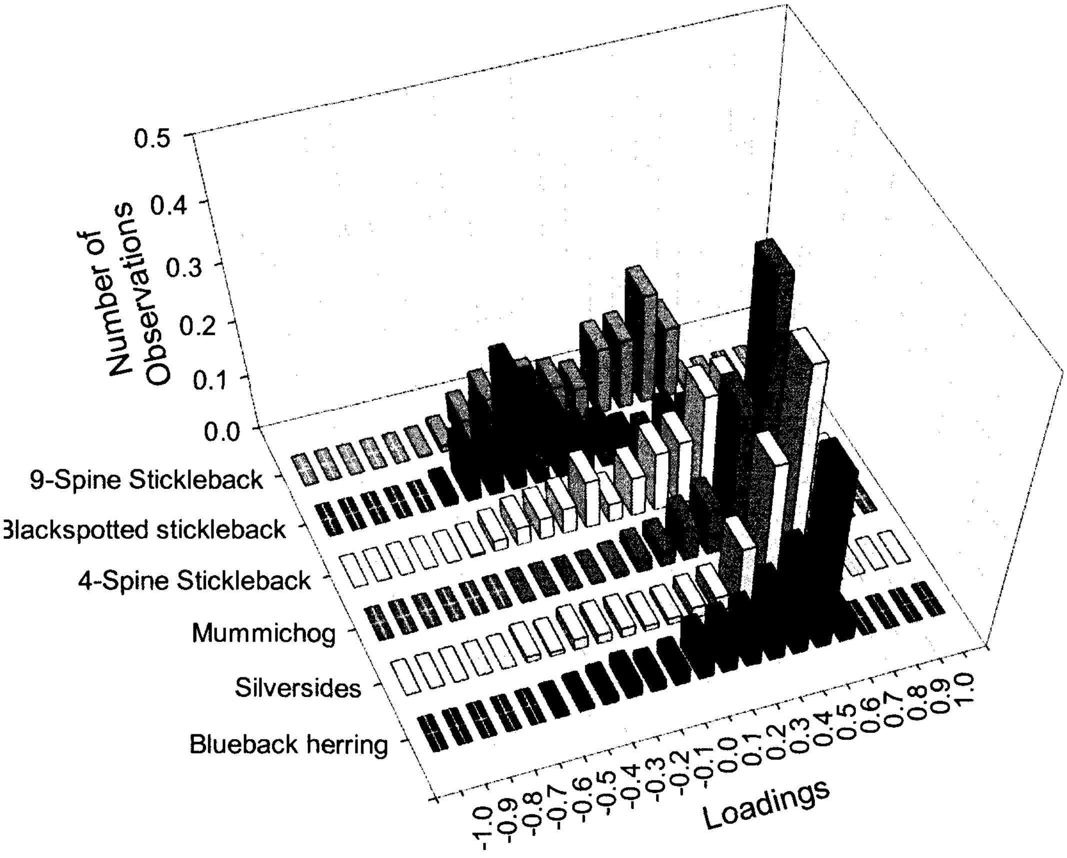

Figure 5.9. Frequency distribution for loading scores from bootstrapped principal component analysis for the outer large seine sites during the second sample period.

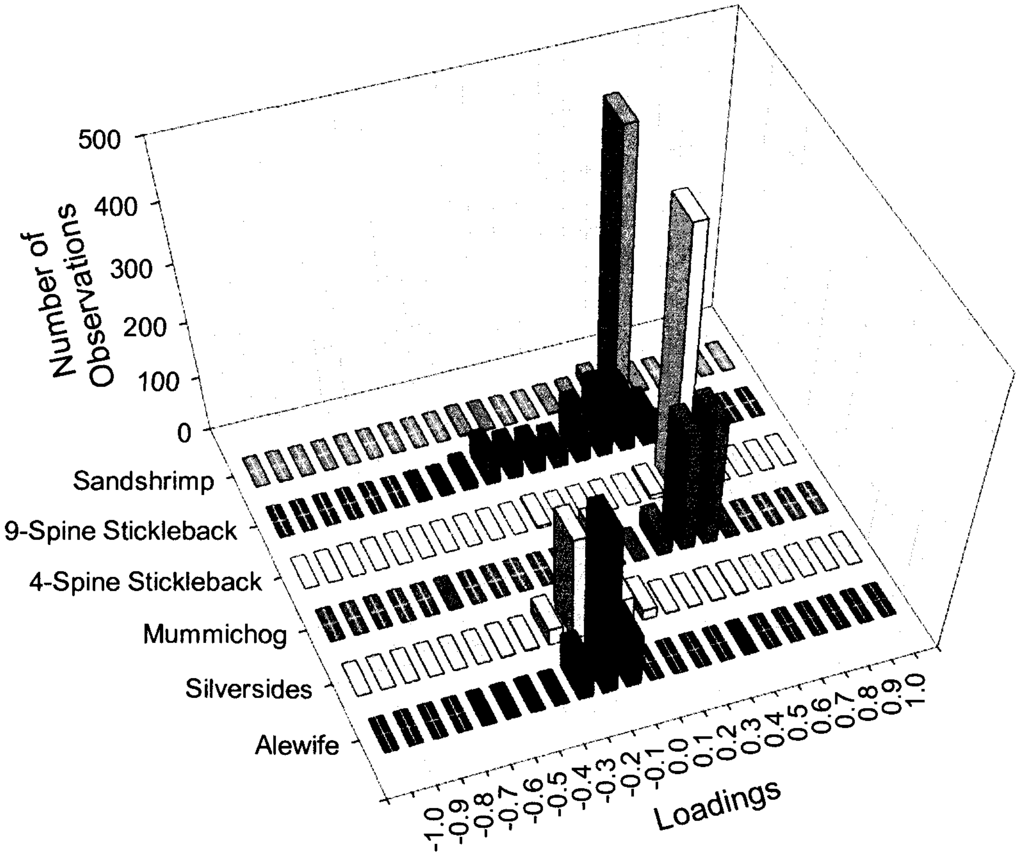

Figure 5.10. Frequency distribution for loading scores from bootstrapped principal component analysis for the outer large seine sites during the third sample period.

there are four types of distributions (Figure 5.7): strong positive loading distribution (*Pugitius pungitus*), strong negative distribution (*Menidia menidia*), intermediate with large number of "0" scores (*Fundulus majalis*), and a more uniform distribution (*Fundulus heteroclitus* and *Apeltes quadracus*).

The outer site analysis for the first sample period there was a more uniform distribution of scores for *Crangon septemspinosa*, while the other species were strongly positive (Figure 5.8). The positive loading species were correlated with one another, except *Fundulus heteroclitus* and *Gasterosteus aculeatus*. In the second sample period the species with distributions that were similar were, for the most part, correlated with one another (Figure 5.9). However, two correlated species, *Fundulus heteroclitus* and *Menidia menidia*, did not share the same relationship with *Gasterosteus wheatlandi*. *Menidia menidia* had a negative correlation with *Gasterosteus wheatlandi* (Figure 5.3), while *Fundulus heteroclitus* had no correlation (Figure 5.2). In the third sample period, a group of correlated species (*Fundulus heteroclitus*, *Apeltes quadracus*, *Pugitius pungitus*, *Crangon septemspinosa*) share positive loading distributions. *Menidia menidia* and *Alosa pseudoharengus* are negatively correlated to the aforementioned group but also with one another, despite having similar loading distributions.

5.4. Discussion

The mummichog is the most widespread species to occur in estuarine/salt marsh habitats (Dionne et al. 1999), and is the only year-round resident species of the estuarine environment (Collette and Klein-MacPhee 2002) with the exception of eels (*Anguilla rostrata*). Mummichogs are particularly abundant in salt marsh, mud flat and estuarine habitats, as well as sites exposed to anthropogenic changes (Dionne et al. 1999; Collette and Klein-MacPhee 2002). This is partly owed to the fact that these fish are capable of breathing air in oxygen-poor environments and tolerating many stressors that are brought into play by the high tides and the variation in oxygen/high temperatures that result (Collette and Klein-MacPhee 2002). This in turn makes the mummichog an extremely abundant inhabitant of the habitats, and also allows for a wide distribution within the brackish water. The wide distribution makes the mummichog a good candidate for monitoring estuarine environments for pollution and other effects on a species. However, they are caught in many places other species with more restricted distributions were and were not, and as a result do not always correlate in a meaningful way with the other species. Therefore, mummichogs may be a good candidate for monitoring changes within a system, but not necessarily for determining the community of fishes present.

When the range of a species was more restricted than *Fundulus heteroclitus*, the result was a negative association with the species. *Menidia menidia* had many negative correlations, in particular using the inner sites. This was caused by the use of increasingly freshwater sites by *Fundulus heteroclitus*, *Pugitius pungitus* and *Fundulus majalis* (Chapter 2). All three of these species were found to use freshwater habitats, and *Fundulus majalis* is a freshwater species. The large number of "0" loading scores for *Fundulus majalis* demonstrates that the species was fairly rare, but this did not reduce the correlation to *Menidia menidia* to a negligible value. Therefore, despite rare detection there was a clear division between the freshwater and more marine species. During the second sample period, Menidia had opposing correlations relative to *Fundulus heteroclitus* between the inner and outer site analysis. During the second sample period, there were large numbers of small young-of-year fish beginning to become susceptible to capture by the seines (Chapter 2; Figure 2.17). The adults were using the salt marsh edges for spawning, placing them in the preferred habitat of mummichogs, while the young were restricted from inner sites.

Crangon septemspinosa and *Gasterosteus wheatlandi* were not identified at the inner sites. The two species are primarily marine species and do not enter those parts of the estuary. *Crangon septemspinosa* is a predator of fish eggs (Taylor and Danila 2005). Since *Crangon septemspinosa* was not detected in any numbers in the freshwater sites, species that can spawn within these areas will have an advantage in avoiding *Crangon* egg predation. This does not preclude that other predators of eggs, such as crabs, are present in the upper reaches of the estuaries since they were not effectively censused using seining techniques.

The loading distributions and the results of the Pearson Correlation analyses were generally in agreement. Species were easily separated into those species that had negative correlations with one another based on opposite loading distributions. However, detecting positive associations was not possible by accepting the premise that "like" distributions were always indicative of similar species. It is important to note that the loadings reflect the relative strength of the species in determining the principal component values, not necessarily the strength of correlations amongst species. Nevertheless, by combining the results of the correlation analysis and the loading scores, it is possible to determine strongly correlating species and identify patterns in community structure.

Edges along the salt marsh provide cover for the mummichogs and the other fish species. The species that primarily reside in the open habitats require some strategy for defense against predation. The sticklebacks have adapted armor and spines to help deter predators and avoid injury once attacked. Anterior plates link dorsal and pelvic spines mechanically, which increases the difficulty of ingestion by predatory vertebrates and protect sticklebacks from injury during manipulation by predatory fish, improving the probability of survival (Reimchen 2000). Stronger selection for fast start performance occurs when sticklebacks are subject to avian predation, as opposed to trout predation, and reduced robustness is associated with enhanced fast-start swimming performance (Bergstrom 2002). Marine populations are robust morphs with many lateral plates, and a full girdle, and are considered to be the ancestral stock. The most robust species (oceanic threespine and blackspotted stickleback) were found in outer sites and the least armored (fourspine stickleback) and most streamlined (ninespine stickleback) were found associated with inner sites. Outer sites are known to be in the range of oceanic predators, while avian predators, such as herons and kingfishers, dominate the inner sites. It is reasonable that the species are following a gradient of low environmental stress/high piscivore predation, which requires robust forms, to high environmental stress/high avian predation, which requires a more agile species. The degree of environmental stress influences biotic interactions with predation dominating in conditions of low environmental stress, competition dominates in environments of intermediate environmental stress and physical factors dominating in high stress environments (Menge and Branch 2001). Water depth decreases towards the freshwater (higher stress) sites, which also suggests more avian and less piscivore predation.

The first limitation from the data used is the number of samples taken using the two gear types during each time period. The reduced number of sites constrains the number of species that could be subjected to the principal component analysis. The second constraint is the inability of the analysis to speak to process. Although identifying structure allows inference or testing of potential processes, there is a requirement of experimentation to extrapolate results to process. Complex interactions among the estuarine species in terms of body morphology, predation pressure and trade-offs in energy acquisition are ultimately important but not testable within the present analysis. The third constraint is that many species are only temporary occupants of habitats during migration into the freshwater systems or into preferred spawning habitats within the estuary. Schooling behaviour adds paucity to capture data for some of the species (silversides, alewives, blueback herring and young sticklebacks) and the result is data that shows many individuals were captured or none. Although presence of zeros in the bootstrap PCA helps identify these species, understanding their relationship to other species will require more sites with finer temporal resolution.

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CHAPTER 6

COMMUNITIES OF FISH DEFINED ACROSS A WAVE ENERGY GRADIENT

6.1. Introduction

There has been debate over the use of environment-recruitment relationships in setting management policies (Tyler 1992). The primary advance in community ecology in the past 50 years has been a shift from the ecology of climax and steady state systems to the concept of "path dependence" (see Gunderson and Holling 2002) and recognition of uncertainty and uncontrollability (Lauck et al. 1998). The former approach leads one to believe that the system can be manipulated or engineered to provide maximum outputs; an example would be the concept in fisheries of maximum sustainable yield (MSY). The latter incorporates the uncertainty and stochasticity, and places humans within ecosystems with multiple states and stabilizing/destabilizing forces. Although path dependence acknowledges uncertainty, there is also a component of the system that is knowable and related to changes across spatial and temporal scales (Gunderson and Holling 2002).

Lauck et al. (1998) advance the concept of marine protected areas (MPAs) to allow maintenance of fish populations under exploitation, and to mitigate the inherent risks (uncertainty and uncontrollability) in MSY-type management. Determining patterns that emerge between environmental parameters and the distribution of fish populations and communities will be a powerful tool when approaching management with a spatial view; such as applying area-management or the use of MPA- type restrictions. The use of MPAs and Marine Sanctuaries depends on the ability to account for species interactions and connectivity of populations, across spatial and temporal scales, with the goal of maintaining the biodiversity and ecological processes (Guichard et al. 2004). This is limited by the understanding of the roles of physical and ecological processes in shaping communities. It is therefore important to determine whether community structure is related to physical processes, and develop techniques to distil that information to a form that can be applied by managers.

It is reasonable to assume that the composition of the local community is initially influenced through the degree of isolation from source habitats and the rates of local extinctions and immigrations (Magnuson et al. 1998). The isolation can be physically or physiologically imposed by gradients in temperature (Jobling 1993), flow rate (Leonard et al. 1998), predation (Witman and Dayton 2001), mechanical force (Vadas et al. 1990; Menge and Branche 2001), land use (Harding et al. 1998) and combinations of these that can vary by season or age of the fish (Labbe and Fausch 2000). Potential wave energy is an overall ecosystem characterization since increasing exposure implies a (1) rocky intertidal zone, (2) steeper reflective beach, (3) hard substrate and associated macroalgae, and (4) well mixed water column. It appears reasonable then to believe that the wave energy experienced by an intertidal site will be related to the structure of the fish communities.

In this paper, I will examine the hypothesis that potential wave energy can be used to estimate the structure of fish communities along the coast of Maine. Principal component analysis will be used to reduce count data of multiple species to fewer new variables and related to estimates of wave energy.

6.2. Methods

6.2.1. Study Design

The sites used in this study are located in the Isle au Haut - Mount Desert Island - Schoodic Peninsula region along the coast of Maine (Figure 6.1, 6.2) and were sampled during the spring to fall in 2004 and 2005. Sampling was completed using an outboard boat. A seine designed for sampling benthic species across a variety of habitats was used. The seine consists of two tapered wings, with the shortest depth (45 cm) at the leader end progressing to a depth of 220 cm in the center of the net. Each wing was 500 cm long and opened gradually into a 315 cm deep cod end centered in a 45 cm section between the two wings. The net uses 0.5 cm mesh, with a 0.5 cm (stretched measure) mesh in the cod end. Each leader end of the seine had a vertical bar that was fixed by 60 m line to the beach. The seine was set in the water off the beach in an arcing manner, by reversing the boat and feeding the net over the bow. Once the entire net was placed in the water, the boat was piloted to shore while keeping the second line to the second leader end of the seine attached to the boat. The boat was kept out of the path of the seine and ended up down the bank from the starting position. Both ends of the seine were retrieved by manually pulling the lines, and eventually net, attempting to maintain the net in a symmetrical formation.

The captured species were gathered in the cod end and placed in a container with small holes to allow for water exchange. All fish species and invertebrates caught in the net were documented. A subset (n=30) of each species caught was measured for total length and the total number of individuals was recorded. If fewer than 30 individuals of a species were caught, all were measured. The analysis is restricted to the vertebrates encountered. Crangon shrimp (*Crangon septemspinosa*) were the sole exception and treated as the fish species. Crabs (*Carcinus maenas*, *Cancer* spp.), lobsters (*Homerus americanus*), periwinkles (*Littorina* spp.) and whelks (*Nucella lapillus*), sea cucumbers (*Cucumaria frondosa*), sea urchins (*Strongylocentrotus droebachiensis*), starfish (*Asterias* spp.), mussels (*Mytilus* spp.), sand dollars (*Echinarachnius parma*) were all counted and measured. Shrimp species such as *Pandalus* spp., *Lebbeus polaris*, and *Mysis* spp., were only identified and counted, in the case of *Mysis* spp. scored with a relative abundance. Algae present in the net were also noted. Handling time was kept to a minimum and each fish or invertebrate was promptly returned after they had been measured or counted.

6.2.2. Estimation of Fetch

Maps supplied by the National Park Service were used to measure available fetch for each site. The measurement application in ArcView^{TM} GIS v.3.2a was used to calculate distances. MB-Ruler v.1.3 for Windows was used for calculating angles. A measure of 0° corresponded to due north, with the angle increasing clockwise until returning to 0° (360° of rotation). The distance to the nearest land mass was measured along the bisection of the angle with new angles and distances created for each change in distance (~50%). If there was no landmass along the bisection until Nova Scotia/Georges Bank, an open Gulf of Maine distance of 250 km was used.

