1983

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John Stevenson Macdonald

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LA THÈSE A ÉTÉ
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FOOD RESOURCE UTILIZATION
BY
FIVE SPECIES
OF
BENTHIC FEEDING FISH
IN
PASSAMAQUODDY BAY, N.B.

by
John Stevenson Macdonald

Department of Zoology

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario.
November, 1982

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ABSTRACT

Feeding relationships of various fish species, and their relationship to the composition of the surrounding sediments, were observed for one year at two sites in the lower Bay of Fundy region. The fishes were the ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus), plaice (Hippoglossoides platessoides), cod (Gadus morhua) and witch flounder (Glyptocephalus cynoglossus). After reducing the size of the data matrix by removing redundant variables (prey items), interspecific diet overlap and the degree to which stomach contents reflect benthic composition were assessed using discriminant functions analysis. Variables were ranked by their power to discriminate among pairwise comparisons of groups: fish species and benthic samples. Many amphipods were utilized to a greater extent than their abundances in the sediments would suggest. Many annelids were underutilized. Each fish species has developed specialized feeding behaviours, digestion techniques and morphologies to segregate food resources. All species tend to increase prey intake at those places and times when benthic abundance of prey common to their diets increases. Visual predators (flounders) show different functional responses towards increased prey abundances than non-visual predators (ocean pout). In some cases availability is determined by prey size rather than prey abundance.

Only a few prey species show benthic density changes as a result of predation. Benthic populations may be held at an early successional, highly productive stage by extreme physical conditions. Large fluctuations in temperature, salinity and current could provide a force regulating benthic species abundance that is at least as important as fish predation.

ACKNOWLEDGEMENTS

I wish to express my gratitude to the many people who have helped at various stages of the research.

The staff and students of the St. Andrews Biological Station and Huntsman Marine Laboratory provided support at every stage of the thesis. Messrs. W. McMullon and C.F. Cunningham prepared many of the figures. Captains J. Allen, D. Hurléy and C. Wright and their crews, provided boat time and helped in many other ways. Drs. K. Waiwood and M. Dadswell provided laboratory and office space and a great deal of constructive criticism. The interest and energy they show towards the field of fisheries science is very contagious. Dr. D. Wildish kindly provided much of the invertebrate feeding habits data. Thanks also to Joanne Powers, Dave Methven, Leslie Linkletter, Ralph Appy, Leslie Davidson and Derek Knox for help with the sampling and the hours of grueling microscope work. Mike Butler helped by being one of the best expeditors I know.

I would like to acknowledge and thank the many people at Western for their help and support throughout the years. The past and present members of the Collip family, Graham Sudbury, Jim Carpenter, Brian Bietz, Bev. Hicks, Keith Somers, Brenda Goodson, Doug Noltie, Greg Goff, Hélène Dupuis and Simon Courtenay, have all contributed stimulating discussion and friendly rivalry. Thanks also to the staff of the computer centre for their patience. Drs. G. Wells and J. Koval of the Statistics and Actuarial Science Department at Western helped in designing and analysing this study.

I am grateful to the members of my committee, Drs. W.B. Scott, M.H.A. Keenleyside and S. Singh for their patience and encouragement. A very special thanks to Dr. R.H. Green, not only my guiding light and source of energy but also a very close friend.

I am grateful to Yvonne Pepper for typing the manuscript on such short notice, Rick van Vloten, who is still a marine biologist at heart, and my father for proof-reading the early drafts.

This work was financed by N.S.E.R.C. operating and strategic grants to Dr. R.H. Green.

THAT LEAVE MIGHT BE GIVEN TO HANG UP THE REPRESENTATION OF A COD FISH IN
THE ROOM WHERE THE HOUSE SIT, AS A MEMORIAL TO THE IMPORTANCE OF THE COD-
FISHERY TO THE WELFARE OF THIS COMMONWEALTH, AS HAD BEEN USUAL FORMERLY.

MOTION PASSED BY THE
HOUSE OF REPRESENTATIVES
OF THE STATE OF
MASSACHUSETTS, BOSTON,
MARCH 17, 1784

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1. INTRODUCTION

In the past few years many researchers have emphasized the importance of the benthos in understanding the dynamics of marine ecosystems. Models of energy flow through the benthos show the need for knowledge of trophic interrelationships between demersal fishes and their benthic prey (Teal 1962; Odum 1971; Steele 1974; Arntz 1975, 1978c; Mearns and Young 1978; Prince et al 1979). In particular we need to know: what macro-benthic items are important for fish food and at what rate they are assimilated, how benthic composition and production affect the production of fishes and in return is the benthos modified by the predation pressure of the fishes, and how effectively and by what mechanisms fishes partition their resources (Mills 1975). Principles used in studies of this nature must be based on theories of competition and niche space as these theories are major structuring forces in animal communities (Schoener 1975; Pianka 1978; Ricklefs 1979).

Information about food habit and food resource partitioning by north-western Atlantic demersal fishes has been collected for more than twenty-five years (Powles 1958; Tyler 1971, 1972; DeGroot 1971; Frame 1974; Bowman 1977, 1980, 1981a, 1981b; Langton and Bowman 1980, 1981; Waiwood et al 1979). However, food habits of most fish species vary with spatial and temporal changes in the available food resources. Knowledge of the benthic composition within the fishes' foraging area is necessary to quantitatively appraise the degree to which fish "select" (this is not meant to imply that fishes select in any deliberate sense of the word) their prey (Ivlev 1961), and to test optimal foraging and niche volume theories. Predictions of degree of niche overlap and optimal foraging

depend on measurements of amounts of available food. MacArthur and Pianka (1966) suggest that predators should prefer more profitable prey and be more selective when profitable prey are common.

In two recent papers, Arntz and Brunswig (1975) and Arntz (1978c) review studies that deal with interrelationships between fishes and macrobenthos. The earliest work was done in the northeastern Atlantic by Peterson (1914, 1924), Blegvad (1928) and Stevens (1930). More recently knowledge of the available food resource has been incorporated into studies involving resource utilization and partitioning by co-occurring fishes (Richards 1963a, 1963b; Frame 1974; Levings 1974; Moore and Moore 1976a, 1976b; Stein 1977; Newsome and Gee 1978; Jackson 1978; Arntz 1978c; Arntz and Finger 1981; Bakanov and Strizhnikova 1979; Ringler 1979; Johansen and Ringler 1980; Macpherson 1981).

Many quantitative methods have been developed to describe the degree of difference between diets of two fish species or between diets and the composition of the food resource. These methods can be divided into four categories.

a) Gabriel (1978) and Berg (1979) review several electivity indices that compare proportion of a single prey species in the digestive tract to the proportion of the same prey species in the environment. Examples are Ivlev's index (1961), the odds ratio (Jacobs 1974) and Shorigin's index (Jones 1952). Although widely used, indices are difficult to interpret statistically (reviewed by Green 1979 and Appendix III). They can only be used to make pairwise comparisons of proportional differences of individual prey species between two groups (a group could be samples of a predator species or of available prey species from a certain area). Proportional measures are adequate when the researcher is interested in

answering questions about fish feeding "selectivity". However, more recently there has been an additional interest in daily rates of assimilation in order to determine what effect fish predation has on the population structure of the food source (Mills 1975). Therefore, diet overlap among predators, and comparisons with the food source, should consider actual prey species abundances.

b) Feinsinger et al (1981) review the development of sample similarity indices (eg. Colwell-Futuyma method 1971):. They differ from electivity indices in that all prey species are compared between two groups at once. The index measures the area of intersection between two frequency distributions. They share many of the disadvantages mentioned in category a).

c) Correlation coefficients have been applied to determine whether there is a significant relationship between ranked prey items in the diets of two predators (Fritz 1974). This method is an improvement on methods already mentioned in that it does allow the establishment of probability estimates and it can be used with actual rather than proportional measures of prey abundance. However, none of the above methods estimates the variation of prey species abundance within each predator species or the environment (ie. no within-group error estimation). Other people have recognized this problem. Horn (1966) noted: "Indices..... are only appropriate in situations in which there is implicit confidence that the proportions of items in each category are adequately characterized." Frame (1974), when comparing percent diet overlap measures between winter flounder stomachs and benthic samples, also compared overlap within stomachs and within grabs. There were greater overlaps within grabs and stomachs than between them.

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d) Analysis of variance (ANOVA) is more appropriate when comparing within group to among group variation. When there are multiple dependent variables (fe. prey species) a multivariate ANOVA (MANOVA) should be used. A MANOVA can consider any number of groups and will determine significance levels of estimates of the group means. Multi-factor MANOVAs can be used to test food composition differences among fish sizes, site and sampling times as well as differences among predator species. However, few researchers on fish feeding have used multivariate techniques to compare diets. Ross (1977) measures similarity among congeneric searobins using cluster analysis to detect group structure based on diets. Ellison (1978) and Dessenle et al (1978) use discriminant analysis and MANOVA techniques to test for significant predator group differences. In their studies variable loadings on discriminant functions are used to isolate which variables differ among groups. There are alternate ways to isolate variables which discriminate among groups (Jancey 1979). These will be discussed later.

Crow, during a recorded discussion at the 1978 Fish Food Habit Workshop, has critized Ellison for violating the assumptions of parametric discriminant analysis. However, Green (1979) and Klecka (1975) discuss the robustness of discriminant analysis and other parametric statistics to many of the violations of parametric assumptions. This will be discussed later in greater depth.

This study is an extension of a five year survey of the distribution of fishes in the lower Bay of Fundy and Passamaquoddy Bay (Appendix I). It attempts to determine what effect temporal and spatial changes of the macrobenthos will have on the food utilization and partitioning by the demersal fish community. The objectives of the thesis can be presented

as four hypotheses.

1. Five fish species, winter flounder (Pseudopleuronectes americanus), plaice (Hippoglossoides platessoides), witch flounder (Glyptocephalus cynoglossus), ocean pout (Macrozoarces americanus) and cod (Gadus morhua) show no "preference" for prey species. Food composition in the stomach is a random sample of the composition of the benthos.
2. Any observed "preference" for food will not change with a spatial or temporal change in the benthic composition.

These hypotheses direct thoughts about the correlation between the benthos and patterns of food utilization by fishes. If benthic composition totally dictates the food composition in fishes' stomachs, hypothesis 1 will be accepted and spatial-temporal changes in the bottom fauna will merely cause the fishes' food habits to change accordingly. If, however, fishes do select food items preferentially then the consequences of the selection process will not be known until the fishes' feeding reactions to a changing benthic composition are determined.

3. All fish species consume the same food at the same space-time combination. Therefore, there is no niche separation among the predators along the prey abundance dimensions.
4. If niche separation does occur then the niche "positions" of all predator species remain the same despite spatial and temporal changes in the benthos.

The importance that spatial and temporal variation in size distributions of common benthic prey species has on patterning food utilization by fishes is also considered.

These hypotheses are important in guiding the direction of data exploration. It is not the purpose of this thesis to test them rigidly at a specified probability level. Rather than a strict decision making approach of the hypothesis testing procedure, a scientific inference approach is taken in which evidence is gathered to support or refute each hypothesis. The complexity of the system is such that formal statistical tests of the hypotheses would probably not be possible in any case. Exploration of these hypotheses has generated many more hypotheses. Some of them are explored in the attached appendices. Appendix I is a summary of a five year survey of the distribution of fishes in the lower Bay of Fundy region. Only two of the fifteen stations included in Appendix I were used in the rest of the thesis but all the information was used to choose five syntopic fish species that would be abundant throughout a one year sampling period.

Variation in the digestion pattern of different prey is an important variable in evaluating diet consumption rates and food preference of wild fishes. The degree to which differential digestion and/or evacuation of prey types influence the researcher's perception of diet composition is presented in Appendix II, as are models used to describe gastric evacuation.

Appendix III describes diel feeding periodicity and the amount of food consumed daily by the fishes in this study. Different feeding times among fish species may serve to reduce interspecific competition.

Appendix IV describes the methods by which winter flounder and ocean pout search and capture prey. Different hunting methods among fish species may be one of the factors involved in resource division.

Appendix V examines the information redundancy associated with three measurement variables: prey abundance, prey weight and percent frequency of occurrence.

At the time of writing all but Appendix III had been submitted for publication. Appendices II, IV and V have been accepted. The data collection, analysis, interpretation and presentation was the sole responsibility of the PhD applicant in all but Appendix I. The first three of five years data collection in Appendix I was made by the co-authors listed.

The reader should be familiar with the contents of the first five appendices before proceeding.

2. MATERIALS AND METHODS

2.1 Study Sites

With the exception of the fish distribution portion of this thesis (Appendix I) all fish and benthic samples were collected along 2 1.6 km transects; one in Passamaquoddy Bay (A) and the other in the Bay of Fundy (B; Appendix I - Fig.1). The sites were 55 and 80-m deep respectively and were relocated each collection period using a depth finder and radar. The annual temperature range was less at site B but the salinity was generally higher (Appendix I - Fig.2). Site A had stronger currents, particularly at the southerly end, due to the tidal flushing effects of Passamaquoddy Bay. Sediment samples taken with a PONAR grab in July 1979 at site B and the northwestern half of site A were composed of silt and clay. The other half of site A is composed of sand (Fig.2.1). Both sieve and hydrometer techniques were used to analyse the sediments (Bowles 1970). Sediment samples were subjected to 550°C temperatures for 2h to burn off the organic fraction. Samples from both sites consisted of approximately 7% organic material. Site A was the same site sampled by Tyler (1971) during 1965 and 1966.

2.2 Data Collection

Fishes were collected using a 3/4 - 35 shrimp trawl constructed of 3.8 cm stretch mesh nylon with a 15.5 m head rope. The net was towed with the 150 h.p., 14 m stern trawler Pandalus II. Repeated tows were made along each transect once a month for 7 months during the period of July 1979 to June 1980 (Table 2.1). Site A was not sampled during December 1979 because of the proximity of lobster trap lines. Within 3 days of each fish collection, 10 benthic

FIGURE 2.1 Grain size distribution of benthic sediments taken from site A and B. Site B samples are consistent along the transect (refer to map, Fig. I-1). Sediment samples from the northern end of site A have a similar grain size distribution to those from site B. They get progressively coarser approaching Deer Island.

----- Site A
_____ Site B

TABLE 2.1 Summary of numbers (n), mean lengths ($\bar{X}_L$, cm), standard deviations of lengths (S.Dev), age ($\bar{X}$ age, years) and sex of all fish species collected at each sampling time. Fish length range within each fish species was minimized and an attempt was made to collect 10 of each fish species at each site and time. This was not always possible. Each male fish was given a value of zero and each female fish a value of one. The means of all values for each species are presented to indicate the proportion of males and females collected at each site and time.

TABLE 2.1

SAMPLING DATES

		July 18-19		Aug. 9-20		Oct. 18-19		Dec. 5	Jan. 28-31		Apr. 3-9		June 23-25	
Site		A	B	A	B	A	B	B	A	B	A	B	A	B
Cod	n	2	4	4	3	0	10	5	10	1	4	0	8	3
	$\bar{X}L$	46	74	40	75		78	93	17	49	15		27	62
	S.Dev.	.63	2.8	7.2	5.8		13	19	2.8	0	1.4		7.6	15
	$\bar{X}$ Age	2	4	2	4		5	7	1	3	1		1	4
	Sex	1	1		1		.7	.6					.8	0
Ocean Pout	n	10	10	10	4	10	2	6	0	1	4	1	10	6
	$\bar{X}L$	45	54	48	56	42	53	51		26	57	58	53	49
	S.Dev.	8.5	4.2	8.2	5.2	10	3.9	8.2		0	3.8	0	3.5	7.2
	$\bar{X}$ Age	7	8	6	8	5	7	7		3	11		.8	.7
	Sex	.5	.7	.5	.8	.4	.5	.1			.3	1	.2	.8
Winter Flounder	n	10	2	10	3	10	4	10	10	10	10	10	10	4
	$\bar{X}L$	32	37	34	40	34	38	32	25	26	28	27	28	38
	S.Dev.	5.9	5.1	8.0	3.2	6.6	4.4	6.0	4.3	8.8	4.4	4.5	4.1	1.1
	$\bar{X}$ Age	5	6	6	7	5	6	5	4	5	5	4	4	7
	Sex	.7	.5	1	1	.7	.5	.9	.5	.6	.4	.4	.6	.8
American Plaice	n	9	10	10	10	10	10	9	3	10	8	10	10	10
	$\bar{X}L$	22	30	26	28	23	30	28	23	20	23	25	27	27
	S.Dev.	2.2	5.2	3.4	4.1	1.0	7.6	5.9	.8	3	3.4	4.9	1.5	2.7
	$\bar{X}$ Age	2	7	3	4	3	4	5	3	3	3	4	3	4
	Sex	1	.5	1	.5	.9	.7	.5		1	1	.4	.5	.6
Witch Flounder	n	0	6	0	10	1	10	10	0	2	0	0	0	10
	$\bar{X}L$		49		47	60	47	39		26				54
	S.Dev.		11		11.1	0	11	16		1.9				2.4
	$\bar{X}$ Age		16		12	12	12	9		5				13
	Sex		1		1	1	.8	.9		1				.9

samples were taken at each site from the RV Miss Michelle using a PONAR grab. Each grab sampled a 23 cm² area.

If sufficient numbers were captured, 10 winter flounder, cod, plaice, ocean pout and witch flounder were selected. Witch flounder were not caught at site A. Total length (to the nearest cm), weight (to the nearest g) and sex estimates were made for each specimen. To reduce the effect of fish size on food habits the size range of fish collected within each species was kept to a minimum (Table 2.1). Unfortunately there was a large size variation in the cod sampled. Cod become increasingly piscivorous as they grow (Powles 1958; Arntz 1974; Lilly and Fleming 1981). This increased the prey species variation within the cod samples.

Immediately after capturing the fishes their stomachs were removed and placed singly in numbered jars of 10% buffered formalin. In the laboratory prey species were transferred to 70% ethanol and later keyed to the lowest possible taxonomic level (Appendix VI).

Mollusk viscera were keyed when valves were not present (Appendix IV). Blotted wet weight (to the nearest 0.01 g) and number of each prey species was recorded directly onto 80 column computer sheets. Otoliths were removed and stored in an equal mix of glycerin and alcohol. Fishes' ages were determined by the aging section of the St. Andrews' Fisheries and Oceans Laboratory (Table 2.1).

Benthic samples were washed through a 1 mm screen and stored in 10% buffered formalin. Laboratory analysis of grab samples was similar to that of stomach samples. In addition, three common benthic species (Casco bigelowi, Leptocheirus pinguis and Yoldia sapotilla) were measured (total length) using a computer linked

measuring device (Tektronix 4954 digitizer). The technique described by Macdonald and Sudbury (1982) was followed. A 2 factor analysis of variance (ANOVA) was used to test for mean length differences of each species between sites and among collection times. Computing was done using the ANOVA subprogram (classical approach) in the statistical packages for the social sciences (SPSS) on a Cyber 170 at the University of Western Ontario computer centre.