Each angle and distance measurement was used to calculate an available fetch area for wind action to work over. The area was determined using the distance measured within each angle, and assuming a perfect triangle, the length of the triangle base was calculated. The fetch area measurements for each site were summed to calculate a total available fetch. The total fetch measure was square root transformed for use in the equation:

6.1. $\zeta^2 = 1.67 \times 10^{-7} (U^2/g) F$,

where ζ^2 is the average variance in sea-level displacement, U the wind speed, g the acceleration due to gravity, and F the linear fetch measurement. The wind speed was calculated for 10° bins from observations made by Gulf of Maine Ocean Observing System (GoMOOS) Buoy F - W. Penobscot Bay (44° 03'20" N, 68° 59'53" W) and GoMOOS Buoy I - Eastern Maine Shelf (44° 06'21" N, 68° 06'31" W), the closest buoys to the MDI region. The years 2000 – 2004 were used to create average wind speeds for each 10° bin. Four year was used in order to develop an average yearly value and lessen the impact of any anomalous year. The orientation of the sites (facing direction) was calculated by the average of the first and last angles measured and the average wind speed experienced by a beach of the orientation of the site was used in the equation. Then the potential wave energy (E) in joules•m^2 was calculated using:

6.2. $E = \rho_w g \zeta^2$,

where ρ_w is the density of seawater (a static value of 1025 g•m^3 was used).

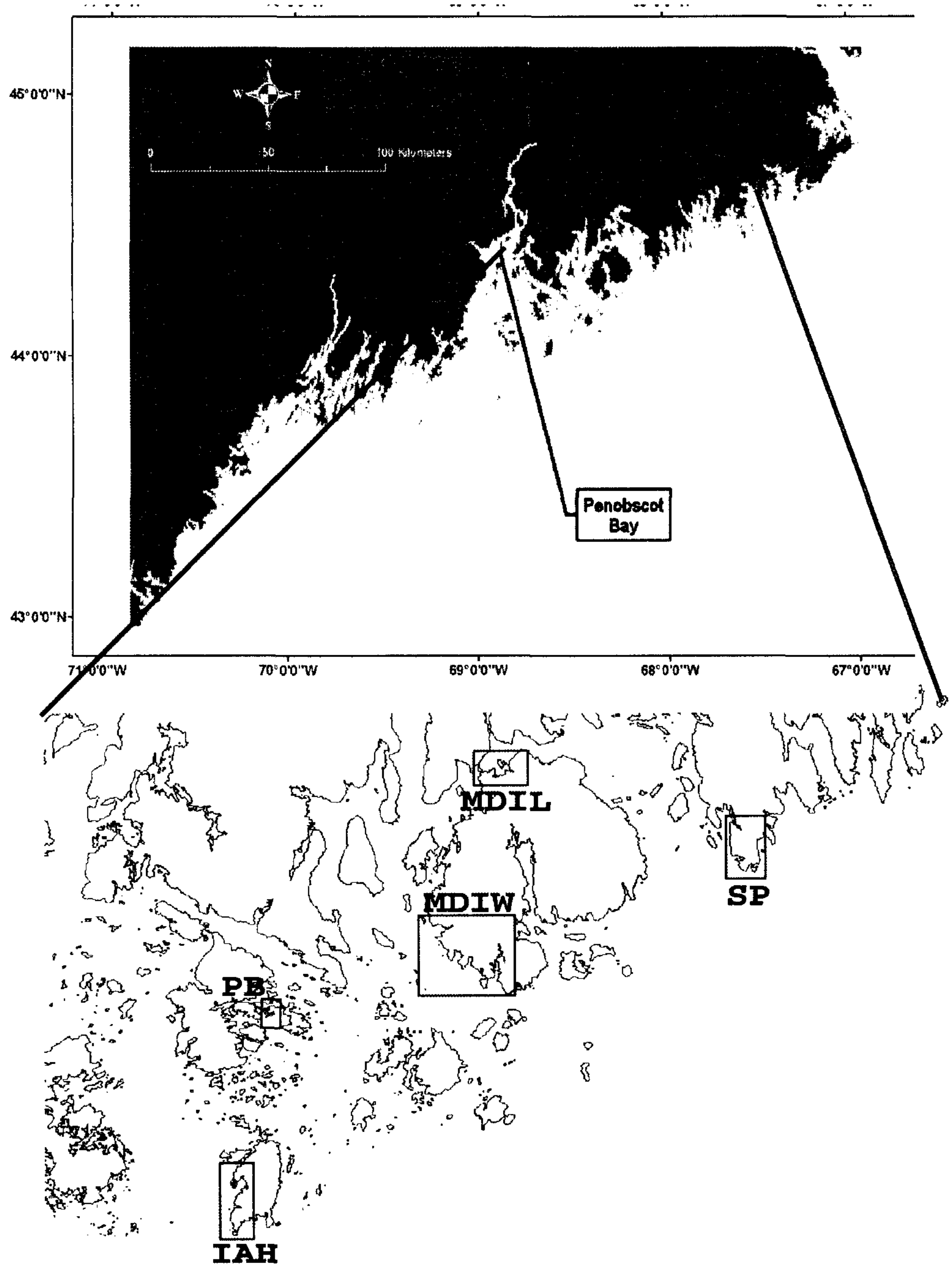

Figure 6.1. Locations of sampling sites used in study in relation to Gulf of Maine and Penobscot Bay. . IAH = Isle au Haut, PB = Penobscot Bay, MDIW = Mount Desert Island windward, MDIL = Mount Desert Island Leeward, SP = Schoodic Point.

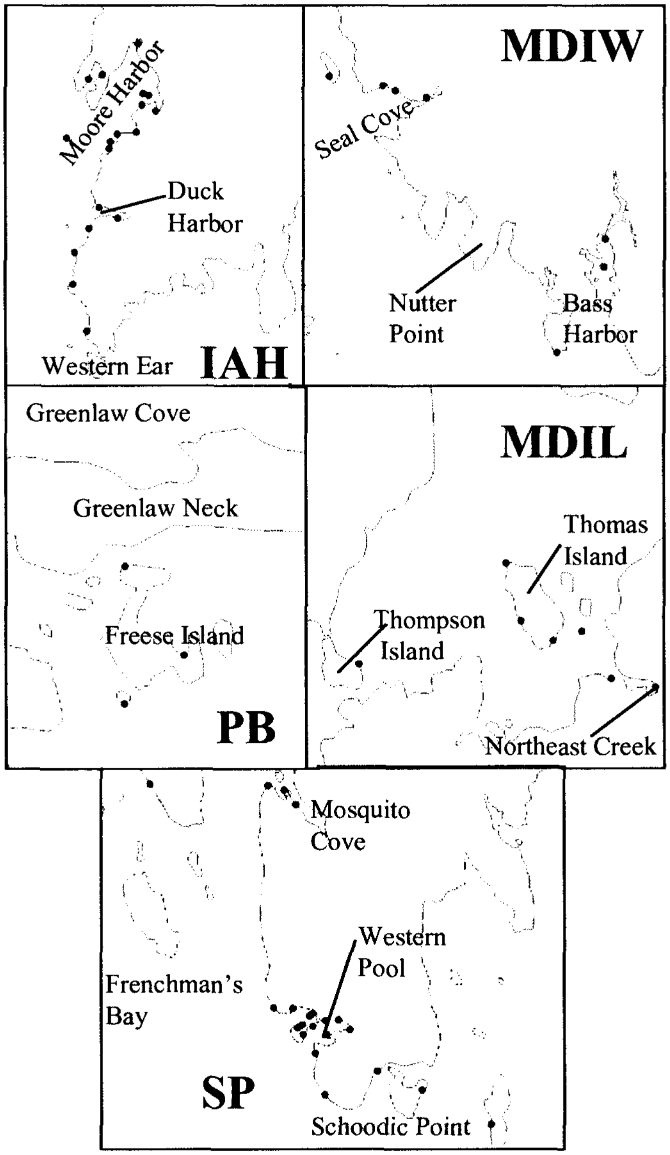

Figure 6.2. Placement of sampling sites within each of the primary locations used in study. Each point represents a seine site. IAH = Isle au Haut, PB = Penobscot Bay, MDIW = Mount Desert Island windward, MDIL = Mount Desert Island Leeward, SP = Schoodic Point.

6.2.3. Analysis

The data on numbers of fish at each site was square root transformed. SYSTAT^{TM} v.10.2 was used for running principal component analysis (PCA) on the transformed data. The analysis was repeated for the full dataset and a reduced random dataset. The full dataset used all samplings, whether a site was resampled more than once or not, and no fish species were removed from the analysis. The random dataset used all the sites sampled, but randomly chose one site from each that was resampled so there were no repeated sites in the analysis. All fish species that were caught in two sites or less, and with two or less total individuals were removed from the analysis. There were 4 sample periods; two in each of 2004 and 2005 and they are referred to as early and late periods in each year.

Once the PCA reduced the data and created components, the eigenvalues were visually studied to determine the relevant components. The inflection in the eigenvalue scores between the first 2-4 components was taken to mean that the remaining components were no longer relevant. The factor scores generated for each of the relevant components were compared to the average wave energy scores (Equation 6.2) for the corresponding site and the location of the sites using a general linear model in SYSTAT^{TM} v.10.2. The locations of the sites were Mount Desert Island windward, Mount Desert Island leeward, Schoodic Point, Penobscot Bay and Isle au Haut. These were chosen since they represent broad locations that are separated for one another by substantial distances and offer little chance of connectedness of intertidal fish communities.

6.3. Results

The estimated wave energies (E) ranged 0.0087, from a site on Mount Desert Island Leeward (MDIL), to 86.00, from a site on Schoodic Point (SP). The low values and variation of E at MDIL resulted in it having the lowest average score. The other sites were typified by higher averages and variation in E values (Figure 6.3).

The principal component analysis using the reduced random dataset identified two components that were considered of importance (Figure 6.4). Principal component 1 and 2 accounted for 23% and 20% of the total variance, respectively. For the analysis of the full dataset, the first three components were considered relevant (Figure 6.4) and accounted for 13%, 11% and 10% of the total variance, respectively.

The results of the general linear model using the random dataset to test for effects of the location and calculated wave energy on PC1 show a lower r^2, and that the sources of variation analyzed (Location, estimated wave energy and their interaction) have a low probability of contributing meaningfully to the model (Table 6.1). The results for PC2 suggest that all three sources contributed to the variation in the component (Table 6.1). For the full dataset, PC1 becomes the component that the three tested sources of variation explain a high probability of contributing to the model.

The species are plotted by the loadings they received in the PCA run on the random dataset in Figure 6.5. The resulting trend suggests two groupings of fish with one a rocky, high-energy group, and the other a mud-flat dominated group. The placement of the pollock (*Pollachius virens*) and rock gunnel (*Pholis gunnellus*) are important rocky

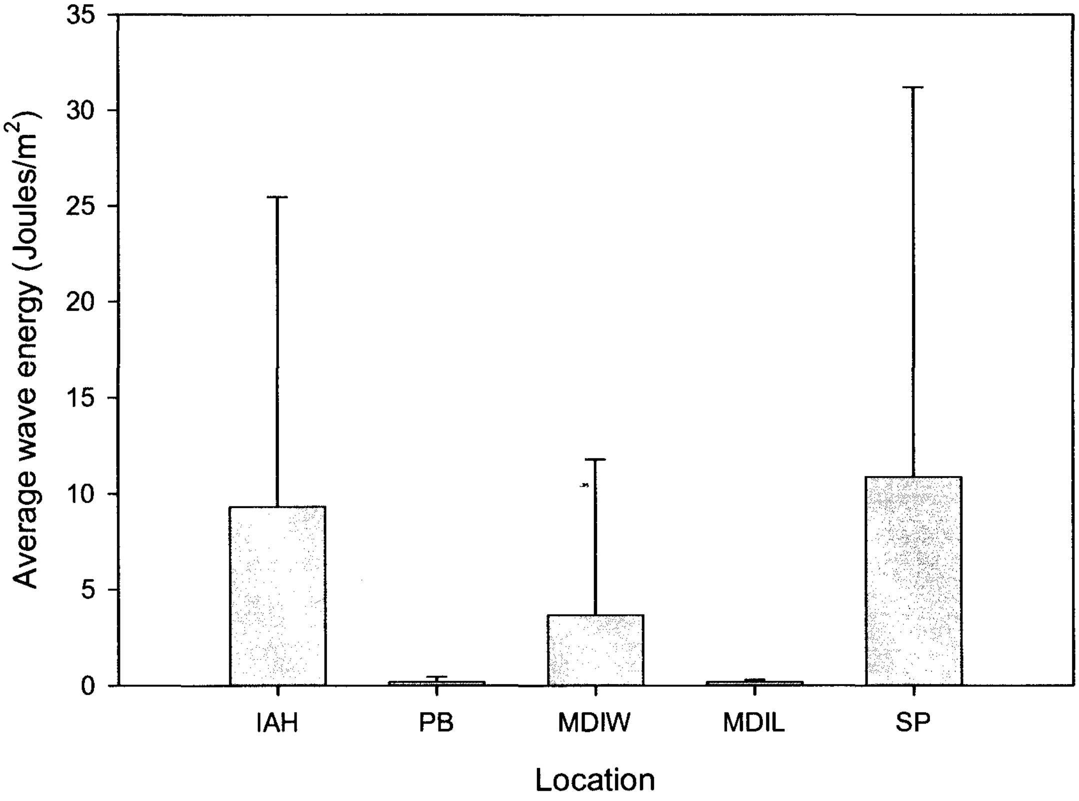

Figure 6.3. Estimated average wave energy (Joules) for each of the three locations of sites. IAH = Isle au Haut, PB = Penobscot Bay, MDIW = Mount Desert Island windward, MDIL = Mount Desert Island Leeward, SP = Schoodic Point

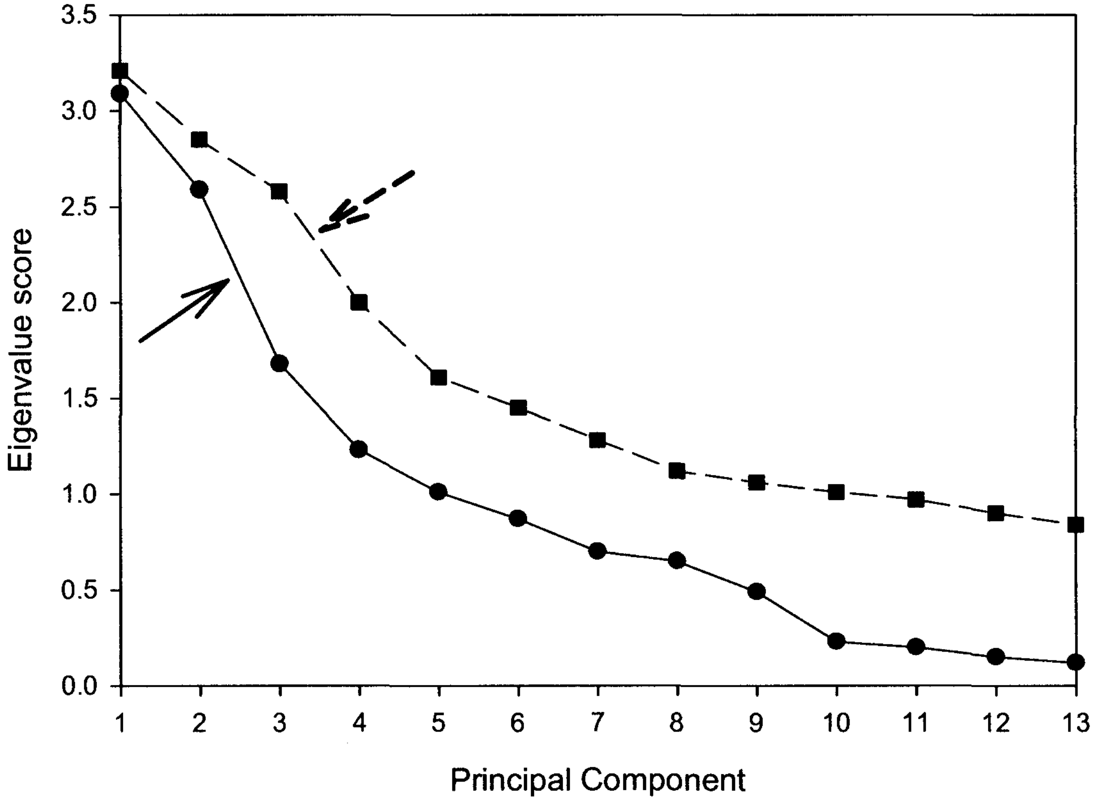

Figure 6.4. Eigenvalue scores for the principal component analysis using the reduced random dataset (circles, solid line) and full dataset (squares, dashed line). The arrows demark where the separation between relevant and non-relevant components was determined.

Table 6.1. General linear model results, testing for effect of location, average wave energy and their interaction on structure of the random full dataset from intertidal survey. The results for the first (PC1) and second (PC2) principal component factor scores calculated are shown. The r^2 value, sum of squares (SS), degrees of freedom (df), mean sum of squares (MS), F-ratio, and p-value (P) are given for each component.

PC1	Source	SS	df	MS	F-ratio	P
$r^2 = 0.18$	LOCATION	7.56	4	1.89	1.91	0.12
	ENERGY	1.89	1	1.89	1.91	0.17
	LOCATION*ENERGY	2.33	4	0.58	0.59	0.67
	Error	44.48	45	0.99		

PC2	Source	SS	df	MS	F-ratio	P
$r^2 = 0.69$	LOCATION	23.75	4	5.94	15.82	0.00
	ENERGY	5.93	1	5.93	15.79	0.00
	LOCATION*ENERGY	8.95	4	2.24	5.96	0.00
	Error	16.89	45	0.38		

Table 6.2. General linear model results, testing for effect of location, average wave energy and their interaction on structure of the full dataset from intertidal data. The results for the first (PC1), second (PC2) and third (PC3) principal component factor scores calculated are shown. The r^2 value, sum of squares (SS), degrees of freedom (df), mean sum of squares (MS), F-ratio, and p-value (P) are given for each component.