To measure the depth-within-the-sediment preferences of common benthic prey species, ten mud samples were collected with a tall Eckman grab (dimensions:- 14 x 14 x 23 cm) at site A during June 1980. The column of mud that resulted from each grab (approximately 10 cm high) was immediately sliced into five - 2 cm sections. Each section was sieved through a 1 mm screen and stored in 10% buffered formalin. Species were identified to their lowest taxonomic level.

A one factor ANOVA followed by an SNK multiple range test was used to examine mean depth differences among the benthic species. The depth information was $\ln(X+1)$ transformed before the analysis to remove dependence of the variance on the mean.

Communication with fellow scientists and literature sources were used to estimate feeding strategies, spawning times, life spans and migratory behaviour of some of the common benthic organisms.

2.3 Data Analysis

This was a three dimensional multivariate study where six sampler-types (five fish species and the bottom grabs) were collected from two sites at seven-times during a year (Fig.2.2). There were 217 prey or potential prey species (dependent variables) identified from one or more of the sampler-types (Appendix VI).

FIGURE 2.2 Data cube showing the 3 dimensional nature of this study. December-site A is empty because lobster lines prevented sampling. Witch flounder were not commonly caught at site A and therefore were not included in the analysis of site A.

G - grab
 F - winter flounder
 O - ocean pout
 P - plaice
 C - cod
 W - witch flounder

FIGURE 2.3 Data as they were prepared for computer analysis. Note that each of the 217 variables (prey species) is expressed as a number and a weight. There were 527 fishes and benthic grab samples (cases). They were divided in groups of each sampler-type at each site-time combination.

VARIABLES (p)										
	1		2				216		217	
	No.	Wt.	No.	Wt.			No.	Wt.	No.	Wt.
1										
2										
3										
4										
CASE (n)										
525										
526										
527										

In preparation for analysis the data were stored on the disk system of the Cyber 170 computer in a two dimensional matrix format (Fig.2.3). A matrix of this size needed to be reduced because there is usually a great deal of information redundancy when large numbers of variables are used (Green 1979). Three methods were used to reduce the size of the matrix:

a) Only number of prey measurements (not weight) were used in the analyses. Measures of number, weight and percent frequency of occurrence for a single variable are highly correlated. Little information is gained by using more than one measurement type (Appendix V).

b) A correlation technique was used to rank the variables (prey species) according to the additional information each one added to the entire data matrix (Green and Macdonald in prep; Orłóci 1978 - program called Rank). The variable given the lowest rank has the highest Pearson product - moment correlation coefficient with the other variables. If two or more variables are highly correlated with one another only the one with the greatest amount of information will be used. In this manner 217 variables were reduced to 126.

c) Variables that occurred in less than 2% of the 527 cases were eliminated because they add very little information to the data matrix. This left the 74 variables that were used in the food habit analyses (Appendix VI). They included most of the 22 principal prey of demersal fish in Passamaquoddy Bay in Tyler's (1972) study.

A series of graphical techniques was used to describe spatial and temporal changes in mean abundance of the major components of the

fishes' diets and benthic samples. A FORTRAN program was used to access mean number, percent frequency of occurrence, and to calculate Ivlev's (1961) electivity indices (Appendix VII). Electivity indices were not used in this thesis because ratio index variables (ie. number of a prey species in stomach divided by number in benthic samples) are difficult to compare statistically. For a more thorough discussion see Green (1979) and Appendices III and V. However, electivity indices are available should they be required by the reader.

Abundance data are generally non-normally distributed (contagious) because of large numbers of variables with zero values in the data matrix. Many, parametric based statistical tests (eg. ANOVA, Discriminant Analysis) are robust to non-normal distribution of variables particularly when there is a large error degree of freedom (Klecka 1975; Green 1979; 1980; J. Koval per.comm.). A more serious violation occurs when the variance is heterogeneous among groups, which often results from dependence of the variance on the mean. This is particularly true when sample sizes are unequal. An $\ln(X+1)$ transformation was used to remove dependence of the variance on the mean. This transformation was determined using Taylor's power law (Elliott 1977; see Appendix V). Log transformations are commonly used when dealing with organism abundance data to stabilize variances and to reduce the skewness and non-additivity of variance components (Sokal and Rohlf 1973; Marriott 1974; Green 1979, 1980).

A three factor multivariate analysis of variance (MANOVA) was used to test for overall significant differences among mean prey

abundances of all site-time-sampler type groups within the data matrix. Then discriminant analysis was performed to compare benthic composition among sites and times. It was used again later, at each site-time combination to find the discriminant functions (DF), and their variable loadings, that gave the maximum separation among groups of fishes and the benthic samples. In this manner diets of all fishes were compared to the potential food components in the sediment. These analyses were made using SPSS at the University of Western Ontario. A portion of the differences among sampler-types, in this analysis, is due to the grab taking a larger number of organisms than the fishes (Fig. 3.2). However, discriminant analysis is legitimate for my purpose. The largest discriminant function coefficients, (loadings) of the first discriminant function of each site-time analysis were generally divided between positive and negative values (Table 2.2). When variables with large loadings have opposite signs it indicates large abundances in opposite groups. The first vector describes differences in benthic species proportions among sampler types as well as sample size differences (Jolicoeur and Mosimann 1959).

The series of discriminant analyses was repeated on fishes only (with benthic grab samples removed) to give a better picture of the degree of feeding niche separation that occurred among fish species. Ninety-five percent confidence ellipses on group centroids were plotted (Sokal and Rohlf 1969). The FORTRAN program used to calculate them is presented in Appendix IX. Loadings on the DF's could have been used to identify the variables which contribute the most to the group differentiation. However, when three or more

TABLE 2.2 Four largest standardized discriminant function coefficients on the 1st DF (loadings) generated from discriminant functions analysis among all sampler types at all times and both site. The loadings are generally divided among positive and negative values.

DISCRIMINANT FUNCTION COEFFICIENTS

	Site A	Site B
	-26.48	-13.92
	25.93	13.40
July	21.64	8.35
	-16.33	- 8.06
	-27.77	-29.43
	-19.57	21.92
Aug	16.62	-17.92
	13.21	16.96
	21.61	25.22
	-18.42	13.37
Oct	16.53	11.69
	15.03	-10.34
		20.68
		-13.27
Dec		-11.97
		-11.01
	19.22	-17.29
	-16.62	-15.11
Jan	11.16	14.60
	- 8.04	-14.05
	-29.29	-10.39
	19.60	- 8.47
April	-17.26	5.95
	-17.19	5.95
	-27.03	-23.58
	18.34	-21.01
June	-17.78	14.97
	-13.26	13.00

groups are involved it is often difficult to determine which groups each variable is discriminating among. Also, the tolerance test screen in the SPSS discriminant analysis removed many rarely occurring variables from the test. Variables that occurred rarely in some groups and abundantly in others were of interest to this study. Therefore variables were ranked, by F-value, on their overall ability to discriminate among pair-wise comparisons of sampler-types (Jancy 1979 - program KRANK). The F-value results from the ratio of between sampler-type to within sampler-type variances (mean squares) of each variable. Variables were said to have significant discriminating power if their alpha values were greater than 0.05 after Bonferroni's inequality equation was used to correct for the increased chance of making a type one error that occurs with repeated F-tests (Snedecor and Cochran 1980).

To illustrate the robustness of discriminant analysis in exploring data which violates parametric assumptions, repeated tests were made on the July-site A observations using four types of fish feeding data. They were: (a) non-logged abundance data; (b) all 217 variables combined into four phyla groups (annelids, arthropods, mollusks and others); (c) binary data and (d) logged weight data. All data types showed significant group separation on DFI, and a high percentage of the groups were correctly classified (Fig.2.4). Gilbert (1968) has found little loss of information when using binary data in discriminant analysis. Discriminant analysis is a good data exploration procedure if the researcher's primary purpose is to explore data shape and structure rather than to test formal hypotheses.

FIGURE 2.4 Repeated discriminant analyses on feeding data from July-site A using 4 data types. The percentage of variation associated with each discriminant function (DF) is presented. Eigenvalues, significance levels and percentages of groups correctly classified are presented. Only variables that pass the tolerance test were used.

Fish used were:_____

- ▲ - winter flounder
- △ - ocean pout
- - plaice

COMPARISONS OF DATA TYPES (July - Site A)

Non-Logged
Abundance
Data

Eigen V.	Chi χ^2 probability	% groups correctly classified
9.47	.0346	93.10
3.09	.313	

- 21 variables used

Binary
Data

Eigen V.	Chi χ^2 probability	% groups correctly classified
13.11	.0001	93.10
4.7	.0223	

- 18 variables used

Data Combined
in 4 Groups
by Phyla

Eigen V.	Chi χ^2 probability	% groups correctly classified
3.79	.0001	96.55
1.87	.0001	

- 4 variables used

Logged
Weight Data

Eigen V.	Chi χ^2 probability	% groups correctly classified
294.1	.0001	96.55
4.30	.296	

- 23 variables used

3. RESULTS

3.1 Fish Distribution - summary of the five year study

During the five year survey of fifteen sites in the lower Bay of Fundy region sixty-two fish species in five groups were identified: an estuarine group, a beach group, a deep hard bottom group, a deep soft bottom group and a pelagic group (Appendix I). Flatfish, gadoids, sculpins, clupeoids and rays dominated all groups, both in species numbers and individuals. Species and/or age-class components of each group varied seasonally, but communities could be recognized at all times. Growth rates of winter flounder, cod, plaice, ocean pout and witch flounder did not differ between sites. There was a progressive seaward displacement of groups from shallow inshore habitats to deeper, offshore habitats in winter and a reverse movement in summer. Changes in species occurrence and abundance recorded during the study period were mostly attributable to ocean climate variation. Changes in abundance since a similar study at site A in 1965 reflect fluctuations in commercial stocks throughout the Maritimes. The beach zone was a major nursery area for juvenile gadoids, flatfishes and clupeoids. A more detailed account of the fish distribution work is presented in Appendix I.