PC1	Source	SS	df	MS	F-ratio	P
r^2=0.47	LOCATION	46.81	4	11.7	20.54	0.00
	ENERGY	8.19	1	8.19	14.38	0.00
	LOCATION*ENERGY	17.09	4	4.27	7.5	0.00
	Error	61.54	108	0.57		

PC2	Source	SS	df	MS	F-ratio	P
r^2=0.13	LOCATION	1.46	4	0.37	0.39	0.82
	ENERGY	1.08	1	1.08	1.14	0.29
	LOCATION*ENERGY	3.62	4	0.91	0.96	0.43
	Error	102.06	108	0.95		

PC3	Source	SS	df	MS	F-ratio	P
r^2=0.14	LOCATION	12.13	4	3.03	3.27	0.01
	ENERGY	2.79	1	2.79	3.02	0.09
	LOCATION*ENERGY	6.57	4	1.64	1.77	0.14
	Error	100.04	108	0.93		

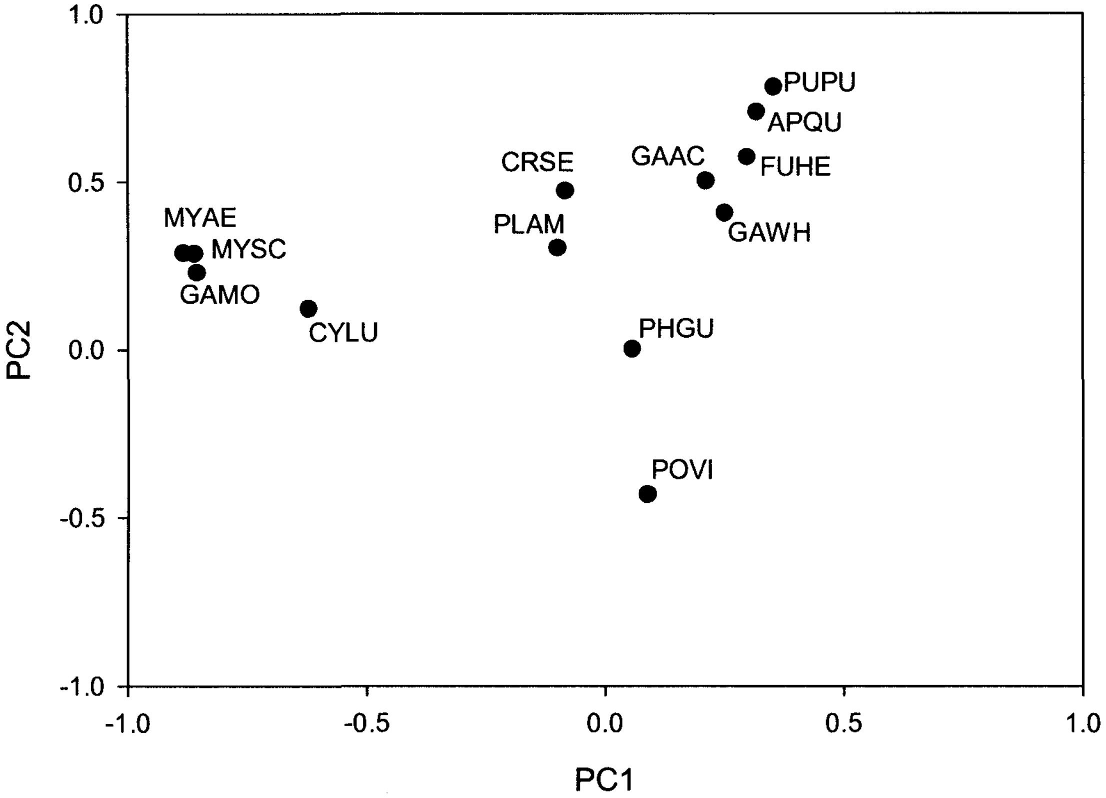

Figure 6.5. Principal component loadings for the first (PC1) and second (PC2) principal components calculated from the reduced random dataset. From left to right along the PC1 axis: MYAE = *Myoxocephalus aenaeus*, MYSC = *Myoxocephalus scorpius*, GAMO = *Gadus morhua*, CYLU = *Cyclopterus lumpus*, PLAM = *Pseudopleuronectes americanus*, CRSE = *Crangon Septemspinosa*, PHGU = *Pholis gunnelus,* POVI = *Pollachius virens*, GAAC = *Gasterosteus aculeatus*, GAWH = *Gasterosteus wheatlandi*, FUHE = *Fundulus heteroclitus*, APQU = *Apeltes quadracus*, PUPU = *Pugitius pungitius*.

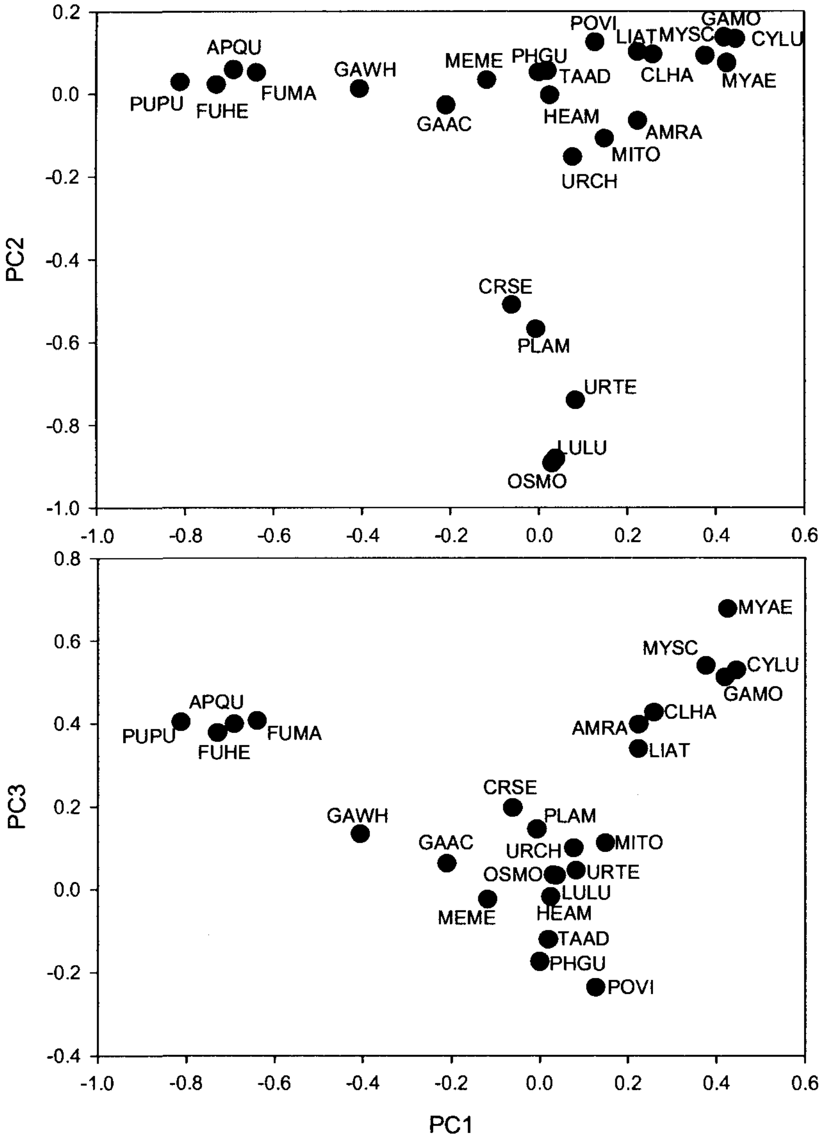

Figure 6.6. Principal component loadings for the first (PC1) and second (PC2) principal components (top) and the first (PC1) and third (PC3) principal components (bottom) calculated from the full dataset. From left to right along the PC1 axis: Species not listed in Figure 6.5 include FUMA = *Fundulus majalis*, MEME = *Menidia menidia*, TAAD = *Tautogolabrus adspersus*, HEAM = *Hemitripterus americanus*, OSMO = Osmerus mordax, LULU = *Lumpenus lumpretaeformis*, URTE = *Urophycis tenuis*, URCH = *Urophycis chuss*, MITO = *Microgadus tomcod*, LIAT = *Liparis atlanticus*, AMRA = Amblyraja radiata.

intertidal species and are an important part of the GLM analysis, suggesting PC2 is strongly related to the wave energy experienced by a site. The results of the analysis based on the full dataset (Figure 6.6) also suggest much the same groupings, in particular the mudflat species demonstrated by Figure 6.5. The cod (*Gadus morhua*) complex of species, including lumpfish (*Cyclopterus lumpus*), and the sculpins (*Myoxocephalus aenaeus*, MYSC = *Myoxocephalus scorpius*) were found with an opposite loadings to the mummichog (*Fundulus heteroclitus*) complex including the stickleback species *Pugitius pungitius*, *Apeltes quadracus*, *Gasterosteus aculeatus*, *Gasterosteus wheatlandi*, and the banded killifish (*Fundulus majalis*).

6.4. Discussion

The results demonstrate that the community of fish occupying the intertidal and upper subtidal (infralittoral) zone within the MDI- Schoodic region can be analyzed successfully using principal component analysis of beach seine collected fish count data. The structure of the fish community is related to the expected average wave energy experienced by the site. A similar trend in species composition was determined through the tidepool surveys but with reduced numbers of species (Chapter 3). Tidepools are in the high intertidal region and some species (cod: *Gadus morhua*) are not found there. High-energy areas are characterized by steep rock ledges with no break in the steepness in the low intertidal, whereas in low energy areas there are extensive mudflats and steep into central thalwegs (Shipp et al. 1987). A decreasing amount of marsh from low to high-energy regions is demonstrated in the tripartite coastal scheme developed for the Maine coast (Kelley 1987, Shipp et al. 1987). The divisions reflect the underlying bedrock structure and the resultant coastal morphology (Duffy et al. 1989). In addition, protected shores of islands near to a coastline can have sediment deposition from both longshore transport growing the coast towards the island and deposition growing the island towards shore (Woodroffe 2002). Species of fish are found to reflect this coastal scheme, progressing from the mummichog estuarine group (Primary species: *Fundulus heteroclitus*, *Apeltes quadracus*, *Pungitius pungitius*. Secondary species: *Fundulus majalis*, *Gasterosteus aculeatus*, *Gasterosteus wheatlandi*) to a gadid complex (*Gadus morhua*, *Myoxocephalus scorpius*, *Myoxocephalus aenaeus*, *Cyclopterus lumpus*). *Crangon septemspinosa* and *Pseudopleuronectes americanus* were separated from, and intermediate to, the other groups. *Pollachius virens* and *Pholis gunnellus* also formed a third group that varied in position compared to the other groups. The reduction of the contributions of location and energy to PC1 compared to PC2 in the general linear model testing the random dataset demonstrate that *Pollachius virens* and *Pholis gunnellus* are found along higher wave energy coastlines than the gadid complex.

Where the mummichog complex was absent the gadid complex invaded despite a low energy environment that should favor the mummichog complex of species. This demonstrates that there are two exposures to consider: the first is at the scale of the site, the second at the regional scale. The site scale is related to the relationship between the morphology of intertidal fish species and microhabitat use, which reflects the physical stress of the environment and life history strategy of the organism (Zander et al. 1999). The regional scale speaks to processes related to exposure between the locations and the resulting chance for populations to persist. It is unlikely that the fish community from the leeward side of MDI can populate the community occupying Isle au Haut. But the reasons are not only because the species may not be suited to those habitats, but also due to the probability of immigration (Magnuson et al. 1988). The species that make up the mummichog-stickleback species complex are restricted to along the coastal mainland, and the result is probably influenced by metacommunity and source-sink dynamics.

Remote island sites have an absence of mummichog and stickleback species while more inter-connected areas along the coast can contain dense populations. Species making up the mummichog complex are also associated with estuaries. The inflow of freshwater will be dependent on the size of the drainage area or watershed. Because of this, larger landmasses will have a better opportunity to create substantial estuarine areas. Northeast Creek and Bass Harbor are the two largest freshwater systems associated with the sampling sites (see Figure 6.2). Both these systems had upper reaches dominated by mummichogs (Chapter 2, 5). Seal Cove and Mosquito Cove also had mummichogs, and the other species in their complex, present but restricted to a much smaller area. In the case of all sites with increased exposure, any estuarine effect was quickly lost due to strong physical forces associated with more exposed coastline. Populations may be controlled by the risks of extinctions, which for example may correlate with increasing exposure to large Nor'easters. Winter mortality has been shown to be an important structuring agent in the Gulf of Maine region (Munch et al. 2003) and may extirpate populations restricted to the intertidal zone in open and unconnected sites. The likelihood of immigration from source populations is lower the further the sites are from source populations or refugia (estuarine sources) with barriers to connectivity established by high wave energy.

The nearshore environment along the Maine coast has been shown to be a nursery ground for marine species (Lazzari et al. 1999, Lazzari and Tupper 2002) and many commercially exploited species use the nearshore during early life histories. Methven and Schneider (1998) use multiple gear types to construct evidence of substantial use of the 4-7 m depth range by juvenile cod. Cote et al. (2004), using sonic tagging to establish that cod kept home ranges concentrated at 19.1 m (standard deviation of 4.1m). This suggests that juvenile cod are found at depths of up to 25 m during the summer. The presence of cod juveniles was also an encouraging development and, combined with widespread anecdotal evidence supplied by lobster fishery members, suggests a population that at the very least is present. The status of the juvenile cod population along the northern Maine coast should be the focus of continuing work.

More mobile species such as herring (*Clupea harengus*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), rainbow smelt (*Osmerus mordax*) silversides (*Menidia menidia*) are know to congregate in heads of bays as the result of observations of small fisheries using large block seines and discussions with local fishermen (Personal Observation). The absence of the species from open coast may be more a result of difficulty of capture along open coastline and the converse within embayments, rather than their limitation to heads of bays. Still, their role in the fish community is overlooked by their omission by the sampling gear, which was developed to effectively capture benthic species. The reason for targeting benthic-associated species was because they are more likely to reflect the environment compared to the schooling and highly mobile species, which are often in the process of migrating between habitats.

The tide height, and therefore the fraction of intertidal or subtidal space being sampled, is also likely to impact the fish species that are retained in the seine, since different species tend to occupy different depths. Pollock (*Pollachius virens*) have been shown to move more freely into the intertidal zone (Rangeley and Kramer 1995) compared to cod, which appear to maintain more site fidelity within the sub tidal zone (Cote et al. 2004). Therefore, upon refinement of the techniques suggested here, the tide height should also be considered in the analysis with different gear types as to better define the full group of species occupying the space.

The sevenspine bay shrimp or sandshrimp (*Crangon septemspinosa*) was the only invertebrate included in the analysis. The reason for inclusion was the dominance of the species in seines across many sites, and the likelihood that, as a result, the species is playing an important role in determining the community structure. Sand shrimp were closely associated with the winter flounder (*Pseudopleuronectes americanus*). Crangon are proven predators of winter flounder smaller than 20 mm (Witting and Able 1995), therefore the overlap in the two species could be attributed to a predator-prey relationship. However, flatfish species have been found to associate to defined sediment types (McConnaughey and Smith 2000), and the relationship between winter flounder and sand shrimp is more likely due to their association to the sediment. Both species were most often caught over mud and sand combinations of sediment, the most often used inshore habitats of winter flounder (Collette and Klein-MacPhee 2002). This does not preclude the notion that predator-prey relationships are important in structuring communities of fishes, only that the type of habitat will play the primary role in determining distributions when considering order of magnitude changes in exposure. A better accounting of invertebrates would also be a positive step towards a more thorough understanding of species divisions along the Maine coast.

The tripartite coastal scheme (Kelley 1987, Shipp et al. 1987) breaks the Maine coast into an outer zone of rocky outcrop, a middle zone characterized by erosion of bluffs and some deposition of sediment in local "quiet" areas, and (3) an inner zone of high sediment accumulation rates with wide tide flats and salt marsh habitat. It is clear that the division of species complexes reflects this coastal scheme and as a result the connectivity of these habitats is likely to be important in controlling the distribution of species along the coast. Vegetation changes also accompany the alteration of the geomorphology. Rockweeds and laminaria spp are encountered along the rocky intertidal, whereas eelgrass was found in moderate (but sediment laden) environments and marsh grasses were common at the head of bays. The use of measurements obtained from GIS as a tool to delineate potential habitats that may be used by complexes of species offers an excellent opportunity for determining valuable habitats and better designing population surveys to account for differing habitat types. Fetch calculations and wind data were used by Ekebom et al. (2002, 2003) and Lundqvist et al. (2006) to generate wave exposure estimates and suggest the technique as a method to describe habitat types. The present research advances this concept by suggesting there is a quantifiable relationship between fetch and the community of fish at a location.

Much of the introduction of this paper focused on the development of marine protected areas as a tool for coastal management. A network of MPAs must allow for essential habitat of juvenile fishes to be included with the understanding of dispersal of egg and larval stages. By accounting for the full potential range of a population and the habitats and species they are associated with rather than focusing on a single habitat will help maintain landscape (larger scale) structure. Labbe and Fausch (2000) give good account of the importance of considering both local and landscape scales in attempting to achieve management objectives.

Focusing on maintenance of discrete MPAs will rely on accurately judging whether enough habitat of the correct type is being put aside. Lauck et al. (1998) suggest bet-hedging as a required strategy, and as a result more than one habitat should be protected. Lauck et al. (1998) also suggest that up to 50% of the original population should be protected in order to hedge successfully against overfishing. These populations then can act as a source for populations targeted for exploitation. Clearly in order to act as a source for other metacommunities, the reserves will have to be constructed with the interconnectedness of habitats and locations of sources of populations incorporated into the design in such a way that species are capable of repopulating habitats after extinction events.

Lobster traps are located in dense numbers across the outer windward sites on MDI, across most of Schoodic and Isle au Haut. Lobsters are generalist feeders shown to prey on fish once they achieve 65 mm carapace length (Sainte-Marie and Chabot 2002). Polis et al. (1997) discuss how importing food into the system can permit consumers to overexploit resident prey. These subsidized consumers can structure systems by suppressing populations of key species. If baited lobster traps offer a food source to lobsters and other predatory species, it could be that juvenile fish at the exposed sites are being preyed upon by populations of juvenile lobsters whose growth and survival are not suppressed by limited productivity. These types of relationships deserve attention and study since they may involve the reduction of populations of fish that are considered ecologically or economically valuable.

This paper links the community of species to a physical gradient in wave energy and offers a potential method to map habitat. The scale of the habitat that needs protection will need to be considered at both local levels, where specific habitats are optimal for certain species, and landscape levels, where interconnectedness and metapopulation dynamics could impair the ability to achieve specified goals.

6.5. Acknowledgments

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CHAPTER 7

DIFFERENCES IN THE FISH COMMUNITY STRUCTURE BETWEEN EASTERN AND WESTERN INSHORE OF THE GULF OF MAINE

7.1 Introduction

The Gulf of Maine (GOM) is a well-studied, semi-enclosed and highly productive coastal ecosystem in the northwest Atlantic Ocean (Figure 7.1). The high levels of production result from estuarine-like circulation patterns and tides (Townsend 1991). The bathymetry of the GOM and Bay of Fundy and the resulting time required for the basin to empty after the flood tide is in a near match with the semidiurnal rhythm of the Atlantic Ocean Basin tide. The result is tidal resonance, where the mean tidal range is greatly amplified (Brooks and Townsend 1989). The strong tidal movement, and to a lesser degree wind stress, result in strong vertical mixing where deeper colder water is brought to the surface. One important area of vertical mixing is the Eastern Maine Coastal Current (EMCC; Figure 7.2). At Penobscot Bay the EMCC moves offshore and under the warmer Western Maine Coastal Current (WMCC), which continues along the southwestern Maine coast (Figure 7.2). This causes a gradient in temperature with approximately Penobscot Bay separating the cold-water EMCC dominating waters to the Northeast and the warm-water WMCC dominating waters to the Southwest.

The pattern in oceanographic processes is coupled with coast-wide differences in geologic structure, progressing from (1) low relief rocky headlands and arcuate embayments, to (2) deep, narrow, elongate estuaries, then (3) broad, deep estuaries and bays with rounded granite islands and (4) a high relief cliff dominated shoreline that

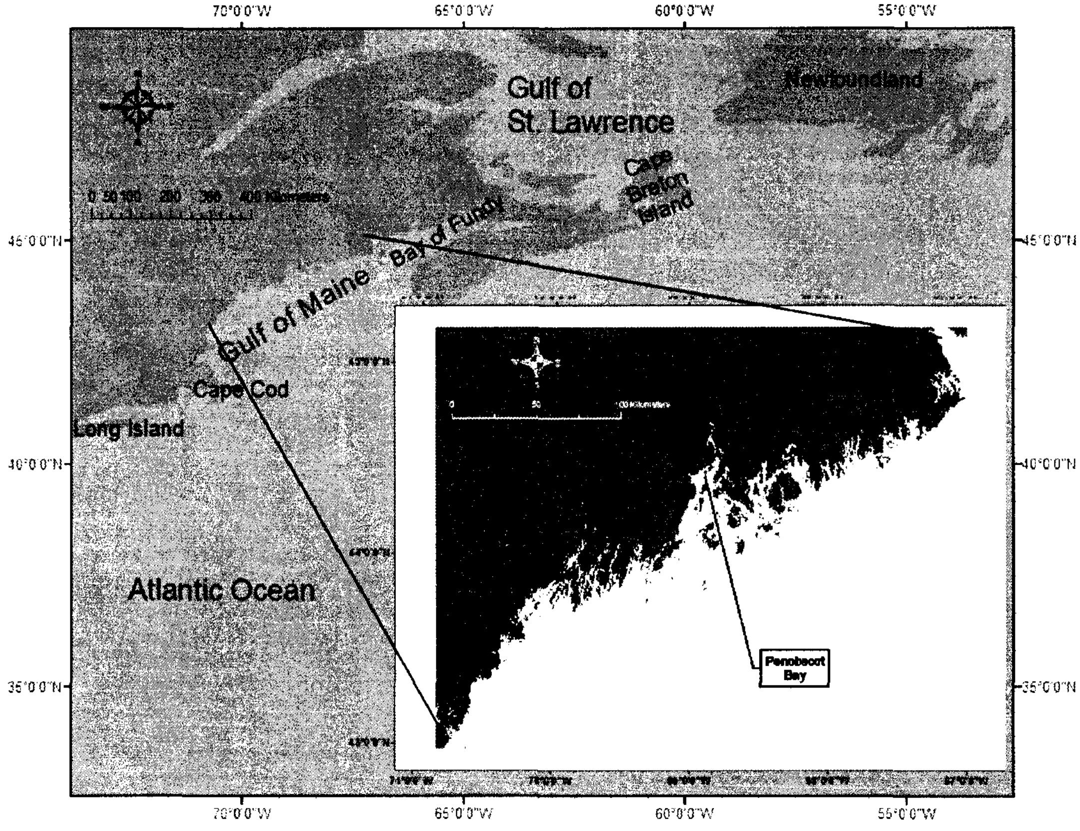

Figure 7.1. The location of the Gulf of Maine, and Maine coastline (inset) in reference to other landmarks along the Northeastern American shelf.

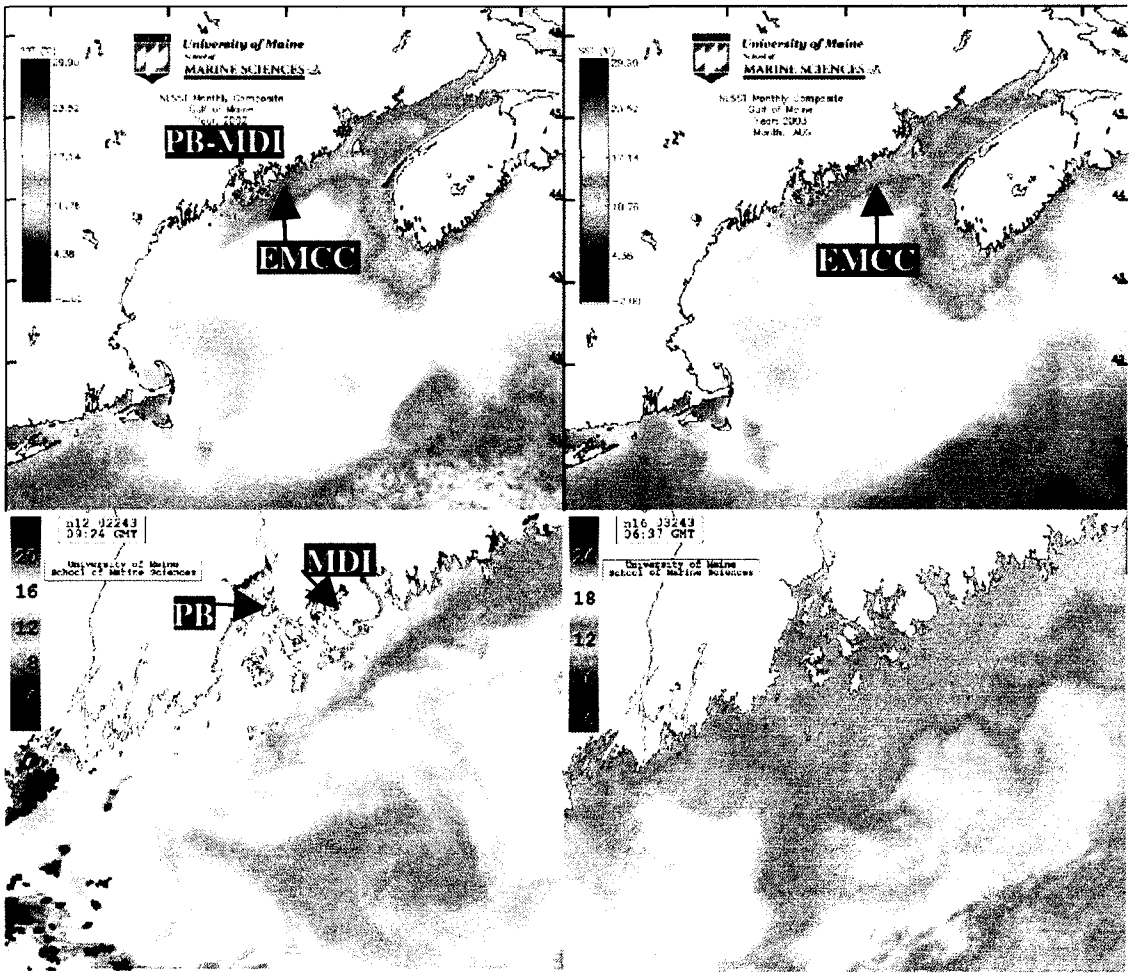

Figure 7.2. Satellite images highlighting temperature differences around Mount Desert Island (MDI) and Penobscot Bay (PB) in 2002 and 2003. In 2002 the entire Gulf of Maine (upper left panel) and the mid-coast of Maine (bottom left panel) experienced cooler water temperatures than in 2003 (Gulf of Maine, upper right; Mid-coast Maine, lower right). The Eastern Maine Coastal Current (EMCC) can be observed as the blue current (arrow) along the Maine coast. The Western Maine Coastal Current (WMCC) dominates south and west of Penobscot Bay. Blue colors represents temperatures near 8°C, orange around 18°C. Images courtesy Dr. Andrew Thomas of the Satellite Oceanography Laboratory, University of Maine.

protects irregular estuaries, as one moves west to east (Jackson 1837; Kelley and Timson 1983; Belknap et al. 1987; Kelley 1987; Duffy et al. 1989).

In addition to the physical controls placed on the distribution of species, there is an interaction among the biological components that can result in structure to an ecosystem. The primary sources of discussion in ecology have been top-down (Hairston et al. 1960), where predators control the abundance and distributions of prey, and bottom-up (Lindeman 1942), where the production at lower trophic levels limits the production at higher trophic levels. The removal of species that are exerting strong top-down forces can influence successive trophic levels, know as a trophic cascade (Strong 1992), as has been suggested with large cod in the Northwestern Atlantic (Frank et al. 2005). Trophic cascades have been suggested as a mechanism controlling species composition in the Gulf of Maine with fishing pressure on specific groups of species being the instigating factor (Steneck et al. 2004; Worm et al. 2005).

The coast of Maine offers a strong environmental gradient to test whether persistent oceanographic processes can help explain community structure of fish. To test for differences in the community of fish in the Eastern and Western coastal waters of Maine, principal component analysis was used to create a new set of variables that explain the correlations amongst species and the new variables are tested for correlations with depth and latitude.

7.2 Methods

7.2.1. Trawl Design

The Maine-New Hampshire Inshore Trawl Survey has been in operation since the fall of 2000, completing a survey every spring and fall since. In 2003, an additional depth stratum was added. This dataset was chosen for analysis of coast-wide ecological structure because a more complete depth range was sampled compared to previous years. The following information regarding the trawl survey design is taken from Sherman et al. (2005). The Maine-New Hampshire Inshore Trawl Survey is a stratified random survey with a fixed component. The inshore area sampled includes four depth strata: 9-37 m, 38-64 m, 65-101 m, and >102 m out to approximately the 12-mile (19 km) limit (for State waters), and five longitudinal regions based on oceanographic, geologic, and biological features. This results in 20 separate strata within the total survey area of ~8640 km^2. A target of 115 stations is selected for sampling in each survey resulting in a sampling density of 1 station for every 74 km^2. Number of tows per stratum is apportioned according to its total area. Trawl design considerations for the survey include effectiveness of the gear for sampling the complex bottom in the nearshore areas of the Gulf of Maine and comparability with previous and ongoing surveys by NMFS and Massachusetts Division of Marine Fisheries. The net is a modified version of the shrimp net design used in Maine waters, designed to fish for a variety of near bottom dwelling species without targeting any specific component. The net is constructed of 5 cm #24 polyethylene mesh; with a 2.5 cm (stretched measure) mesh liner in the cod end. The 2003 survey concluded with 101 sites sampled in the spring and 78 in the fall sample period.

7.2.2 Tests and Statistics

The dataset was divided into three different groups: benthic vertebrates, benthic invertebrates and pelagic species. Each of the three categories was treated separately and then compared once all principal component analyses were completed.

Bootstrap-PCA procedures were completed in SAS. Bootstrap 95% confidence limits for eigenvalues were used as the stopping rule to determine which principal components were "significant" and to be included in further analysis (Jackson 1993). Bootstrap-PCA techniques were then used to identify species that were driving the PCA results by examining the distribution of component loadings, and identifying significant correlations in the loadings amongst species. The bootstrap loading distributions were compared to one another using Kolmogorov – Smirnov two sample tests with Bonferroni corrections for multiple comparisons in SYSTAT™ v.10.2. Groupings of fish were designated on the basis of the Kolmogorov – Smirnov two sample tests, which tests whether two sampled frequency distributions are from the same population. The three species with the highest component loading scores where compared for trends in species correlations against the full group of species using mean bootstrap-created Pearson correlation coefficients and standard deviations.

SYSTAT™ v.10.2 was used to calculate principal components for the spring and fall surveys. Only the principal components identified as unique by for each group (benthic vertebrates, benthic invertebrates and pelagic species) for each the spring and fall surveys were used. The scores generated for each site were compared for differences in relation to longitude, depth and temperature (and interactions) using a general linear model (GLM). Pearson correlations between species were performed, for principal

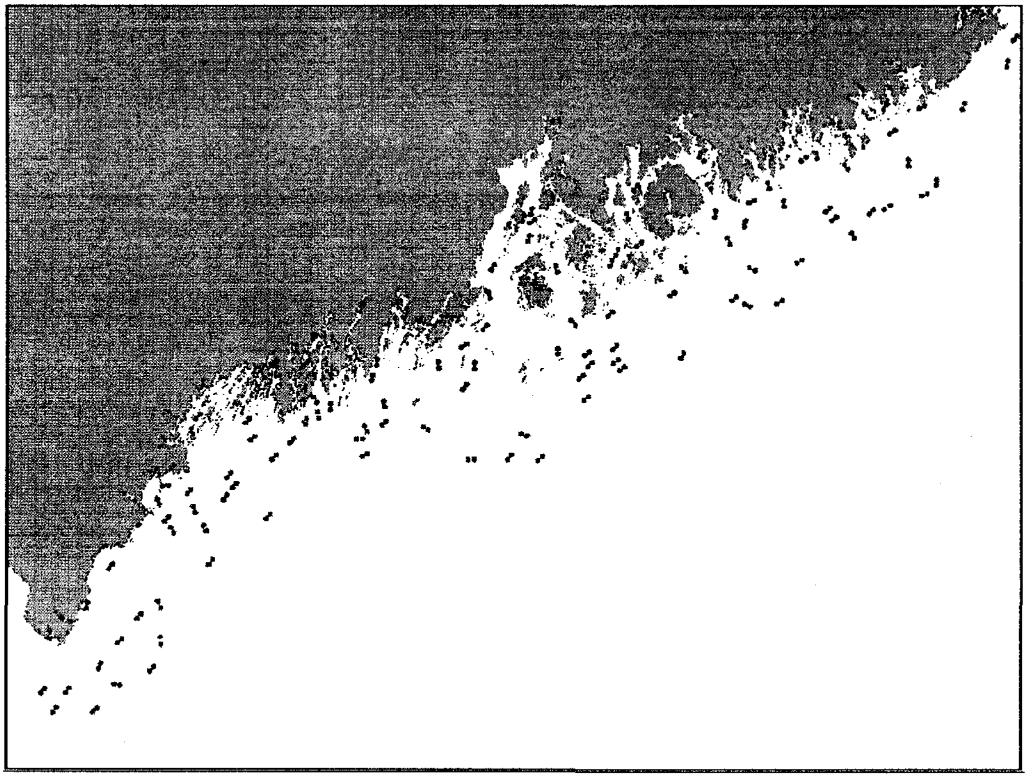

Figure 7.3. Sites used by the spring and fall inshore trawl survey. See Figure 7.1 for position relative to other landmarks in Northwest Atlantic Ocean.

components that demonstrated uniqueness, to determine those principle component scores from different groups (fish, invertebrates, pelagics) correlated with one another.

7.3 Results

The species lists for the groups of species are found in Table 7.1, 7.2 and 7.3. The principal component analysis produces the same number of new variables as was present in the original data. There were 29 species of benthic vertebrates, 24 species of benthic invertebrates and 10 pelagic species in the spring and 11 in the fall. The eigenvalue scores for the principal components indicate that first principal components of the species groups explain 16-23% of the total variance in the spring and 17-24% in the fall (Table 7.4). The eigenvalue scores are higher for the bootstrap results than for the initial analysis in all but one case (Table 7.4), although the initial analysis scores are within the 95% confidence limits of the bootstrapped values. The bootstrap generated 95% confidence limits for the eigenvalues scores provided a stopping rule by comparing across PC values and establishing overlapping confidence limits (Jackson 1993). Analysis of fish data, from both the spring and fall surveys, demonstrated that PC1, PC2 and PC3 were all different from one another and PC4 onwards were similar. Neither invertebrate dataset provided unique value suggesting a lack of structure to the data or equivalence to a randomly generated dataset. Analysis of the pelagic data identified PC1 and PC2 as unique values.