3.2 Benthic Composition and Food Utilization - one year feeding study with the fishes described in Table 2.1.

3.2.1 Graphical Analysis

Food utilized by the fishes and benthic samples consisted of 217 infaunal and epifaunal invertebrate species. Very few fish species and no plants were consumed (Appendix VI). The fishes,

particularly cod and plaice, did not utilize all the prey species that were sampled from the sediment (Fig. 3.1). Cod and plaice also consumed fewer prey items (Fig. 3.2). The species diversity and number of individuals in the sediment peaked at both sites in late fall or early winter. However, as the water temperature declined in the fall, cod, ocean pout and winter flounder consumed decreasing numbers of prey species and individuals (Appendix I - Fig. 2). The plaice and witch flounder did not show the same trend. There was a greater species diversity and number of individuals in the sediment at site A than at site B. However, there was no between-site difference in the number of items or species taken by each predator with the possible exception of the winter flounder consuming more items at site A.

Ninety-seven percent of the number of benthic invertebrates at both sites were either annelids (35%) mollusks (20%) or arthropods (42%). Site A had large numbers of arthropods (45%) and annelids (50%) but few mollusks (5%). Site B was annelid (65%) and mollusk (20%) rich with fewer arthropods (15%). At both sites more worms were sampled from the sediment in the winter and early spring than during the warmer months (Fig. 3.3).

Winter flounder fed on large numbers of annelids at site B and large numbers of arthropods at site A. Cod fed primarily on arthropods at both sites and times. Plaice fed on large numbers of annelids and arthropods throughout the year. They also took mollusks at most times of year. Plaice fed more heavily on arthropods at site A than site B. Ocean pout sampled during the summer and fall held large numbers of mollusks. Those sampled in

FIGURE 3.1 Graph of mean number of prey species sampled from each sampler-type at each collection time. Vertical lines indicate 95% confidence limits of the mean. Site B bars are shaded and site A are clear. A dot without a bar indicates that fishes caught had empty stomachs.

<u>Gadus morhua</u>	- cod
<u>Macrozoarces americanus</u>	- ocean pout
<u>Pseudopleuronectes americanus</u>	- winter flounder
<u>Hippoglossoides platessoides</u>	- plaice
<u>Glyptocephalus cynoglossus</u>	- witch flounder

FIGURE 3.2 Graph of mean number of items sampled from each sampler-type at each collection time. Vertical lines indicate 1 standard error of the mean. Site B bars are shaded and site A are clear. A dot without a bar indicates that fishes caught had empty stomachs.

FIGURE 3.3 Percent by number of individuals in Annelid, Arthropod and Mollusk phyla collected by each sampler-type at each site and time.

<u>SYMBOLS</u>		
<u>TIME</u>	<u>SITE A</u>	<u>SITE B</u>
July	1	A
Aug.	2	B
Oct.	3	C
Dec.	-	D
Jan.	5	E
Apr.	6	F
June	7	G

Ponar Grab ***Pseudopleuronectes americanus*** ***Gadus morhua*** ***Hippoglossoides platessoides*** ***Macrozoarces americanus*** ***Glyptocephalus cynoglossus***

the spring contained larger numbers of arthropods (site A) or annelids (site B). Witch flounder fed on arthropods at all times of year (Fig. 3.3).

The following variables had lower densities in the winter at both sites: Thyasira flexuosa, Yoldia sapotilla, Nucula delphinodonta, Sternaspis scutata, Ninoe nigripes and many amphipod species. Leptocheirus pinguis, Syrrhoe crenulata, Praxillella praetermissa, Nucula proxima, Arctica islandica, Nuculana tenuisulcata and Owenia fusiformis had lower densities in the winter at site A only. Cerastoderma pinnulatum had a lower density in the winter at site B only (Appendix VIII).

Many benthic species were commonly found at both sites (eg. Lumbrineris fragilis, Nephtys incisa, Scalibregma inflatum and Y. sapotilla etc.). Others were particular to one of the two sites. Site A the annelid - arthropod community, had a dense assemblage of the annelids: P. praetermissa, Harmothoe imbricata, Eteone trilineata, Amphipolis squamata, family Ampharetidae, Melinna cristata, the arthropods: L. pinguis, Diastylis quadrispinosa, three species of Unciola and the mollusks: C. pinnulatum and N. proxima. Site B, the annelid community, had a dense assemblage of the annelids: S. scutata, Heteromastus filiformis, Rhodine loveni, Chaetozone setosa; the mollusks: N. tenuisulcata, N. delphinodonta, Periploma fragile; and the arthropod: Casco bigelowi.

The macrobenthos was divided into three groups according to their feeding methods (Table 3.1). Until more autecological information is available a rough food classification scheme was

TABLE 3.1

Table of benthic species that occurred in large numbers at both sites (C), site B (B) or site A (A). An 'S' marks species that show seasonal fluctuations in abundance. Where available, feeding methods (D - deposit, SU - suspension and C - carnivore), spawning times, life spans (SH 1 - 2 yrs, L 2 + yrs.) and diel vertical migration patterns within the water column (+ migrates, - does not migrate) are indicated.

TABLE 3.1

Species	Occurrence	Feeding Method	Spawning Times	Life Span	Vertical Migrations
<u>Praxillella praetermissa</u>	S-A	D			-
<u>Harmothoe imbricata</u>	A	C	April	SH	+
<u>Eteone trilineata</u>	C	D			-
<u>Amphipholis squamata</u>	C	SU			-
<u>Ampharetidae</u>	A	D	May	SH	-
<u>Melinna cristata</u>	A	D			-
<u>Heteromastus filiformis</u>	B	D	Apr.-May		-
<u>Rhodine loveni</u>	B	D			-
<u>Chaetozone setosa</u>	B	D			-
<u>Sternaspis scutata</u>	S-B	D	Sept.		-
<u>Cerastoderma pinnulatum</u>	S-A	SU			-
<u>Nucula sp.</u>	S	D			-
<u>Nuculana tenuisulcata</u>	B	D			-
<u>Astarte sp.</u>	A	SU		L	-
<u>Periploma fragile</u>	B	SU			-
<u>Leptocheirus pinguis</u>	S-A	SU	Jan. or July	SH	-
<u>Diastylis sp.</u>	A	D		SH	+
<u>Unciola sp.</u>	A	D		SH	-
<u>Casco bigelowi</u>	S-B	D	July	SH	-
<u>Arctica islandica</u>	S-C	SU			-
<u>Syrrhoe crenulata</u>	S-C	D		SH	-
<u>Nephtys incisa</u>	C	D/C	May	L	-
<u>Lumbrineris fragilis</u>	C	C	July-Aug		-
<u>Scalebragma inflatum</u>	C	D			-
<u>Yoldia sapotilla</u>	S-C	D	Winter		-
<u>Harpina propinqua</u>	C	D		SH	-
<u>Thyasira flexuosa</u>	S-C	SU			-
<u>Haploops fundiensis</u>	S-C	SU		SH	-
<u>Orchomonella minuta</u>	C	D		SH	-
<u>Ninoe nigripes</u>	S-C	D	Sept.		-
<u>Owenia fusiformis</u>	S-C	SU/D		SH	-

all that was possible. The majority of the benthic invertebrate species were omnivorous, feeding on bacteria, algae, other micro-organisms and non-living detritus that accumulates in the sediment (Arntz 1975). Surface and subsurface deposit feeders feed on living and non-living micro-organisms on or within the sediment. Suspension feeders filter detritus and organic material suspended above the sediment surface. Carnivores are predators on other benthic invertebrates (Barnes 1968; Wildish and Linkletter pers. comm.). Many cumaceans and Harmothoe imbricata ascend at night and are therefore available to fish predators.

Most benthic animals in Passamaquoddy Bay spawn in spring or mid-summer and their life span is usually less than two years (Lacalli 1981). Leptocheirus pinguis sampled from the mud were smallest (0.56 - 0.76 cm) in summer ($P < 0.05$) and therefore probably spawned in late winter or early spring (Fig. 3.4). Wildish (1980) reports this species to spawn twice, in January and August. Casco bigelowi spawns once, in July at both sites, with juveniles appearing in the spring (0.57 - 1.0 cm). Casco bigelowi lives longer than most other amphipods (3-yr) (Wildish). The presence of several age classes explains the variability in size at each collection time. Yoldia sapotilla are largest in late summer or early fall (0.68 cm) and smallest in early spring (0.17 cm) at both sites. Spawning probably occurs over winter. Individuals at site A are larger than those at site B ($P < 0.05$, Site by time 2 Factor ANOVA; Fig. 3.4).

Generally, the fishes' food resource habits were a function of

FIGURE 3.4 Mean size of 3 common benthic species collected throughout the year at two sites (only L. pinguis from site A were measured). Vertical lines are 95% confidence limits about each mean. Sample sizes are: L. pinguis $n = 426$, Y. sapotilla $n = 359$ and C. bigelowi $n = 218$.