The results of the GLM demonstrate that there are differences in the structure of the datasets associated with longitude, temperature, depth and their interaction. For the spring benthic vertebrates, PC1 produced a significant regression model (F-ratio = 29.9, d.f. = 7, 93, $P < 0.001$, $r^2 = 0.47$) with longitude ($T = 3.0$, $P = 0.003$), temperature ($T = 2.47$. $P = 0.015$) and the temperature-longitude interaction ($T = -2.46$, $P= 0.016$) were all significant contributors to the model with depth and all other interaction not significant ($P> 0.95$). For the spring pelagics, PC1 produced a significant regression model (F-ratio = 11.7, d.f. = 7, 93, $P < 0.001$, $r^2 = 0.47$) with longitude ($T = 2.24$, $P = 0.028$), depth ($T = 2.12$. $P = 0.036$) and the depth-longitude interaction ($T = -2.14$, $P = 0.035$) were all significant contributors to the model with temperature and all other interaction not significant ($P > 0.1$). For the spring pelagics, PC2 also produced a significant regression model (F-ratio = 3.38, d.f. = 7, 93, $P = 0.003$, $r^2 = 0.20$) with all factors and interactions significantly contributing to the model ($P < 0.035$), except for temperature ($T = 1.8$, $P =0.07$) and the temperature-longitude interaction ($T = -1.8$, $P =0.07$). For the fall benthic vertebrates, PC1 produced a significant regression model (F-ratio = 23.9, d.f. = 7, 66, $P < 0.001$, $r^2 = 0.72$), only longitude was marginally significant ($T = 3.0$, $P = 0.08$). By removing all depth associated factor (none had $P < 0.68$) the model is significant (F-ratio = 28.6, d.f. = 3, 66, $P < 0.001$, $r^2 = 0.55$) and longitude ($T = -3.1$, $P = 0.003$), temperature ($T = -2.6$. $P = 0.013$) and the temperature-longitude interaction ($T = 2.7$, $P = 0.01$) are significant. The benthic vertebrate PC2 was also significantly explained by the model (F-ratio = 3.8, d.f. = 7, 66, $P = 0.002$, $r^2 = 0.29$).Only the depth-temperature interaction ($T = 2.5$, $P = 0.016$) and longitude-depth-temperature interaction ($T = -2.5$, $P = 0.015$) were judged significant, but depth ($T = -1.8$, $P = 0.07$) and longitude-depth interaction ($T = 1.8$, $P = 0.07$) were marginal. Depth ($T = -2.2$, $P = 0.03$) and longitude-depth interaction ($T = 2.2$, 0.03) were significant for the PC3 benthic vertebrate GLM (F-ratio = 6.9, d.f. = 7, 66, $P < 0.000$, $r^2 = 0.42$). Although not considered "structured" by the stopping rules, the PC2 invertebrate GLM analysis for the fall sample period produced a significant model (F-ratio = 6.6, d.f. = 7, 66, $P < 0.001$, $r^2 = 0.41$), with longitude as the only significant variable (T = -2.5, P =0.015) although temperature (T = -1.8, P = 0.073) and temperature-longitude (T = 1.8, P = 0.077) were marginal. The GLM for the pelagic PC1 analysis produced a significant model (F-ratio = 20.0, d.f. = 7, 66, $P < 0.001$, $r^2 = 0.68$), with all factors and interactions significantly contributing ($P< 0.001$).

Simply comparing the east and west components of the coast, using roughly the position of Penobscot bay for dividing the coast, using t-tests with Bonferroni corrected p-values demonstrate that there are strong east-west differences for PC1 (T = -4.48, df = 58.6, P = 0.00032) and PC3 (T = 4.27, df = 94.4, P = 0.00042) for the benthic vertebrates (PC1VERT and PC3VERT) and PC2 (T = 4.52, df = 90.6, P = 0.00017) for the benthic invertebrates (PC1INV) during the spring survey. East-west differences demonstrated by principal components from the fall survey data were PC1 (T = 4.62, df = 52.2, P = 0.00023) for the benthic vertebrates (PC1VERT), PC2 (T = -5.29, df = 32.8, P = 0.000071) from the pelagic species group (PC2PEL), and to a lesser degree the PC1 from the benthic invertebrates (PC1INV; T = -2.67, df = 35.7, P = 0.10).

The results of the Pearson correlations coefficients amongst spring survey principal components demonstrated coherence of PC1INV (Pearson correlation coefficient (CC) = 0.32, P = 0.033), PC2INV (CC = -0.42, P = 0.00036) and PC1PEL (CC = -0.30, P = 0.09) with PC1VERT, and PC3VERT with PC1INV (CC = -0.32, P = 0.031). For the fall survey generated principal components, groups that show coherence

Table 7.1. Species list for benthic vertebrate group including abbreviations used in text.

Species	Abbreviation	Common name
Raja erinacea	RAER	Little Skate
Raja senta	RASE	Smooth Skate
Raja radiata	RARA	Thorny Skate
Merluccius bilinearis	MEBI	Silver Hake
Gadus morhua	GAMO	Atlantic Cod
Melanogrammus aeglefinus	MEAE	Haddock
Pollachius virens	POVI	Pollock
Urophycis tenuis	URTE	White Hake
Urophycis chuss	URCH	Red Hake
Enchelyopus cimbrius	ENCI	Fourbeard Rockling
Reinhardtius hippoglossoides	REHI	Greenland Halibut
Hippglossus hippoglossus	HIHI	Atlantic Halibut
Hippoglossoides platessoides	HIPL	American Plaice
Paralichthys oblongus	PAOB	Fourspot Flounder
Limanda ferruginea	LIFE	Yellowtail Flounder
Pseudopleuronectes americanus	PSAM	Winter Flounder
Glyptocephalus cynoglossus	GLCY	Witch Flounder
Scophthalmus aquosus	SCAQ	Windowpane
Sebastes fasciatus	SEFA	Acadian Redfish
Myoxocephalus scorpius	MYSC	Shorthorn Sculpin
Myoxocephalus octodecemspinosus	MYOC	Longhorn Sculpin
Hemitripterus americanus	HEAM	Sea Raven
Aspidophoroides monopterygius	ASMO	Alligatorfish
Cyclopterus lumpus	CYLU	Lumpfish
Tautogolabrus adspersus	TAAD	Cunner
Lumpenus lumpretaeformis	LULU	Snakeblenny
Cryptacanthodes maculatus	CRMA	Wrymouth
Macrozoarces americanus	MAAM	Ocean Pout
Lophius americanus	LOAM	Goosefish

Table 7.2. Species list for benthic invertebrate group including abbreviations used in text.

Species	Abbreviation	Common name
Crangon septemspinosa	CRSE	Sevenspine Bay Shrimp
Pasiphaea multidentata	PGSH	Pink Glass Shrimp
Dichelopandalus leptocerus	DILE	Bristled Longbeak
Pandalus montagui	PAMO	Aesop Shrimp
Homarus americanus	HOAM	American Lobster
Pandalus borealis	PABO	Northern Shrimp
Geryon quinquedens	GEQU	Red Crab
Cancer borealis	CABO	Jonah Crab
Cancer irroratus	CAIR	Rock Crab
Stomatopod sp.	STSP	Mantis Shrimp
Lithodes sp.	LISP	Northern Stone Crab
Chionectes opilio	CHOP	Snow Crab
Echinoidae sp.	ECSP	Sand Dollar
Stronglyocentrotus droebachiensis	STDR	Sea Urchin
Mytilus edulis	MYED	Blue Mussel
Placopecten magelanicus	PLMA	Sea Scallop
Arctica islandica	ARIS	Ocean Quahog
Venercardia borealis	VEBO	Northern Cardita
Astarte undata	ASUN	Waved Astarte
Cephalopoda spp.	CESP	Octopus (unclass.)
Hyas araneus	HYAR	Toad Crab
Yoldia thraciaeformis	YOTH	Ax Head Clam
Caudina arenata	RAAR	Rat-tail Cucumber
Cucumaria frondosa	CUFR	Sea Cucumber

Table 7.3. Species list for pelagic group including abbreviations used in text.

Species	Abbreviation	Common name
Squalus acanthias	SQAC	Spiny Dogfish
Clupea harengus	CLHA	Atlantic Herring
Alosa pseudoharengus	ALPS	Alewife
Alosa aestivalis	ALAE	Blueback Herring
Alosa sapidissima	ALSA	American Shad
Brevoortia tyrannus	BRTY	Atlantic Menhaden
Osmerus mordax	OSMO	Rainbow Smelt
Scomber scombrus	SCSC	Atlantic Mackerel
Maurolicus muelleri	MAMU	Pearlsides
Loligo pealei	LOPE	Longfin Squid
Euphausuid spp.	EUSP	Krill

Table 7.4. Eigenvalues (EG) and percent explained variance (%) for the first three principle components generated for the three species groupings for the spring and fall surveys. Benthic vertebrates = VERT, benthic invertebrates = INV, pelagic species = PEL. Both the SYSTAT generated and SAS-bootstrap generated values are given.

		Spring						Fall					
		PC1		PC2		PC3		PC1		PC2		PC3	
		EV	%	EV	%	EV	%	EV	%	EV	%	EV	%
SYSTAT	VERT	4.7	16	3.2	11	2.3	8	5.5	19	3.3	11	2.7	9
	INV	4.3	18	2.9	12	2.5	11	4.2	17	3.0	12	2.5	10
	PEL	2.3	23	1.6	16	1.2	12	2.7	24	2.2	20	1.3	12
SAS-bootstrap	VERT	5.1	18	3.4	12	2.5	9	5.9	20	3.6	12	2.8	10
	INV	4.5	19	3.0	12	2.3	10	4.5	19	3.2	13	2.5	10
	PEL	2.4	24	1.7	17	1.2	12	2.9	26	2.2	20	1.4	12

The component loadings generated by the PCA bootstrap technique and the initial PCA run were not equal in value. There is agreement in the division of species with the bootstrap-PCA loadings dampened compared to the SYSTAT generated loadings (Tables 7.5 – 7.10). Still, the bootstrap loadings support the general trend in species. For the spring sample period, silver hake were the most common averaging 440 individuals per tow. The most important species according to the loading data are the 3 highly correlated monkfish, redfish and American plaice (Figure 7.5), which averaged 1.0, 7.8 and 67.0 individuals per tow, respectively. The fish were found to show the same general trend in relation to the other species (Figure 7.5).

Component loadings did display some flip-flopping of loading scores, but the relative position of the scores was conserved. For the benthic vertebrates in the fall sample period, the initial PCA scores were opposite to the majority of scores given by the bootstrap-PCA (Table 7.8). Still, the bootstrap-PCA did identify the same pattern in species loadings. The initial PCA gave the species *Lophius americanus* a loading opposite to that of the spring sample (Table 7.5). The details of flip-flopping PCA loadings is discussed in Chapter 3.

Rare species did in some cases score high loadings, and these species were easily identified from the correlation coefficients. This because receiving "0" scores during the bootstrap process becomes more likely the rarer the species is. Correlations coefficients less than 1 with error bars indicate species were this occurred. The fall invertebrate analysis (Figure 7.9) displays this tendency with *Venercardia borealis* picking up the most "0" scores and therefore having the lowest correlation coefficient with itself compared to *Chionectes opilio* and *Cephalopoda spp*. The increased number of "0" scores also reflected in the component loadings (Table 7.9).

Table 7.5. Frequencies of component loadings for 29 species of benthic vertebrates estimated using 500 bootstrap samples from the spring inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov-Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	GAMO	MEAE	POVI	MEBI	URTE	URCH	ENCI	REHI	HIHI	HIPL	PAOB	LIFE	PSAM	GLCY	SCAQ
LOAD	0.33	0.48	0.41	0.37	0.52	0.54	0.31	0.09	-0.16	0.71	0.48	0.63	-0.21	0.59	-0.49
GRP	G,H	D	F	E	C	B	H	U	U	A,B	C,D	U	U	U	U
-0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.4	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	2	0	0
-0.2	0	0	0	0	0	0	0	0	1	0	0	0	33	0	331
-0.1	1	0	3	0	0	0	0	0	103	0	0	0	210	0	168
0	6	0	26	2	0	0	1	115	367	0	3	1	207	1	1
0.1	97	13	67	43	20	1	117	341	28	0	28	3	42	5	0
0.2	326	208	214	321	146	76	314	41	1	4	173	23	5	59	0
0.3	69	272	189	132	306	405	67	3	0	158	276	312	1	301	0
0.4	1	7	1	2	28	18	1	0	0	336	20	161	0	133	0
0.5	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0

Table 7.5.(cont) Frequencies of component loadings for 29 species of benthic vertebrates estimated using 500 bootstrap samples from the spring inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov-Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	SEFA	MYSC	MYOC	HEAM	ASMO	CYLU	TAAD	LULU	CRMA	MAAM	RAER	RASE	RARA	LOAM
LOAD	0.71	-0.30	-0.08	0.00	-0.11	-0.09	0.19	0.04	-0.03	0.35	0.26	0.36	0.39	0.72
GRP	A	U	J	U	I,J	I	U	U	U	D,E,F,G	U	E	E	A
-0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.4	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	0	0
-0.2	0	8	12	1	2	0	0	0	0	0	0	0	0	0
-0.1	0	416	111	43	71	41	2	17	17	1	0	0	0	0
0	0	76	226	220	319	376	116	171	296	7	19	6	1	0
0.1	0	0	129	190	94	83	184	253	175	102	196	101	60	0
0.2	2	0	17	41	13	0	147	59	12	262	256	264	274	2
0.3	133	0	4	5	1	0	51	0	0	126	27	125	162	120
0.4	365	0	1	0	0	0	0	0	0	2	2	4	3	378
0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 7.6. Frequencies of component loadings for 24 species of benthic invertebrates estimated using 500 bootstrap samples from the spring inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	CRSE	PGSH	DILE	PAMO	HOAM	PABO	GEQU	CABO	CAIR	STSP	LISP	CHOP	ECSP	STDR	MYED
LOAD	-0.26	-0.05	0.33	-0.01	-0.40	0.50	0.01	0.45	-0.32	-0.03	0.35	0.60	-0.12	-0.17	-0.08
GRP	C	U	U	U	U	U	U	U	D	U	U	U	U	U	U
-0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
-0.3	2	0	0	0	10	13	0	1	9	0	0	0	0	0	0
-0.2	17	0	14	3	197	22	0	1	57	0	2	22	0	6	0
-0.1	277	1	20	22	230	2	0	24	320	0	18	14	20	116	0
0	160	489	2	217	27	0	279	10	74	494	42	1	447	328	480
0.1	6	10	68	183	3	3	221	4	1	6	100	0	32	20	20
0.2	1	0	325	57	3	77	0	172	0	0	114	32	1	16	0
0.3	19	0	65	12	21	349	0	285	1	0	144	234	0	11	0
0.4	16	0	6	5	9	34	0	3	29	0	73	196	0	3	0
0.5	2	0	0	1	0	0	0	0	8	0	7	1	0	0	0

Table 7.6.(cont) Frequencies of component loadings for 24 species of benthic invertebrates estimated using 500 bootstrap samples from the spring inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	PLMA	ARIS	VEBO	ASUN	CESP	HYAR	YOTH	RAAR	CUFR
LOAD	0.50	0.70	0.71	0.82	0.64	-0.33	0.54	0.12	-0.27
GRP	U	A	A,B	U	B	D	U	U	C
-0.5	0	0	0	0	0	0	0	0	0
-0.4	0	0	0	0	0	0	0	0	0
-0.3	11	0	0	0	0	12	0	0	2
-0.2	19	2	0	15	0	66	9	2	31
-0.1	5	18	6	13	9	327	12	10	304
0	1	94	28	4	82	58	6	165	126
0.1	32	54	138	2	83	0	6	84	1
0.2	89	14	16	4	18	1	12	107	2
0.3	178	81	63	21	89	0	198	88	15
0.4	154	180	182	308	183	24	209	39	17
0.5	11	57	67	133	36	12	48	5	2

Table 7.7. Frequencies of component loadings for 10 pelagic species estimated using 500 bootstrap samples from the spring inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	SQAC	CLHA	ALPS	ALAE	ALSA	OSMO	SCSC	MAMU	LOPE	EUSP
LOAD	-0.21	0.67	0.74	0.79	0.33	0.53	0.10	-0.23	0.09	-0.38
GRP	U	U	U	U	U	U	U	U	U	U
-0.5	0	0	0	0	1	0	0	0	0	0
-0.4	0	0	0	0	0	0	0	1	0	1
-0.3	0	0	1	0	0	0	0	4	0	69
-0.2	27	0	0	0	0	1	0	104	2	337
-0.1	323	1	0	0	13	1	1	269	24	91
0	132	0	0	1	37	8	208	109	142	2
0.1	18	1	2	0	63	27	205	13	196	0
0.2	0	1	2	0	100	67	74	0	108	0
0.3	0	17	19	2	117	79	9	0	21	0
0.4	0	131	56	5	124	149	3	0	5	0
0.5	0	305	195	124	44	136	0	0	2	0
0.6	0	44	216	367	1	32	0	0	0	0
0.7	0	0	9	1	0	0	0	0	0	0

Table 7.8. Frequencies of component loadings for 29 species of benthic vertebrates estimated using 500 bootstrap samples from the fall inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

SPP	GAMO	MEAE	POVI	MEBI	URTE	URCH	ENCI	REHI	HIHI	HIPL	PAOB	LIFE	PSAM	GLCY	SCAQ
LOAD	0.35	0.36	0.28	-0.59	-0.03	-0.73	-0.76	0.05	0.12	-0.76	-0.31	0.11	0.76	-0.79	0.44
GRP	H	H	U	U	U	U	C	E	F	A,C	D	F	U	B	I
-0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.3	0	0	0	2	0	1	5	0	0	8	0	0	352	8	0
-0.2	36	33	3	17	0	17	17	0	0	14	0	0	126	14	163
-0.1	340	358	301	3	26	3	0	9	91	0	11	51	0	0	298
0	100	78	170	0	195	1	0	298	289	0	19	332	0	0	18
0.1	2	11	12	1	234	0	0	192	107	0	150	101	0	0	3
0.2	14	9	14	88	43	7	2	1	13	0	274	14	0	0	16
0.3	8	11	0	369	2	202	121	0	0	79	46	2	0	44	2
0.4	0	0	0	20	0	269	355	0	0	398	0	0	22	434	0
0.5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Table 7.8.(cont) Frequencies of component loadings for 29 species of benthic vertebrates estimated using 500 bootstrap samples from the fall inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	SEFA	MYSC	MYOC	HEAM	ASMO	CYLU	TAAD	LULU	CRMA	MAAM	RAER	RASE	RARA	LOAM
LOAD	-0.30	0.15	0.50	0.44	0.10	-0.23	0.03	0.08	-0.20	0.09	0.45	-0.29	-0.20	-0.80
GRP	U	U	U	I	G	U	E	U	U	F,G	I	D	U	A,B
-0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-0.4	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	0	16
-0.2	0	0	261	156	2	0	0	0	0	3	154	0	0	6
-0.1	14	42	213	303	81	8	8	2	13	95	303	7	9	0
0	8	429	4	18	212	31	292	479	20	249	21	32	77	0
0.1	53	29	0	1	161	215	170	19	287	105	0	154	178	0
0.2	358	0	3	0	40	244	26	0	172	45	0	259	204	0
0.3	65	0	19	21	4	2	4	0	8	3	20	48	32	73
0.4	2	0	0	1	0	0	0	0	0	0	2	0	0	405
0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 7.9. Frequencies of component loadings for 24 species of benthic invertebrates estimated using 500 bootstrap samples from the fall inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	CRSE	PGSH	DILE	PAMO	HOAM	PABO	GEQU	CABO	CAIR	STSP	LISP	CHOP	ECSP	STDR	MYED
LOAD	-0.29	-0.06	0.41	0.10	-0.34	0.61	0.59	0.37	-0.40	-0.11	0.59	0.69	-0.08	-0.29	-0.17
GRP	G	U	D	U	G	U	B	D	U	E	B	A	U	F	E
-0.3	4	0	2	0	1	9	1	0	23	0	0	0	0	6	1
-0.2	50	0	27	3	36	23	13	1	132	0	15	6	0	50	12
-0.1	307	1	10	19	346	8	3	4	283	28	12	15	0	207	82
0	98	488	1	131	83	1	68	16	22	443	31	23	477	196	373
0.1	1	11	59	227	14	4	31	60	0	18	43	4	23	2	0
0.2	0	0	231	95	15	57	62	247	0	9	79	11	0	3	3
0.3	21	0	145	18	3	253	151	167	1	1	132	97	0	5	14
0.4	17	0	25	6	2	138	128	4	22	1	168	302	0	23	14
0.5	2	0	0	1	0	7	43	0	15	0	20	42	0	8	1
0.6	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0

Table 7.9.(cont) Frequencies of component loadings for 24 species of benthic invertebrates estimated using 500 bootstrap samples from the fall inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	PLMA	ARIS	VEBO	ASUN	CESP	HYAR	YOTH	RAAR	CUFR
LOAD	0.54	0.46	0.64	0.55	0.67	-0.32	0.05	-0.09	-0.23
GRP	U	C	A	C	A	F,G	U	U	U
-0.3	4	0	0	0	0	10	0	0	3
-0.2	19	0	1	0	6	70	2	6	31
-0.1	14	1	5	2	10	217	40	92	145
0	3	139	46	161	30	163	161	341	295
0.1	7	45	26	21	28	0	114	47	0
0.2	149	56	12	26	12	2	80	8	1
0.3	231	122	104	104	105	3	47	4	11
0.4	58	124	242	139	280	25	52	1	13
0.5	15	13	64	47	29	10	4	1	1
0.6	0	0	0	0	0	0	0	0	0

Table 7.10. Frequencies of component loadings for 11 pelagic species estimated using 500 bootstrap samples from the fall inshore trawl survey placed in 0.1 bins. All loading data is for principle component 1. Included are the non-bootstrapped loadings for each species (LOAD) and the grouping of species based on Kolmogorov - Smirnov two sample tests of the bootstrap loading distributions (GRP), with like letters indicating similar distributions. U grouping = unique distribution, not correlated to any other species loading distribution. Yellow bar depicts the bins adjacent to 0.

	SQAC	CLHA	ALPS	ALAE	ALSA	BRTY	OSMO	SCSC	MAMU	LOPE	EUSP
LOAD	-0.49	0.75	0.65	0.05	0.13	0.83	0.83	0.20	-0.13	-0.03	-0.04
GRP	U	U	U	C	B	A	A	B	U	C	U
-0.5	0	0	0	0	0	0	0	0	0	0	0
-0.4	1	1	0	0	0	4	4	0	0	0	0
-0.3	177	2	0	1	0	1	1	0	0	0	0
-0.2	232	3	0	25	2	2	3	0	1	25	0
-0.1	57	3	0	99	25	2	3	6	100	123	23
0	12	9	2	112	93	9	12	64	376	131	439
0.1	11	19	0	69	139	15	18	147	19	59	38
0.2	2	22	7	46	112	25	23	110	3	45	0
0.3	4	33	35	36	65	24	27	67	1	46	0
0.4	4	73	175	44	41	41	41	64	0	47	0
0.5	0	288	212	44	22	234	159	42	0	23	0
0.6	0	47	69	24	1	143	209	0	0	1	0

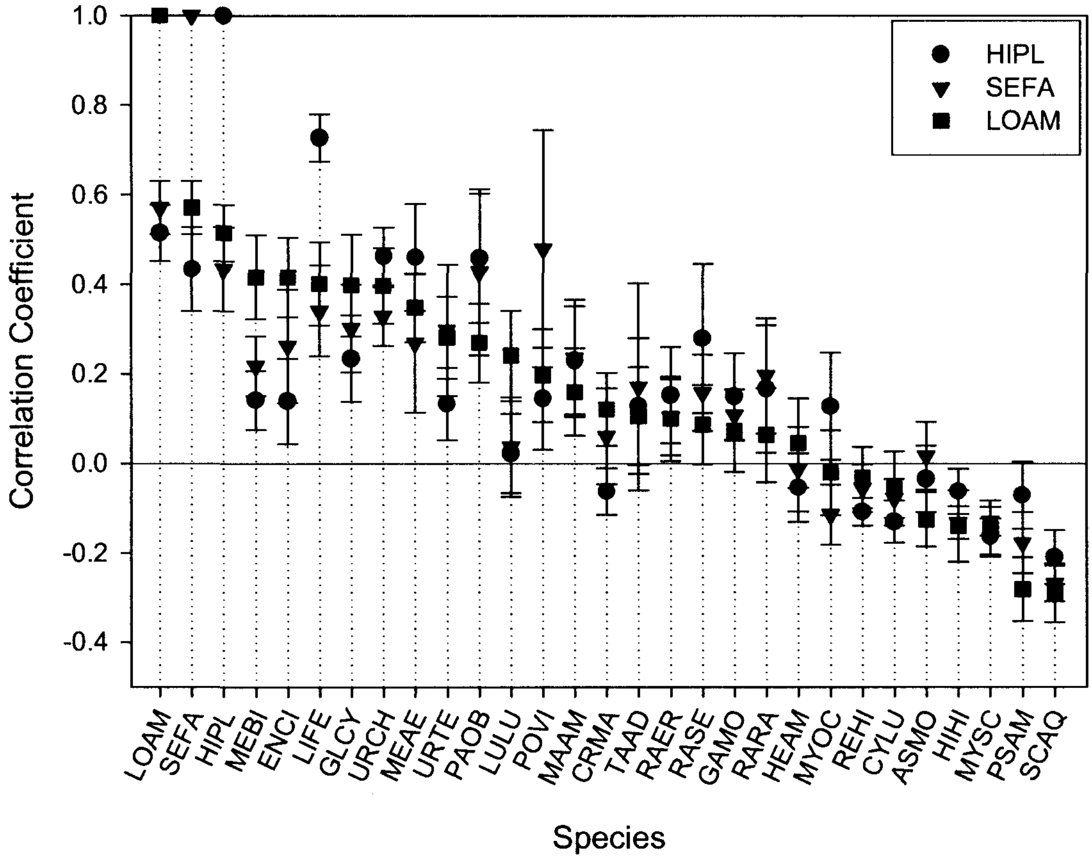

Figure 7.4. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three species of fish with the highest component loadings in the spring sample period (HIPL = *Hippoglossoides platessoides*, SEFA = *Sebastes fasciatus*, LOAM = *Lophius americanus*). Order is determined by the highest loading species (LOAM, Table 7.2) and by decreasing correlation with the other sampled species, left to right on x-axis.

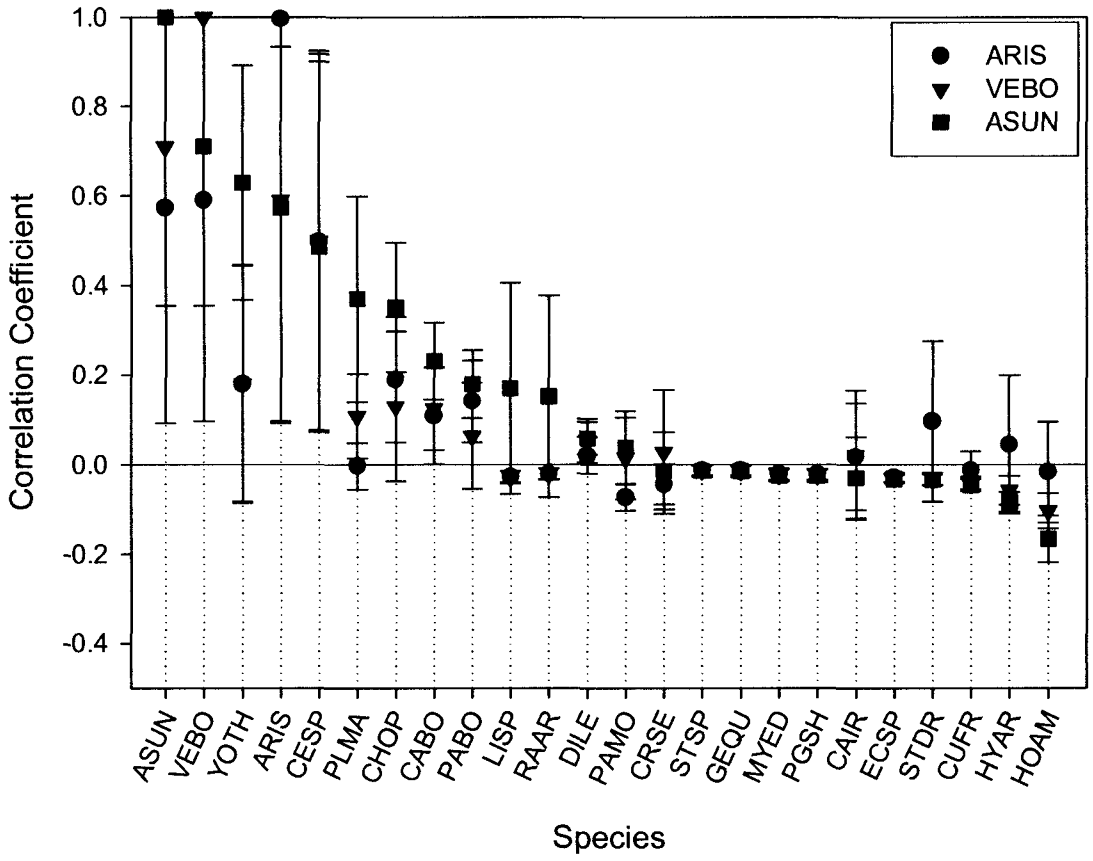

Figure 7.5. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three invertebrate species with the highest component loadings in the spring sample period (ARIS = *Arctica islandica*, VEBO = *Venercardia borealis*, ASUN = *Astarte undata*). Order is determined by the highest loading species (ASUN, Table 7.3) and by decreasing correlation with the other sampled species, left to right on x-axis.

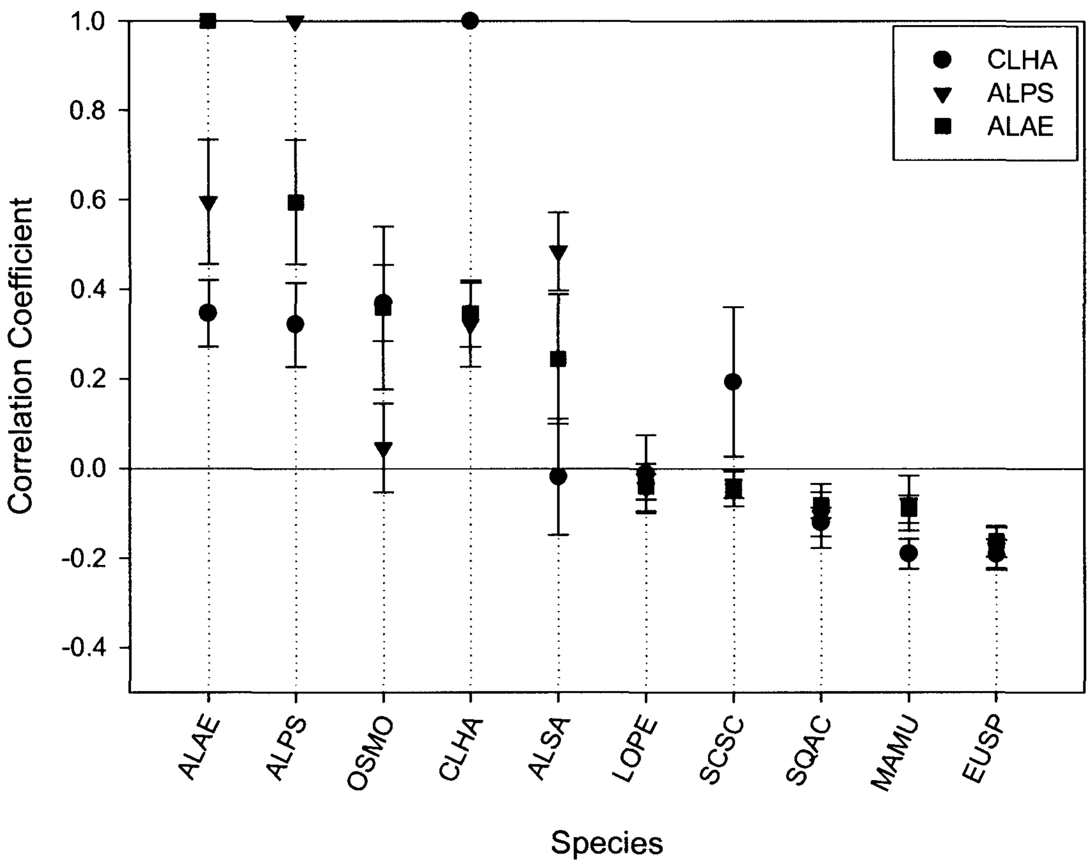

Figure 7.6. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three pelagic species with the highest component loadings in the spring sample period (CLHA = *Clupea harengus*, ALPS = *Alosa pseudoharengus*, ALAE = *Alosa aestivalis*). Order is determined by the highest loading species (ASUN, Table 7.4) and by decreasing correlation with the other sampled species, left to right on x-axis.

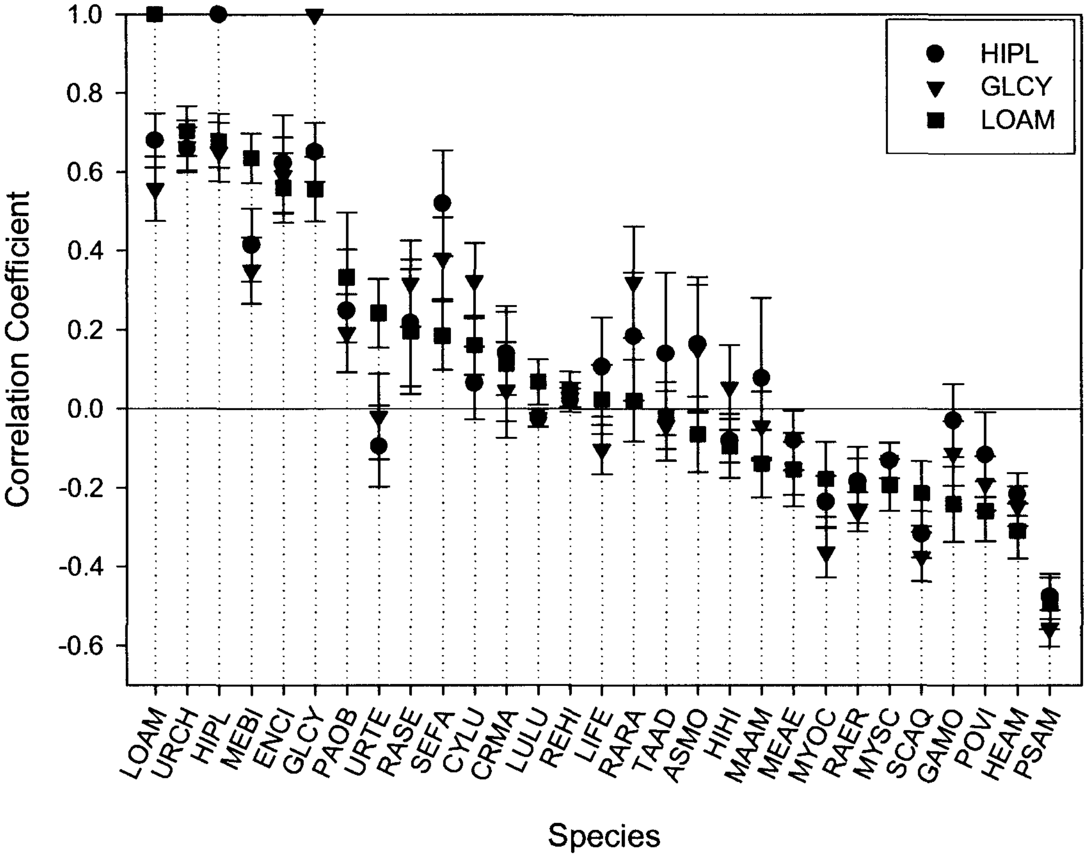

Figure 7.7. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three species of fish with the highest component loadings in the fall sample period (HIPL = *Hippoglossoides platessoides*, GLCY = *Glyptocephalus cynoglossus*, LOAM = *Lophius americanus*). Order is determined by the highest loading species (LOAM, Table 7.5) and by decreasing correlation with the other sampled species, left to right on x-axis.