● - site A

○ - site B

CASCO BIGELOWI

LEPTOCHERIUS PINGUIS

YOLDIA SAPOTILLA

fish species and of spatial and temporal fluctuations in benthic prey species density. Examples and exceptions to this are introduced at this point using details from Appendix VIII. However, the fishes' reactions to benthos density changes is the major theme of the next section of the results (3.2.2 Statistical Analysis).

Praxillella praetermissa, H. imbricata, E. trilineata, Ampharetidae, D. quadrispinosa, L. pinguis, C. bigelowi and S. scutata are all consumed in the largest quantities by winter flounder at those times and sites where they are most abundant. However, despite large quantities at site B, mollusk consumption was restricted to Y. sapotilla at site A. More Yoldia were consumed in the summer and early fall than in spring.

Cod consumed the amphipods L. pinguis and Unciola sp. at site A, mysids and the euphausiid Meganctiphanes norvegica at site B. Unfortunately mysids and euphausiids cannot be sampled accurately with a benthic grab but both types of amphipods were more abundant at site A. Unciola spp., were consumed in the largest quantities when they were least abundant in the sediment, during spring. However, the smallest cod were caught in the spring and crustaceans are eaten more frequently by small cod than larger ones (Arntz 1974; 1978a). Annelids and mollusks were consumed in large numbers in the summer.

Praice utilize N. incisa, S. scutata, L. pinguis, E. rubrocincta, C. bigelowi, A. squamata and Ampharetidae in relative quantities that reflect benthic abundance at most times and sites. There is, however, an exception to this. At site B

in July, plaice reduced their intake of Y. sapotilla and S. scutata to consume C. bigelowi. At approximately the same time, at both sites, ocean pout switched from arthropods (Unciola spp., C. bigelowi, L. pinguis) to mollusks and annelids (S. scutata, C. alba, Y. sapotilla, Nucula spp.). Neither of the shifts coincided with changes of benthic prey density in the sediments.

Witch flounder consumed S. scutata, L. fragilis, N. nigripes, Ampharetidae, C. bigelowi, Hippomedon propinquus in quantities that reflect benthic abundance. Yoldia sapotilla is the only mollusk consumed in large numbers and is taken more often in the summer while arthropods are favoured in the spring.

3.2.2 Statistical Analysis

Significant three way interaction occurred among sites, times and all sampler-types ($P < 0.01$, MANOVA). Before the analysis could be performed, the data from December and the data from witch flounder were removed to give a fully crossed design. Bartlett's test for homogeneity of variances was significant due, partially, to skewness of the data ($P < 0.05$). Partitioning the matrix into all possible two-way designs and one-way designs at each site-time combination showed there to always be significant data structure to be explored in this study ($P < 0.01$).

With the aid of three dimensional stereograms (Fewster and Orloci 1978) and discriminant analysis, spatial and temporal fluctuations in benthic composition were displayed (Figs. 3.5 and 3.6). Species compositions in the mud at sites A and B are significantly different (DFI, $P < 0.01$). Both sites show temporal variation although composition of species in the mud at site A

FIGURE 3.5. A three dimensional stereogram, when viewed with a stereoscope, shows separation in five distinct clusters. One cluster corresponds to discriminant scores for all collection times at site B. The other four show the separation that occurs among the temporal groups at site A. A reference map to identify the groups is presented in Fig. 3.6.

FIGURE 3.6 Reference map to identify the clusters from the stereogram in Figure 3.5. The chi-square and classification test results associated with the first 3 discriminant functions are presented in Table 3.4.

<u>SYMBOLS</u>		
TIME	SITE A	SITE B
July	1	A
Aug.	2	B
Oct.	3	C
Dec.	-	D
Jan.	5	E
Apr.	6	F
June	7	G

45
varies to a greater degree (DFII, $P < 0.01$). The months of July, October and January are the most different. The first three D.F.'s account for 67% of the variation among the groups, although significant discriminating power exists on eight dimensions in this analysis (Table 3.4). The arthropods and annelids, H. imbricata, M. cristata, D. quadrispinosa and Ampharetidae were more abundant in the mud at site A at most times. The annelids and mollusks S. scutata, R. loveni, P. fragile and N. tenuis were more abundant at site B at most times ($P < 0.05$; Table 3.2). A number of benthic species show significant seasonal fluctuations (Table 3.3). L. pinguis, S. scutata, Ampharetidae and N. tenuis have high densities in August and Y. sapotilla in June.

Food composition in the stomachs of the five species of fish does not duplicate the composition of the benthos at most sites and times (discriminant analysis $P < 0.05$; Fig. 3.7; Table 3.4). Many annelids (N. nigripes, N. incisa, L. fragilis, T. acutus and others - Table 3.5) are underutilized at most sites and times by most species of fish. Many mollusks and amphipods are consumed in numbers that are similar to or greater than benthic abundance (Y. sapotilla, L. pinguis, N. tenuisulcata, N. tenuis and Diastylis spp.).

The type of functional response exhibited by a predator to changing prey species density depends on the species of predator and the species of prey. When the abundances of L. pinguis, S. scutata and Ampharetidae increase significantly (Tables 3.2 and 3.3) either winter flounder or ocean pout increase their intake

TABLE 3.2

Ranked log abundance variables that discriminate between sites using the F-statistic (Jancey 1979). Variables are significant at the 0.05 level after Bonferroni's inequality equation was applied. Letters indicate site at which each variable was most abundant during each collection period.

Discriminators (between sites, grabs only)	M O N T H S					
	July	Aug	Oct	Jan	Apr	June
<u>Ampharetidae</u>	A	A	A			A
<u>Sternaspis scutata</u>	B	B	B	B	B	A
<u>Diastylis quadrispinosa</u>	A	A	A		A	A
<u>Periploma fragile</u>			B	B	B	
<u>Harmothoe imbricata</u>			A	A	A	
<u>Rhodine loveni</u>		B	B	B	B	
<u>Nucula tenuis</u>		B	B		B	
<u>Melinna cristata</u>			A	A	A	
<u>Praxillella praetermissa</u>		A	A			A
<u>Unciola irrorata</u>			A		A	
<u>Leptocheirus pinquius</u>		A	A	A		
<u>Diastylis cornuifer</u>		B				
<u>Ninoe nigripes</u>				B		
<u>Micrura spp.</u>					A	
<u>Alvania pelagica</u>			B			
<u>Terebellides stroemii</u>				B		
<u>Diastylis sculpta</u>		A				
<u>Thyasira flexuosa</u>		A				A
<u>Lumbrineris fragilis</u>						A
<u>Astarte borealis</u>			A			
<u>Yoldia sapotilla</u>				B		B
<u>Edotea montosa</u>			A			
<u>Unciola leucopis</u>			A			
<u>Erichthonius difformis</u>					A	
<u>Dentalium entale</u>		B				

TABLE 3.3 Variables are ranked by their ability to discriminate between all pairwise comparisons of successive collection times at each site using the F-statistic (Jancey 1979). Variables are significant at the 0.05 level, after Bonferroni's inequality equation was applied. Letters in brackets indicate the month at which each variable was most abundant. Variables were logged to reduce skewness.

TIME	SITE A - DISCRIMINATORS		SITE B - DISCRIMINATORS	
July-Aug	<u>Diastylis quadrispinosa</u>	(J)	<u>Diastylis cornuifer</u>	(A)
	<u>Ampharetidae</u>	(J)	<u>Sternaspis scutata</u>	(A)
	<u>Praxillella praetermissa</u>	(A)	<u>Nucula tenuis</u>	(A)
	<u>Periploma fragile</u>	(J)	<u>Maldanidae</u>	(J)
	<u>Diastylis sculpta</u>	(A)	<u>Ampharetidae</u>	(A)
	<u>Lumbrineris fragilis</u>	(A)	<u>Rhodine loveni</u>	(A)
	<u>Leptocheirus pinquis</u>	(A)	<u>Diastylis quadrispinosa</u>	(A)
	<u>Harmothoe imbricata</u>	(A)	<u>Nucula delphinodonta</u>	(A)
Aug-Oct			<u>Brada villosa</u>	(A)
	<u>Edotea montosa</u>	(O)	<u>Alvania pelagica</u>	(O)
	<u>Phyllodoce groenlandica</u>	(O)	<u>Diastylis cornuifer</u>	(A)
Oct-Dec	-----		<u>Chaetozone setosa</u>	(D)
			<u>C. pinnulatum</u>	(O)
Oct-Dec	<u>Diastylis quadrispinosa</u>	(O)	<u>Chaetozone setosa</u>	(D)
-Jan	<u>Astarte borealis</u>	(O)	<u>Nephtys incisa</u>	(D)
Jan-Apr	<u>Ninoe nigripes</u>	(A)	<u>Terebellides stroemii</u>	(J)
Apr-June	<u>Ucaiola irrorata</u>	(A)		
	<u>Yoldia sapotilla</u>	(J)		
	<u>Lumbrineris fragilis</u>	(J)		

FIGURE 3.7 Results of discriminant analysis on collections of fishes and benthos at each site and time. The percentage of variance explained by each significant discriminant function are presented above each graph. For purposes of comparison the sediment sample centroid is always on the left. The chi-square values and classification test results associated with each collection site and time are presented in Table 3.4.