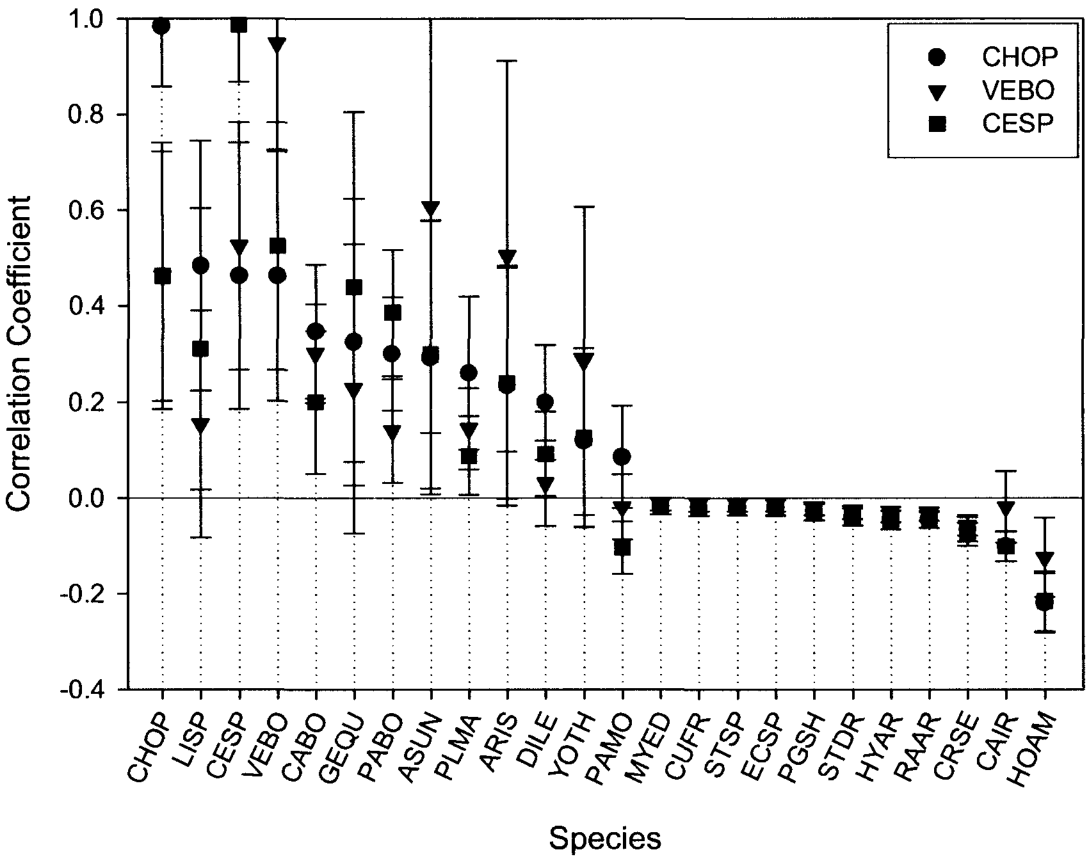

Figure 7.8. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three invertebrate species with the highest component loadings in the fall sample period (CHOP = *Chionectes opilio*, VEBO = *Venercardia borealis*, CESP = *Cephalopoda spp.*). Order is determined by the highest loading species (CHOP, Table 7.6) and by decreasing correlation with the other sampled species, left to right on x-axis.

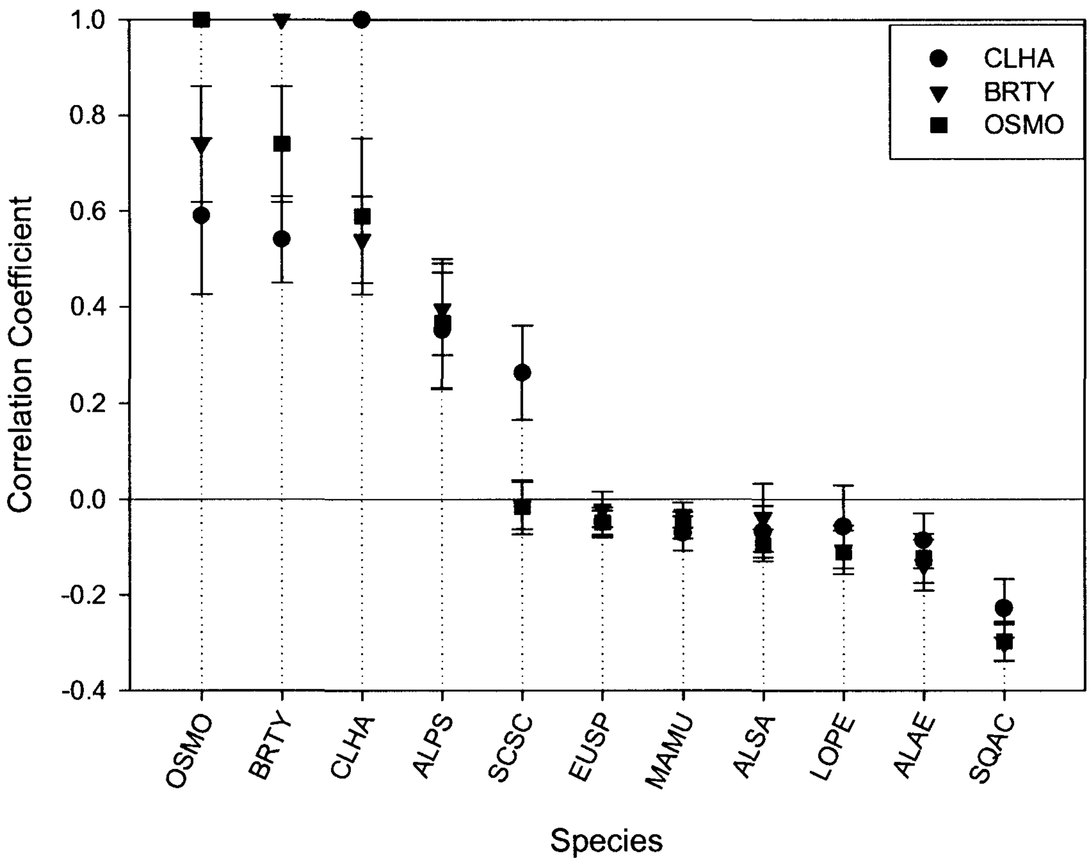

Figure 7.9. Bootstrap created mean Pearson correlation coefficients and standard deviation for the three pelagic species with the highest component loadings in the fall sample period (CLHA = *Clupea harengus*, BRTY = *Brevoortia tyrannus*, OSMO = *Osmerus mordax*). Order is determined by the highest loading species (OSMO, Table 7.7) and by decreasing correlation with the other sampled species, left to right on x-axis.

7.4 Discussion

New variables generated by principal component analysis of fish abundance data collected by inshore trawl survey showed east-west differences in community structure. The structure was seen in both the testing of the primary principal components for east-west differences, and in the coherence amongst different groups of organisms. To discuss the correlation of species in terms of correlation coefficients and loading distributions, the fall benthic vertebrate sample will be used (see Table 7.8, Figure 7.5). The top three species of fish *Hippoglossoides platessoides*, *Glyptocephalus cynoglossus*, *Lophius americanus* and the species associated with them (*Urophycis chuss*, *Enchelyopus cimbrius*, and to lesser extent *Merluccius bilinearis*) all had the highest loadings, were amongst the highest correlation coefficients of all the species and correlated the highest with one another. *Pseudopleuronectes americanus* was heavily correlated with *Aspidophoroides monopterygius* (0.26), *Pollachius virens* (0.42) and *Hemitripterus americanus* (0.39), *Gadus morhua* (0.35), and strongly negatively correlated with the list of species in the high positive loading group above (-0.47, -0.56, -0.49, -0.51, -0.32, respectively). The association between the highest loading species and correlation coefficients were consistent and suggest that groups of species are important in determining structure, at present, rather than any one species. For 2003 in the nearshore waters along the coast of Maine, I suggest species groupings that are important in identifying ecological structure and that heavily correlate to one another (see Table 7.11). Ecological structure is the organization of species into groups that correspond to a spatial pattern. These could be compared to the results of other work using the same surveys but including gut content analysis, to help determine potential biological causes of the patterns.

Flip-flopping of scores also occurred in the larger datasets, with few rare species, used in the present study. This demonstrates that the flip-flopping of loadings shown in Chapter 3 is not limited to those datasets. The consequences of these results are that subtle differences in the collection of data can influence the direction of scores, but not the magnitude of differences. Therefore, less emphasis should be placed on the direction of the scores, and rather the focus should be placed on relative differences among the species and how those species are correlated.

The values from the bootstrap-PCA procedure produced eigenvalues that were higher than the initial PCA run, but this did not translate into higher species loading scores. On the contrary, the bootstrapped PCA created distributions of loading scores that were dampened compared to the initial PCA. The lower magnitude in loading scores did not influence the percent of variance explained by the principal components.

In some ways, the dependence of the analysis on the rare species causes a weaken confidence in the identified structure. However, rare species are more likely to be at risk to extinction (Atlantic salmon, *Salmo salar*) or invasive species establishing reproductively viable populations (Asian shore crab, *Hemigrapsus sanguineus*). In addition, because the Gulf of Maine is a transition zone between faunal regions, it may be a place where this type of change would be expected. Being able to identify rare species, their correlations to other species, and how those relationships change within seasonal and decadal time periods has enormous potential. These species will often be harder to identify when collected and mis-identification will be a potential error.

Table 7.11. Species that determined community structure in the spring 2003 inshore trawl survey. (V = benthic vertebrates, I = benthic invertebrates, P = pelagic species). Species in each of the positive and negative loading positions were heavily correlated to one another and negatively correlated to those in the adjacent cell, and as a result can be viewed as groups of species (complex, assemblage). Separations within groupings designate larger differences amongst the groups of more related species. Only the first principal component and Pearson correlation coefficients were used to generate species groupings.

	Positive loading		Negative loading	
	LOAM	*Lophius americanus*	SCAQ	*Scophthalmus aquosus*
	SEFA	*Sebastes fasciatus*		
	HIPL	*Hippoglossoides platessoides*	MYSC	*Myoxocephalus octodecemspinosus*
	URCH	*Urophycis chuss*		
			PSAM	*Pseudopleuronectes americanus*
V	LIFE	*Limanda ferruginea*		
			HIHI	*Hippglossus hippoglossus*
	URTE	*Urophycis tenuis*		
	POAB	*Paralichthys oblongus*		
	MEAE	*Melanogrammus aeglefinus*		
	ARIS	*Arctica islandica*	HOAM	*Homarus americanus*
	VEBO	*Venercardia borealis*		
	ASUN	*Astarte undata*	CRSE	*Crangon septemspinosa*
I				
			CAIR	*Cancer irroratus*
			HYAR	*Hyas araneus*
	CLHA	*Clupea harengus*	SQAC	*Squalus acanthias*
P	ALPS	*Alosa pseudoharengus*	EUSP	*Euphausuid spp*
	ALAE	*Alosa aestivalis*		

Table 7.12. Species that determined community structure in the fall 2003 inshore trawl survey. (V = benthic vertebrates, I = benthic invertebrates, P = pelagic species). Species in each of the positive and negative loading positions were heavily correlated to one another and negatively correlated to those in the adjacent cell, and as a result can be viewed as groups of species (complex, assemblage). Separations within groupings designate larger differences amongst the groups of more related species. Only the first principal component and Pearson correlation coefficients were used to generate species groupings.

	Positive loading		Negative loading	
V	PSAM	*P. americanus*	LOAM	*Lophius americanus*
			GLCY	*Glyptocephalus cynoglossus*
	MYOC	*M. octodecemspinosus*	HIPL	*Hippoglossoides platessoides*
			ENCL	*Enchelyopus cimbrius*
	RAER	*Raja erinacea*		
	HEAM	*Hemitripterus americanus*	URCH	*Urophycis chuss*
	SCAQ	*Scophthalmus aquosus*		
	GAMO	*Gadus morhua*		
	MEAE	*Melanogrammus aeglefinus*		
I	CHOP	*Chionectes opilio*	CAIR	*Cancer irroratus*
	VEBO	*Venercardia borealis*		
	CESP	*Cephalopoda spp*	HOAM	*Homarus americanus*
			HYAR	*Hyas araneus*
			STDR	*Stronglyocentrotus droebachiensis*
P	OSMO	*Osmerus mordax*	SQAC	*Squalus acanthias*
	BRTY	*Brevoortia tyrannus*		
	CLHA	*Clupea harengus*		
	ALPS	*Alosa pseudoharengus*		

Sea temperatures have been shown to be major indirect and direct causes of species abundances and catch fluctuation of fisheries along the Maine coast (Dow 1981). Targett and McCleave (1974) related the presence and absence of fish in a Maine tidal cove to water temperatures and the thermal tolerances of the species. The thermal tolerance of a species, particularly during early life stages, is a critical component in development, growth and survival (Jordaan and Kling 2003). Changes in species distributions and abundances in the GOM have led to the identification of the area as a transition zone between the northerly cold-temperate faunal province and southern warmer mid-Atlantic bight and potentially sensitive to climate change (Frank et al. 1990). Just because some species are defining the structure along the Maine coast at present, does not mean that they will always do so. Of interest is whether the structure changes, and what may cause the change. Changing population demographics, of all the species, and year-year (cloud cover) to multi-decade (sea-level) environmental changes that accompany them could alter the basic relationships amongst the species. This is particularly true for species on the edges of the distributions. Frank et al. (1990) suggest species shifts, such as loss of groundfish populations and increased numbers of pelagic species, will accompany increasing ocean temperatures. Changes could be monitored through the techniques described in this study, however in recognition of lags in the response of species to environmental changes there will need to be analysis done for longer term surveys to better understand how to incorporate time as a variable in the analysis.

Variations in the North Atlantic Oscillation (NAO) are believed to be related to changes in the makeup of the source water for the EMCC, with negative NAO years bringing colder, less saline, and nutrient depleted water (Thomas et al. 2003). How large atmospheric forcing events can influence the observed structure in the biological community is unknown. The influence of physical changes in the system, how species population shifts according to season and how these influence observations will be important in making multivariate analysis of survey data an extremely useful tool. The work detailed here strongly suggests that structure is present along the coast of Maine, that species can be grouped to some degree, and that the ecological structure is potentially robust.

Although principal component analysis does extract information regarding correlations or covariance amongst variables across sites, it does not give information regarding abundance. Therefore, to appropriately apply the information from a multivariate analysis it will be necessary to incorporate analyses of abundance to determine whether trends in species correlations are in fact related to increasing or decreasing numbers. For example, in Chapter 5 the mummichog was found to correlate with some species and not with others, often as a result of having a ubiquitous distribution. This type of observation will be important in determining expansion of species or shifts in interactions with other species.

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CHAPTER 8

DRIVERS OF COMMUNITY STRUCTURE IN THE GULF OF MAINE: APPLICATION AND CAVEATS

8.1 Introduction

The primary goal of the studies presented in this thesis was to evaluate whether the structure of fish assemblages can be identified and related to constraining physical variables. Ultimately, key drivers that influence the distribution and abundance of fish in the Gulf of Maine can be incorporated into management decision making. This is required because, under an ecosystem-based adaptive management regime, there will be a need to identify manageable components of the system and how human behaviour interacts with them (defining ecosystem boundaries). Second, with the system being managed rather than individual species, it will be necessary to develop ecosystem indicators that can be used to gain a sense of the health, or state, of an ecosystem and the populations of fish that form the basis for exploitation of the marine environment (monitoring ecosystems).

In order to develop ecosystem indicators, it is necessary to discuss the drivers that have been identified as important modifiers of fish communities' distribution in the Gulf of Maine. Then those drivers that can be employed to address management concerns such as identifying regions within the gulf that are distinct, defining areas that are critical habitats for numbers of species, and identifying times of the year where regions within of the gulf are better for fishing in terms of bycatch of populations of fish with low abundance.

8.2. Identification of indicators and tools for management

There has been ample discussion regarding the ineffectiveness of past and current fisheries management schemes and the resulting negative consequences on ecosystems (Jackson et al. 2001). In the State of Maine there has been a shift from multi-species to single-species (lobster – *Homerus americanus*) fishing practices over the past decades. Presently, there is significant concern about both the socioeconomic dependence on lobster and the consequences of past and present fishing activities on the ecological structure of the region. The concept of adaptive management was advanced to reconcile the often-competing goals of natural resource extraction and conservation (Schreiber et al. 2004). Development of modeling techniques is critical to adaptive management for elucidating the quantities, uncertainties and complexities involved in ecological systems (Schreiber et al. 2004). The identification and use of environmental indicators, which summarize large amounts of information and provide a signal that informs stakeholders of the state of the system (Garcia et al. 2000), will be an important part of developing adaptive management strategies.

The National Academy of Sciences (2000) gives a detailed framework for indicator selection. They detail 9 general areas to consider in indicator selection: (1) a conceptual basis, (2) reliability in indicator performance, (3) appropriate temporal and spatial scales of applicability, (4) sound statistical properties, (5) minimal data requirements, (6) availability of necessary skills for application, (7) robustness to external noise, (8) international compatibility, and (9) cost-effectiveness, which as a practical matter will dominate over everything else. In order for both multi-species and ecosystem-based management to work there needs to be involvement from government, industry, other user groups, and scientists. Constanza (2001, from Daly 1992) identifies three important goals in managing economic systems in a sustainable way: (1) matching the scale of human activities to those of the ecosystem, (2) distributing access to resources fairly among current and future stakeholders, and (3) efficiency of allocation, constrained by the first goals, including both non-marketed and marketed resources. Incorporating scale considerations into management decisions, and reconciling different scales as they interact, will be difficult.

An important step in outlining how the proposed species and divisions of species can be used in developing indicators is to present some of the potential processes present in the Gulf of Maine and suggest possible indicators of those processes (Figure 8.1). In the presented figure, the present research can be seen as developing community-based indicators (methods of determining community structure). The division of species along a wave energy gradient (Chapter 6) could be used as a habitat index to determine which habitats are best suited for species. In chapter 7, the results point towards an oceanographic index (temperature, currents) as a potential way to monitor changes or delineate "ecosystems". By considering both of these indicators it is possible to consider multiple scales, ranging from measures within embayments to coast-wide differences. However, identifying the relevant scale can be difficult (Figure 8.2), due to the differing importance of certain drivers as one considers the different scales.