- - PONAR grabs
- ▲ - winter flounder
- △ - ocean pout
- - cod
- - plaice
- - witch flounder

TABLE 3.4 Eigenvalues (variances), cumulative percent variation, chi-square test significance levels and results of the SPSS classification test results for the discriminant analyses performed on benthic and fish species groups collected at each site-time combination.

DISCRIMINANT ANALYSIS RESULTS
PONAR GRABS AND ALL FISH SPECIES

DISCRIMINANT FUNCTIONS

Month- Site	Eigenvalue	Cum.% Variation	Chi -square prob.	% sampler- types correctly classified
PONAR	41.09	42.01	.0001	
GRABS	12.51	54.81	.0001	100%
(all times and sites)	11.50	66.57	.0001	
July A	1762.99	98.91	.0001	
	11.87	99.57	.0019	97.44%
July B	927.76	88.44	.0001	
	91.34	97.15	.0001	100%
Aug A	7175.15	99.75	.0001	
	9.94	99.88	.0151	93.18%
Aug B	1798.77	84.94	.0001	
	307.88	99.48	.001	90.00%
Oct A	648.02	75.55	.0001	
	186.13	97.25	.0001	90.24%
Oct B	6294.47	99.51	.0001	
	23.78	99.58	.0001	84.78%
Dec B	378.53	98.69	.0001	72.00%
Jan A	26.11	80.63	.0016	100.00%
Jan B	209.82	99.99	.0001	91.30%
Apr A	1889.78	99.69	.0001	
	5.00	99.91	.0207	83.33%
Apr B	314.14	99.92	.0001	80.00%
June A	6061.89	99.77	.0001	
	10.15	99.93	.0036	91.67%
June B	1978.45	92.16	.0001	
	153.08	7.13	.0001	95.35%

TABLE 3.5 Prey species ranked by F-values on their overall ability to significantly discriminate among sampler types ($P < 0.05$ after Bonferroni's inequality equation was used to obtain an overall confidence probability from a series of tests - Snedecor and Cochran 1980). Numbers assign ranks to each species at that particular site and time. Horizontal bars join sampler-types with similar numbers of prey. Sampler-types are labelled, G-grab sample, F-winter flounder, O-ocean pout, P-plaice, C-cod and W-witch flounder. Numbers of each prey in each sampler-type decrease from left (+) to right (-). Variables that do not appear in this table show no significant abundance differences among sampler-types.

		SITE A			SITE B		
		Discriminators	⊕	⊖	Discriminators	⊕	⊖
JULY		<i>Ninoe nigripes</i>	1	<u>G F O C P</u>	<i>Ninoe nigripes</i>	1	<u>G W F C O P</u>
		<i>Nephtys incisa</i>	2	<u>G F O C P</u>	<i>Nephtys incisa</i>	6	<u>G F P C O W</u>
		<i>Sternopsis scutata</i>	11	<u>O G F C P</u>	<i>Sternopsis scutata</i>	3	<u>G F W O C P</u>
		<i>L. fragilis</i>	4	<u>G F C O P</u>	<i>Voldia sapotilla</i>	2	<u>O G W F C P</u>
		<i>Voldia sapotilla</i>	5	<u>O G C F P</u>	<i>Rhodine loveni</i>	4	<u>G F C O P W</u>
		<i>Tharynx acutus</i>	6	<u>G F C O P</u>	<i>Periploma fragile</i>	5	<u>G F C O P W</u>
		<i>Ampharetidae</i>	7	<u>G F C P O</u>	<i>Thyasira flexuosa</i>	8	<u>G C F W P O</u>
		<i>D. quadrispinosa</i>	8	<u>G O C F P</u>	<i>N. tenuisulcata</i>	7	<u>O G C F P W</u>
		<i>P. praeterrmissa</i>	10	<u>G F C O P</u>	<i>Nucula tenuis</i>	9	<u>O G F W C P</u>
		<i>L. pinguis</i>	3	<u>G F O C P</u>			
		<i>Malidanidae</i>	9	<u>G P C F O</u>			
AUGUST		<i>Ninoe nigripes</i>	8	<u>G F C P O</u>	<i>Ninoe nigripes</i>	7	<u>G F O C W P</u>
		<i>Nephtys incisa</i>	1	<u>G F P O C</u>	<i>Nephtys incisa</i>	10	<u>G F O C W P</u>
		<i>L. fragilis</i>	3	<u>G F P O C</u>	<i>Sternopsis scutata</i>	1	<u>G O F W C P</u>
		<i>Voldia sapotilla</i>	7	<u>O G F P C</u>	<i>Voldia sapotilla</i>	3	<u>G O W F C P</u>
		<i>Tharynx acutus</i>	9	<u>G C P F O</u>	<i>Rhodine loveni</i>	5	<u>G F C W P O</u>
		<i>Ampharetidae</i>	6	<u>G F C P O</u>	<i>D. cornuifer</i>	2	<u>G O F W C P</u>
		<i>D. quadrispinosa</i>	4	<u>G O F P C</u>	<i>C. pinnulatum</i>	8	<u>O G C F W P</u>
		<i>P. praeterrmissa</i>	2	<u>G F P O C</u>	<i>Nucula tenuis</i>	6	<u>G F C O P W</u>
		<i>L. pinguis</i>	10	<u>F G C O P</u>	<i>Ovenia fusiformis</i>	11	<u>G P O C F W</u>
		<i>Thyasira flexuosa</i>	5	<u>G C F O P</u>	<i>Brada villosa</i>	4	<u>G P W C O F</u>
		<i>Diastylis sculpta</i>	11	<u>G O C P F</u>	<i>A. hasata</i>	9	<u>O G C F W P</u>
					<i>N. delphinodonta</i>	12	<u>G F O C W P</u>
OCTOBER		<i>Ninoe nigripes</i>	12	<u>G F P O</u>	<i>Ninoe nigripes</i>	10	<u>G W F O P C</u>
		<i>Nephtys incisa</i>	13	<u>G F O P</u>	<i>Nephtys incisa</i>	11	<u>G F O P W C</u>
		<i>L. fragilis</i>	7	<u>G F P O</u>	<i>Sternopsis scutata</i>	3	<u>G W O F P C</u>
		<i>Tharynx acutus</i>	5	<u>G F P O</u>	<i>L. fragilis</i>	12	<u>G F W O C P</u>
		<i>Ampharetidae</i>	2	<u>G F P O</u>	<i>Voldia sapotilla</i>	4	<u>O G W P F C</u>
		<i>D. quadrispinosa</i>	4	<u>G O P F</u>	<i>Rhodine loveni</i>	2	<u>G C W P O F</u>
		<i>P. praeterrmissa</i>	6	<u>G F P O</u>	<i>Periploma fragile</i>	8	<u>G O F C P W</u>
		<i>L. pinguis</i>	14	<u>G F O P</u>	<i>D. cornuifer</i>	5	<u>O G F W C P</u>
		<i>Melinna cristata</i>	3	<u>G F O P</u>	<i>N. tenuisulcata</i>	6	<u>O G F P C W</u>
		<i>H. imbricata</i>	1	<u>G O F P</u>	<i>C. pinnulatum</i>	7	<u>O G F C P W</u>
		<i>Unicola irrorata</i>	10	<u>G F P O</u>	<i>Alvania pelagica</i>	9	<u>G O F C P W</u>
		<i>Astarte borealis</i>	8	<u>G F P O</u>	<i>Nucula tenuis</i>	1	<u>O G F W C P</u>
		<i>Eteone trilineata</i>	9	<u>F G P O</u>	<i>W. breviculcar</i>	13	<u>G F O W C P</u>
		<i>H. fundiensis</i>	11	<u>G F P O</u>			