8.3. Issues of Scale

The extent and grain of a survey will have a marked effect on the results, and as a result on the management of the fishery. Stanley (1992) used bootstrap calculations on catch per unit effort (CPUE) data generated from different surveys to discuss the number

Figure 8.1. Simplified flowchart of possible ecosystem indicators for the Gulf of Maine from broad scale (top) to specific habitats (bottom), with boxes indicating observations and arrows indicating processes. Arrows in both directions indicate that feedbacks are possible (i.e.: a fish community, in the lowest box, influences what fish can survive in a habitat, next box up, through competition and predation). Large fonts outside the boxes give types of indicators that may be derived from observations in the adjacent box. The present studies focused on defining species distributions and community structure (lowest box) and offers principal component analysis as a measure of the structure or a community-based indicator. Community-based indicators are affected by the probability (P) of retention and dispersal within a specific habitat, probability of extinction from and or immigration into a habitat due to differential survival and behavior, and connectivity between habitats or presence of physical and physiological barriers including processes involved in reproduction. The remaining indicators will be referred to in text.

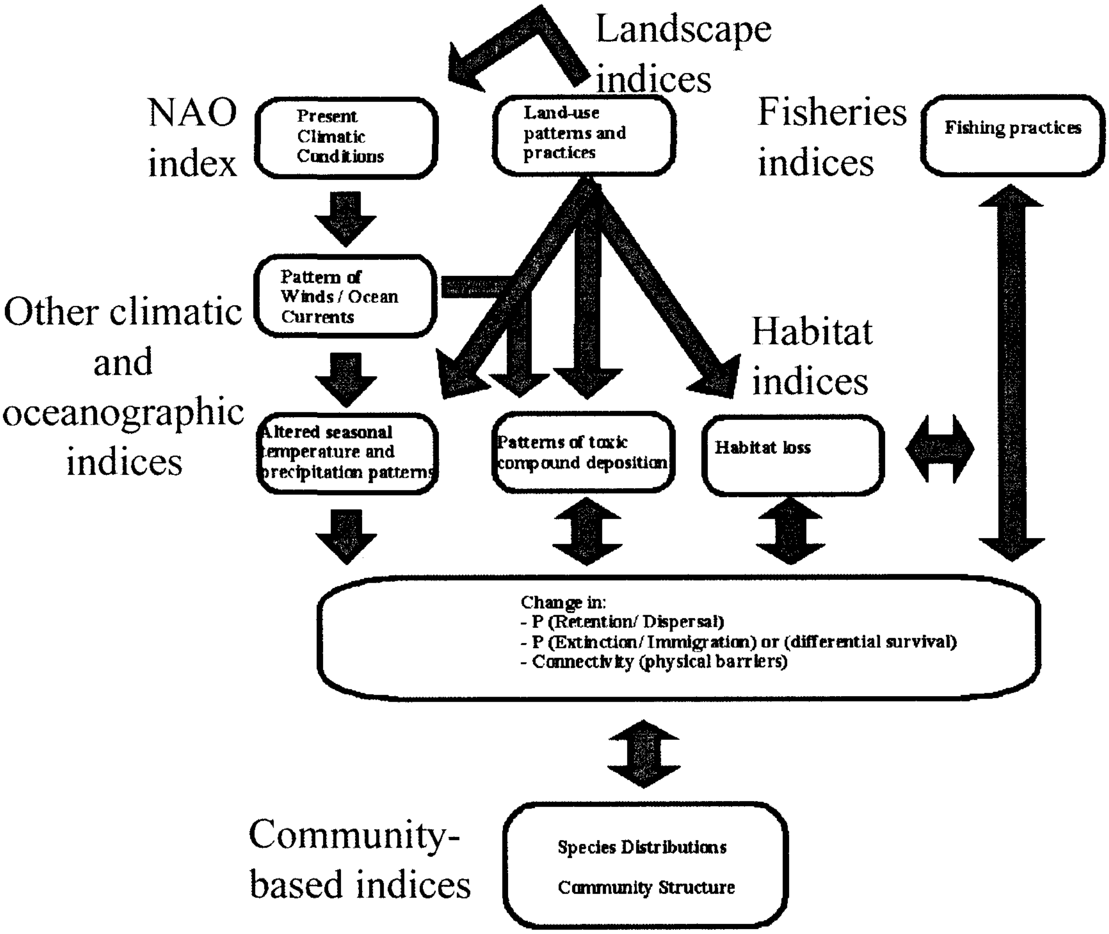
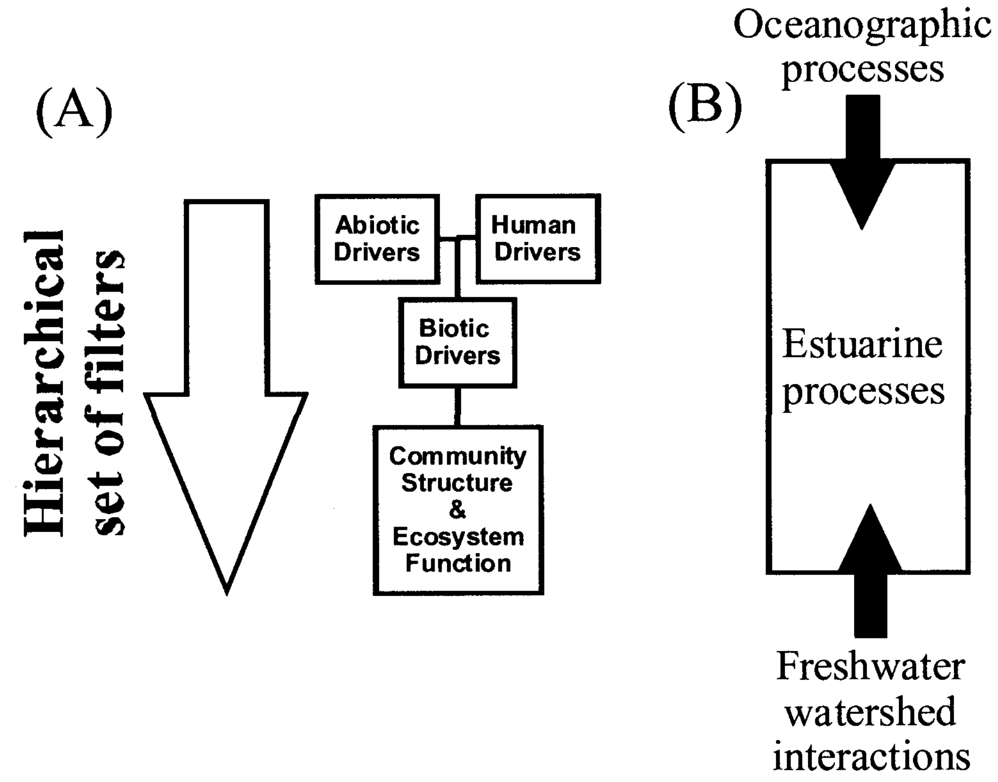

Landscape indices
NAO index
Present Climatic Conditions
Land-use patterns and practices
Fisheries indices
Fishing practices
Pattern of Winds / Ocean Currents
Other climatic and oceanographic indices
Habitat indices
ltered seasonal emperature and recipitation patterns
Patterns of toxic compound deposition
Habitat loss
Change in:
- P (Retention/ Dispersal)
- P (Extinction/Immigration) or (differential survival)
- Connectivity (physical barriers)
Community-based indices
Species Distributions
Community Structure

Figure 8.2. Hypothesized drivers for a typical Maine estuary from a broad scale perspective. (A) Abiotic drivers are paralleled with human drivers because in that system the two are controlling biotic drivers. Heavy fishing pressure, climate change, eutrophication, habitat modification, obstructions to flow, introduction of invasive species, pollution and stocking of non-native anadromous fish populations and their management have fundamentally altered ecosystem function. Many of these processes are linked with abiotic factors such as "natural" or background climate change, currents, latitudinal gradients and geologic setting. If one were to look at year-year variation, biotic drivers would find a more prominent position in the hierarchy of drivers. Further complicating the designation of positions in a hierarchy is the link between the different scales, and cycles that may be nested within the complex system (Panarchies – see Chapter 1).

(B) At a most basic level, freshwater and marine systems are the mixing of two systems with their respective species. The resulting gradient in human, abiotic and biotic drivers from marine to freshwater end-members result in estuarine processes. Of note is that freshwater human drivers have been more significant than human drivers from the marine end member, but the interaction of the two has had far reaching effects. The loss of anadromous fish due to freshwater habitat destruction and marine fisheries is the primary example. It is estimated that the historic populations in the St. Croix River of 7000 - 18,000 salmon and 31,700,000 alewives have been reduced to populations presently less than 1% those values (Lotze and Milewski 2004).


(A)
Hierarchical set of filters
Abiotic Drivers
Human Drivers
Biotic Drivers
Community Structure & Ecosystem Function
(B)
Oceanographic processes
Estuarine processes
Freshwater watershed interactions

of sites required to effectively estimate stock size. The results suggest that some fisheries only have precision enough (estimate is ± 25% of the actual value 80% of the time) to detect major changes over a few years or general trends over long time series (Stanley 1992). Furthermore, it is important to have better estimates as a species becomes less abundant with a consequent reduction in statistical power. Stanley (1992) acknowledges that the assumptions of constant catchability and accuracy are often of greater concern. These observations reaffirm the importance of matching the sampling design to the ecosystem characteristics of interest.

Coherence between sites will also be important and relates to whether important processes are large-scale phenomena as opposed to local impacts. Mertz et al. (1994) discuss local winds and their impact of coastal upwelling, and show coherence among sites is restricted to distances of less than 200 km. They also suggest that local beach orientation and bathymetry will have important roles in the translation of wind energy to water column properties (upwelling and alongshore currents). Still, other processes will be more structured along larger regions of the coast.

The result of the effect of scale is that specific management questions will require analysis of appropriate datasets collected at appropriate scales. As an example, Labbe and Fausch (2000) demonstrate that management of the threatened Arkansas darter (*Etheostoma cragini*) must be considered at multiple scales. Deep pools are important refugia for the darters but are largely ephemeral, while flow regimes within the watershed, which are controlled by water management practices, are important in the overall availability of deep pools. Therefore, management and monitoring efforts focused on the maintenance of pools will have to be employed at the landscape scale, rather than individual pools (Labbe and Fausch 2000). Although stream habitats are in many ways vastly different than marine systems, the general conclusions can be applied to both. Maintenance of single populations within a defined area may or may not be appropriate depending on the scale of interactions among the species, environment and anthropogenic impacts.

8.4. Issues of Gear

Directly related to issues of catchability and accuracy is the effect of gear selectivity. This is because fish are distributed unevenly (Polis et al. 1997; Marshall and Frank 1995) and the ability of a specific gear type to catch specific species (or size class) is also biased (Layman and Smith 2001, Methven and Schneider 1998; Cote et al. 2004). Gear biases are related to habitat type as well, as evidenced by the use of different gears to construct the depth preferences of cod in Methven and Schneider (1998).

8.5. Ecosystems and oceanography

The results of the work can be viewed in light of hierarchal patch dynamics. Relationships between pattern and process were shown across scales. Local differences in vertical position and wave energy constrained populations and assemblages of species, while gradients in temperature driven by currents correlated with structure of fish assemblages across a coast-wide scale. Because identification of patches and tangible boundaries allows understanding of discrete, but interactive, components (Wu and Loucks 1995), the result of the studies outlined can be used to improve overall understanding of how scales interact and which processes should be the focus of more research.

Two important observations relate to comments of hierarchal patch dynamics. First, that it appears that pattern in relation to environmental gradients occurs at all scales, but the species involved change. Because process rates become important as scale is considered, the scale which is deemed important will determine the pattern seen. Teasing out what scale is actually driving patterns will involve approaching the system with naivety. The dynamic mosaic of patches is considered to have pattern and process operating at different spatial and temporal scales resulting in different levels of succession within a specific patch (Wu and Loucks 1995). Determining the physical constraints on populations across scales will involve improving knowledge of processes by conducting experiments such as those by Labbe and Fausch (2000), Leonard et al. (1998), Trussell et al. (2002) and outlined in Menge and Branch (2001). By doing so, the species defined as assemblages can be functionally related to one another and defined as communities.

By using the methods outlined, collections of interacting populations within some boundary can be defined. The role of subordinate species can be viewed objectively and species importance can be related to structure defined at a specific scale. O'Neill (2001) criticizes the loss of objectivity accompanying the adoption of the ecosystem concept paradigm. This can be avoided by approaching ecological units with an understanding of scale, with analyses of all species and relating the results to gradients within the geographic boundaries of interest. Then structure can be documented and process understood without necessarily placing boundaries on the space and time scales of interest.

8.6. Conclusions

The studies outlined in this thesis were able to demonstrate divisions of species with varying degrees of success. Observations from three surveys demonstrated that changes in the distribution of species are measurable. It also appears that the changes are related to gradients in abiotic, biotic and human drivers, if one considers multiple scales. Although the results are encouraging, it is important to emphasize that divisions of species are expected, and the ability to detect these differences is based on the extent (spatial coverage) and grain (number of sites) of the survey. The analyses were not designed to indicate the best divisions of the species to base management decisions upon. In other words, although there were divisions of species detected by the surveys, those divisions may or may not be aligned with the best environmental gradients by which to base delineations to ecosystem boundaries and nominate marine protected areas. However, the techniques described within this manuscript can certainly be used to help design better surveys by taking into account what environmental gradients are responsible for observed patterns of fish distributions and what variables should be considered as strata. Any survey should be designed to incorporate fisheries-dependent data into the analysis to increase the power of the analysis, run for numbers of years, and be at a scale by which socioeconomic concerns are also taken into account. Of perhaps even greater importance is the governance structure, and as Hilborn (2002) states, the implementation of a system that provides incentives for user groups, scientists and managers to make decisions that are in line with societal goals. The reason for this is because stock sizes and yields for conserving long-term sustainability are much lower than when based on short-term objectives (Mardle and Pascoe 2002).

In this framework, the use of multivariate analyses on fisheries datasets will allow for a better understanding of how species overlap, and how those distributions are altered by environmental gradients and over time, and how best to monitor the ecosystem for change.

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APPENDIX

BOOTSTRAP PROGRAM FOR SAS

Using tidepool dataset presented in Chapter 3, from the fourth sample period.

c:\Tidepools\FIS4R.prn refers to a space delimited spreadsheet. “pool$” is the tidepool identification and “phgu cylu liat mysc myae fuhe apqu” is the list of species (variables).

Program Starts.

```
options ls=240 ps=500 nocenter nonumber nodate;
data a;
infile 'c:\Tidepools\FIS4R.prn' lrecl=240;
input pool$ phgu cylu liat mysc myae fuhe apqu;

* two macros that are defined before the actual program;

%macro loop(count);
 %do i=2 %to &count;
  %boot(37);
   * 37 represents the number of cases (or observations);
 %end;
%mend loop;


%macro boot(n);
 data b;
 do i=1 to &n;
  rnd=int(1+&n*uniform(0));
   set a point=rnd;
   output;
   end;
 stop;
 proc princomp out=c outstat=temp2 prefix=pca noprint n=5;
 * first 5 PCAs;
  var phgu cylu liat mysc myae fuhe apqu;
 data temp1; set c; drop I phgu cylu liat mysc myae fuhe apqu;
 proc append base=result1 data=temp1;
 proc append base=result2 data=temp2;
 run;
%mend boot;


* the start of the actual program ;
```

```
* need to start the analysis in this way so that we can use the "PROC APPEND" (above);

 data _null_;
 do i=1 to 37;
  rnd=int(1+37*uniform(0));
   set a point=rnd;
   output;
   end;
 stop;

 proc princomp out=c outstat=result2 prefix=pca noprint n=5;
  var phgu cylu liat mysc myae fuhe apqu;
 data result1; set c; drop phgu cylu liat mysc myae fuhe apqu;


%loop(100);
* define the number of bootstraps ... in this case 100 times;
* formating the datasets for output;
* scores;
data _null_;
set result1;
file 'c:\Tidepools\scor.p' lrecl=240;
put no (pca1-pca5) (8.4,+2);

* eigenvalues;
data _null_;
set result2;
if _TYPE_='EIGENVAL';
file 'c:\Tidepools\eval.p' lrecl=240;
put (phgu cylu liat mysc myae fuhe apqu) (8.4,+2);

* pearson correlation and eigenvectors;
data _null_;
set result2;
if _TYPE_='CORR' or _TYPE_='SCORE';
file 'c:\Tidepools\cvec.p' lrecl=240;
put _TYPE_ _NAME_ (phgu cylu liat mysc myae fuhe apqu) (8.4,+2);

run;
```

BIOGRAPHY OF THE AUTHOR

Adrian was born in Calgary, Alberta during a snowstorm on the 20th of January, 1972. During the early years of his life, his parents began unknowingly training him for a career in biology through many camping trips across the Canadian Rocky Mountains to the Pacific coast. Then, in 1986, his family moved to Newfoundland on the East coast of Canada. After high school at Holy Heart of Mary, he began attending Memorial University of Newfoundland in St. John's and completed an honours degree in Biology. During his studies, he was lucky to be taken into the aquaculture and fisheries research laboratory of Dr. Joe Brown, where he was quickly trusted with many responsibilities.

Adrian moved "south of the border" and received a Master of Science degree in Marine Biology from The University of Maine in December, 2002, working on larval fish. Although the larval cod world had been a good one for Adrian, including 5 publications to date (1 from his undergraduate days, and 4 from work at the University of Maine), the research had lead him to believe that there is value in working on multiple species rather than focusing on one. He then turned his eye on the management failures in fisheries and questions regarding scale in ecology. In order to understand these problems, some new statistical techniques were required, as well as data from various surveys on fish populations. Dr. John Moring had allowed Adrian to collect the first two datasets, and with some small amount of funding, and some collaboration, it was possible to secure a few more. This thesis represents the culmination of that work. Adrian started a postdoctoral fellowship at Stony Brook University, New York, in June 2006. Adrian is a candidate for the Doctor of Philosophy degree in Marine Biology from The University of Maine in December, 2006.