SITE A			SITE B		
Discriminators	+	-	Discriminators	+	-
DEC					
			<i>Ninoe nigripes</i>	8	<u>G C W O F P</u>
			<i>Nephtys incisa</i>	1	<u>G W C O F P</u>
			<i>Sternopsis scutata</i>	2	<u>G W C O F P</u>
			<i>L. fragilis</i>	4	<u>G W G O F P</u>
			<i>Voldia sapatilla</i>	3	<u>G W C O F P</u>
			<i>Tharynx acutus</i>	7	<u>G C W O F P</u>
			<i>N. tenuisulcata</i>	6	<u>G C W O F P</u>
			<i>Chaetozone setosa</i>	5	<u>G W C O F P</u>
JAN					
<i>L. fragilis</i>	5	<u>G P C</u>	<i>Ninoe nigripes</i>	1	<u>G P W</u>
<i>Tharynx acutus</i>	4	<u>G P C</u>	<i>Nephtys incisa</i>	4	<u>G P W</u>
<i>Ampharetidae</i>	2	<u>G P C</u>	<i>Sternopsis scutata</i>	3	<u>G P W</u>
<i>L. pinguis</i>	1	<u>C G P</u>	<i>L. fragilis</i>	8	<u>G P W</u>
<i>Melinna cristata</i>	3	<u>G P C</u>	<i>Tharynx acutus</i>	6	<u>G P W</u>
<i>E. rubrocincta</i>	6	<u>G P C</u>	<i>Periploma fragile</i>	5	<u>G P W</u>
<i>H. imbricata</i>	7	<u>G P C</u>	<i>Rhodine loveni</i>	7	<u>G P W</u>
			<i>T. stroemii</i>	2	<u>G P W</u>
APR					
<i>Ninoe nigripes</i>	8	<u>G C O F P</u>	<i>Ninoe nigripes</i>	3	<u>G P F</u>
<i>L. fragilis</i>	1	<u>G F P C O</u>	<i>Nephtys incisa</i>	1	<u>G P F</u>
<i>Tharynx acutus</i>	2	<u>G O F P C</u>	<i>Sternopsis scutata</i>	2	<u>G P F</u>
<i>Ampharetidae</i>	5	<u>G C O F P</u>	<i>Voldia sapatilla</i>	9	<u>G P F</u>
<i>D. quadrispinosa</i>	4	<u>G C O F P</u>	<i>Tharynx acutus</i>	5	<u>G P F</u>
<i>P. praetermissa</i>	7	<u>G C O F P</u>	<i>Periploma fragile</i>	4	<u>G P F</u>
<i>Melinna cristata</i>	6	<u>G C O F P</u>	<i>Thyasira flexuosa</i>	8	<u>G P F</u>
<i>H. imbricata</i>	3	<u>G C O F P</u>	<i>Nucula tenuis</i>	7	<u>G P F</u>
			<i>Micrura sp.</i>	6	<u>G P F</u>
JUNE					
<i>Ninoe nigripes</i>	2	<u>G F C O P</u>	<i>Ninoe nigripes</i>	4	<u>G W F C O P</u>
<i>Nephtys incisa</i>	6	<u>G F P O C</u>	<i>Nephtys incisa</i>	2	<u>G F P W O C</u>
<i>Sternopsis scutata</i>	8	<u>G O F P C</u>	<i>Sternopsis scutata</i>	1	<u>G W F O C P</u>
<i>L. fragilis</i>	1	<u>G F C O P</u>	<i>Tharynx acutus</i>	5	<u>G F W C O P</u>
<i>Voldia sapatilla</i>	7	<u>G O F P C</u>	<i>Periploma fragile</i>	3	<u>G F C O W P</u>
<i>Tharynx acutus</i>	3	<u>G F C O P</u>	<i>Owenia fusiformis</i>	6	<u>G F W C O P</u>
<i>Ampharetidae</i>	4	<u>G F P O C</u>			
<i>D. quadrispinosa</i>	10	<u>G F O P C</u>			
<i>P. praetermissa</i>	9	<u>G F O P C</u>			
<i>L. pinguis</i>	12	<u>O C F G P</u>			
<i>Thyasira flexuosa</i>	5	<u>G O F C P</u>			
<i>Melinna cristata</i>	15	<u>G F C P O</u>			
<i>N. tenuisulcata</i>	14	<u>G O P C F</u>			
<i>Owenia fusiformis</i>	11	<u>G F C O P</u>			
<i>Unicola irrorata</i>	13	<u>C F O P G</u>			
<i>Nucula proxima</i>	16	<u>G F C P O</u>			

to consume significantly more than the other fish and occasionally more than the number sampled by the grab (Table 3.5). Ocean pout tend to consume a constant proportion of mollusks (Y. sapotilla, N. tenuis) and other hard-body prey regardless of density unless an upper limit is set by satiation (eg. D. quadrispinosa; Fig. 3.8). Winter and witch flounder show a lag response at low densities of many prey species, and a rapid increase in consumption rate at higher densities. Exceptions to this may be D. quadrispinosa, where there are no data at intermediate prey densities, and L. fragilis. Other predators respond much less dramatically to increasing prey density. Functional response by cod may be independent of prey density. However, some of the common prey species of cod could not be sampled efficiently with a PONAR grab (eg. mysids and euphausiids) and therefore abundance measures of availability could not be made.

After repeating the series of discriminant analyses without the benthic grab samples it was clear that there was a great deal of food resource partitioning among the predators ($P < 0.05$; Fig. 3.9; Table 3.6). The prey species that show a significant difference in degree of utilization among sampler-types are listed in Table 3.5. The results agree quite closely with the findings from Appendix VIII. In fact, Table 3.5 applies significant levels to the results already presented from Appendix VIII.

The smallest amount of resource partitioning occurred during the collections when feeding rates were low (Fig. 3.2 - December,

FIGURE 3.8

Mean number of eight common species of prey consumed at different prey densities by the five predator species. Only prey that show significant changes in density among the sites and times sampled are exhibited (Table 3.2, 3.3). Data is not recorded for months when fishes were not feeding (Fig. 3.2) or for fishes feeding on prey not common to their diet. Lines are fitted through the points by eye.

- ▲ - winter flounder (F)
- △ - ocean-pout (O)
- - cod (C)
- - plaice (P)
- - witch flounder (W)

FIGURE 3.9

Results of discriminant analysis on fish stomach collections at each site and time. The percentage of variance explained by each significant discriminant function is presented above each axis. Each centroid is surrounded by a 95% confidence ellipse. Asterisks refer to fish species where the variance was too low to calculate ellipses. Low variance may be caused by low sample number or empty stomachs. A discriminant score scale is presented in the lower left hand corner of the figure.

- ▲ - winter flounder
- △ - ocean pout
- - cod
- - plaice
- - witch flounder
- N/S - no significant difference between the fish

TABLE 3.6 Eigenvalues (variances), cumulative percent variation,
Chi -square test significance levels and results of the
classification test results for the discriminant analyses
performed on fish species groups collected at each site-
time combination. Benthic samples have been removed.

ALL FISH SPECIES - AT ALL SITES AND TIMES - GRAB SAMPLES EXCLUDED

DISCRIMINANT ANALYSIS RESULTS

DISCRIMINANT FUNCTIONS

Month-Site	Eigenvalue	Cum.% Variation	Chi-square prob.	% sampler-types correctly classified
July A	14.92	61.37	.0031	
	9.39	100.00	.0377	100.00
July B	627.74	94.29	.0001	
	32.99	4.96	.0015	100.00
Aug A	10.50	52.76	.0210	91.18
Aug B	1171.00	97.48	.0001	
	24.49	99.52	.0332	96.67
Oct A	189.39	90.00	.0001	
	20.25	99.62	.0003	87.10
Oct B	28.25	78.72	.0001	
	6.00	95.36	.0204	80.56
Dec B	147.52	98.51	.0001	70.00
Jan A	13.97	100.00	.0402	100.00
Jan B	1.09	91.09	.9018	84.62
Apr A	5.06	74.46	.0063	76.92
Apr B	.39	100.00	.2620	70.00
June A	168.87	96.69	.0001	
	3.95	98.96	.0184	94.74
June B	193.41	59.04	.0001	
	128.46	98.25	.0001	93.94

January and April) or during August (site A) and October (site B). In most cases niche overlap among two or more predators was the result of the sharing of many prey species. This makes it difficult to develop a direct link between benthic change and changes in niche overlap among predator species. For instance, winter flounder in August (site A) and October (site B) share similar abundances of almost all prey species with cod and plaice (Table 3.5; Appendix VIII). At most other times and sites there was at least one prey species that was consumed in greater abundances by winter flounder (eg. N. nigripes - July B; L. fragilis - October A). Ocean pout and witch flounder differ from the other predators in August and October; ocean pout because it consumes mollusks (Y. sapotilla, N. tenuisulcata) and witch flounder by consuming annelids (N. nigripes, S. scutata). The similarities between feeding patterns of ocean pout and plaice were traced to months when they both feed primarily on arthropods (Fig. 3.3 - October and June, site A) or an arthropod - annelid mix (June, site B). Unciola spp., D. quadrispinosa and C. bigelowi were among the prey being shared (Appendix VIII).

3.3. Feeding behaviour of the Ocean Pout and Winter Flounder

Observations of winter flounder and ocean pout feeding on a variety of natural prey items provide an example of feeding methods influencing food resource division among syntopic fish (Appendix IV). The ocean pout sorts mouthfuls of bottom sediment to obtain infaunal prey species such as bivalves. The winter flounder relies more on vision to select prey exposed on the surface of the substrate. Winter flounder were also seen to

remove the viscera from shells of bivalves that presumably were too large to swallow; however, the required increase in handling time may make bivalves a suboptimal prey.

3.4 Prey species depth within the sediment

Mean sediment depths at which prey are found differ significantly among prey species ($P < 0.01$). Ten samples were taken in June at site A only (Fig. 3.10). Amphipods, Ampharetids and S. scutata live in the upper sections of the mud and some species of mollusks (Pitar morrhuana, Cylichna alba, and Periploma fragile) and Nemerteans (Micrura sp. and Cerebratulus sp.) in the lower sections ($P = 0.05$, SNK multiple range test). Yoldia sapotilla had a shallower mean depth than the other mollusks. The variances of the prey groups were homogeneous after Ln-transformation (Bartlett-Box F test, $P < 0.05$). The cumaceans sampled were mainly D. quadrispinosa and the amphipod category was C. bigelowi and Byblis gaimardi.

3.5 Rates of digestion of different prey

A visual index method of evaluating prey evacuation shows that polychaete worms followed by amphipods become unrecognizable before bivalves do. Factors to correct for variability in digestion rates of prey (Table II - 4) were not applied to the stomach contents of fishes collected in this thesis. They show the degree to which variability of digestion characteristics among prey species can affect the researcher's perception of diet composition. Before corrections can be made to stomach content data the digestion characteristics of more prey species at many temperatures must be made.

FIGURE 3.10 Mean sediment depths of twelve species of benthic invertebrates ranked in order of descending depth at site A in June. Depths are $\log(X+1)$ transformed. Vertical bars show 95% confidence limits of benthic species mean depths.

From plots of percentage of each prey recovered versus time since feeding, it can be seen that annelids and amphipods were evacuated at a significantly greater rate than bivalves. Of three models fitted to the decay curves the exponential model gave the best overall fit to the data. However, a linear model gave a good or better fit to the decay rate of the bivalve. The evacuation rates of different prey should be considered when estimating daily rations of fish in their environments (Appendix II).

3.6 Feeding chronology and daily ration calculations

Using three methods to estimate feeding periodicity discussed in Appendix III, it was found that winter flounder, plaice and ocean pout are diurnal feeders with plaice feeding more heavily later in the day. Cod show no change in feeding activity with time of day. Winter flounder and cod consume the most food per gram of fish followed by ocean pout and plaice. The winter flounder daily ration estimate (1.65% body wt/day) was similar to the estimates of Tyler and Dunn (2% for daily fed fish) and Huebner and Langton (1.8 - 2.4%) for laboratory studies at a similar temperature.

4. DISCUSSION

4.1 Annual Feeding Cycles

It is likely that cooler temperatures and approaching spawning times are responsible for the decrease in feeding activities of winter flounder, ocean pout and cod during the months between December and April (Fig. 3.2). Similar responses have been recorded for plaice (Pleuronectes platessa), cod, and flounder (Platichthys flesus) in the western Baltic (Arntz 1974, 1978a, 1978b; Arntz and Finger 1981), dover sole (Microstomus pacificus) off Oregon (Pearcy and Hancock 1978), and winter flounder and ocean pout in the western north Atlantic (Olsen and Merriman 1946; Pearcy 1962; Richards 1963a; Tyler 1971; Hacunda 1979). These species first feed in April or May when temperatures reach 3 or 4°C (Appendix I, Fig. 3.1). Seasonal food quantity trends were less evident for plaice and witch flounder (Tyler 1971; Fig. 2). Lower temperatures slow metabolism and ingestion rates and reduce the amount of food required by all fishes in the winter community in the lower Bay of Fundy (Tyler 1970; Edwards 1971; Persson 1979, 1981).

Comparisons of number of items per stomach among fish species are misleading, (Fig. 3.2). Mean sizes of the fish species (Table 2.1) and type of prey species eaten will affect daily ration estimates (Appendices II, III).

4.2 General Feeding Habits

Literature reports suggest that demersal fish species' food habits vary from region to region. Winter flounder feed primarily on polychaetes (Richards 1963a; 1963b; Tyler 1972; Langton and Bowman 1981), mollusks and amphipods in the New England region

(Frame 1974) and amphipods and polychaetes in the Bay of Fundy region (Figure 3.3). Ocean pout feed on echinoderms and crustaceans in the Gulf of Maine (Hacunda 1979) and the Cape Cod (Olsen and Merriman 1946) regions. They feed primarily on mollusks in Passamaquoddy Bay (Tyler 1972). Plaice feed on mollusks, fishes and crustaceans in the western Baltic (Arntz 1981) and Passamaquoddy Bay (Tyler 1972), polychaetes, off southern New England (Bowman 1981a, 1981b) and echinoderms on the Grand Banks (Macdonald unpublished). Cod less than 40 cm in length feed on crustaceans in the western Baltic and the northwestern Atlantic. Fishes and mollusks become increasingly important to cod as they grow (Powles 1958; Tyler 1972; Arntz 1974; Hacunda 1979; Bowman 1981a). DeGroot (1971) describes the witch flounder as a polychaete, mollusk and amphipod feeder in the North Sea. They feed primarily on annelids off the New England states (Langton and Bowman 1981) and arthropods in the Bay of Fundy (Fig. 3.3).

Variation in the size of each fish species collected in each study, and perhaps differences in feeding behaviour among years and in rates of evacuation among different prey species, partially explain the differences in food habits reported in the literature (Appendix II - Table 4). However, demersal fishes are opportunistic feeders and therefore food habit differences among different studies are primarily the result of differences in the available food source at each site (Fig. 3.3; Percy and Hancock 1978; Moore and Moore 1978a). Seasonal and spatial changes in diets are best examined after spatial and temporal changes in the benthic composition are discussed.

4:3 Ben

Many studies of benthic animal abundance, at latitudes similar to this study, have found annelids to outnumber arthropods or mollusks (Fig. 3.3; Richards and Riley 1967; Ziegelmeier 1978). However, crustaceans are more susceptible to losses resulting from sampling device pressure waves and leakage, and are therefore under-represented in most benthic collections (Word 1976). Provided sampler bias remained constant, spatial and temporal benthic abundance fluctuations can be attributed to many biological and hydrographic factors including spawning times, settlement patterns, sediment type, hydrographic factors (temperature, salinity, depth), predator-prey relationships and environmental stability (Arntz 1975; Ziegelmeier 1978; Rachor and Gerlach 1978).

Short-lived species have fluctuations that reflect seasonal cycling of their populations (Arntz 1975; Ziegelmeier 1978). Many of the benthic species at site A and B have short life spans (Table 3.1). Spring and mid-summer spawnings were common for Passamaquoddy Bay invertebrates (Lacalli 1980; and this study), and provided large abundances of animals of a size that were retained by a 1.0 mm sieve in late summer and early fall (Fig. 3.2). Ampharetidae, Harmothoe sp., S. scutata, most amphipods and other invertebrates provide examples of this (Appendix VIII). In regions where temperature and salinity show little fluctuation (eg. abyssal depths) species reproduce throughout the year and do not show seasonal abundance changes (Rokop 1974). Larger species abundance variations at site A probably reflect the more extreme fluctuations in temperature, salinity and possibly current at that location (Fig. 3.5).

Abnormally low temperatures have the direct effect of eliminating both infaunal and epifaunal animals, particularly bivalves (Ziegelmeier 1978). More extreme yearly temperatures may explain the lower densities of bivalves at site A (Appendix I - Fig. 2, Fig. 3.3). Other spatial faunal composition differences may reflect depth and sediment type differences. Sediments become coarser with decreasing depth and increasing currents (site A; McIntyre 1978). Arntz and Brunswig (1975) found the highest faunal diversity to occur in conditions similar to those at the northern half of site A (Fig. 2.1). However, while individual physical features undoubtedly control spatial and temporal benthic patterns, the critical controlling factor is the degree of environmental stability. Sanders (1968) has shown how all communities are a result of their physical and biological components. Physical conditions are of primary importance when each species has to adapt to a broad spectrum of physical changes. To survive, each species must utilize large portions of the environment and therefore fewer species can exist than when physical conditions are more constant. With constant physical conditions biological interrelationships develop and community control occurs through biological accommodation. Biologically accommodated communities usually have a higher species diversity. Both sites were primarily controlled by physical hydrographical conditions (currents and fluctuations in temperature and salinity). Levinton (1972), Racher and Gerlach (1978) and Rhoads et al (1978) have shown how extreme temperatures and wind, wave and current erosion can prevent successional advancement to a later successional stage. The fauna of early

successionary stages feed on newly settled or suspended organic matter (bacteria) by filter feeding or surface deposit feeding (Rhoads et al 1978). Both sites had many animals with these feeding strategies (eg. S. scutata, Nucula spp., most small crustaceans, Ampharotidae, Owenidae; Table 3.1). Fewer sub-surface deposit feeders and carnivorous species, which are common in later successionary stages, were present (eg. Nephtys sp., Glycerids, Pectinerids, Lumbrinerids). The fauna at both sites show other re-selected characteristics that are common to colonizing species. Most animals were small, had high reproduction rates, high dispersability and short life spans (Table 3.1; Odum 1971; Levinton 1972; Rhoads et al 1978; Wildish 1980).

Many pioneering species live near the sediment surface and are therefore more susceptible to fish predation and wave erosion (eg. S. scutata, Ampharotidae, Y. sapotilla, Maldanidae; Fig. 3.10. Rhoads et al 1978). Most of these animals are surface suspension or deposit feeders. Many deeper animals are subsurface deposit feeders (Lumbrineridae, Nucula sp. and Nemerteans) or filter feeders (P. morrhuana, P. fragile). Despite their depth Rhoads describes many as pioneering species.

Unfortunately measurements of the depths at which animals live in the sediment were made only at one site and time. Seasonal depth variation was not measured. Reading and McGrorty (1978) found Macoma balthica to be deepest in the winter. This may be an evolutionary response to avoid the eroding effects of winter storms and bird predation.

It is difficult to detect successional stage differences between

sites because little information is available on feeding methods and habitation depths of many of the invertebrates. Site B may support species that are at a higher successional stage. It has slower currents, fewer extreme hydrographic factors, more consistent sediment structure and was deeper so less susceptible to wave erosion. Surface feeding animals (eg. amphipods) were less abundant at site B. The dominant amphipod at site B (C. bigelowi) was a large relatively long-lived species which shows other K-selected characteristics. It can rework sediments to depths of 20-25 cm (Wildish 1980). The fish species assemblage was more sedentary at site B than at site A (Appendix I). However, site A had a higher species diversity than site B which is a characteristic of biologically accommodated, stable communities that are at later successional stages.

Site A was a better fish feeding ground. The benthic animals were more abundant (Fig. 3.2) and potentially lived shallower in the sediment. Amphipods, which were more abundant at site A, have higher caloric values than most other prey species (Tyler 1973). A great number of demersal fishes make seasonal migrations into Passamaquoddy Bay (site A) to feed (Appendix I).

The degree to which fish feeding affects the benthos is of interest to many researchers (Huebner and Langton 1981; J. Grassle and M.J. Dadswell pers.comm.). Richards (1967), Levings (1974) and Arntz and Brunswig (1975) have found the density of a few prey species populations to be reduced by demersal fish predation. Accurate estimates of fish predation, expressed as a percentage of benthic production, are hampered by lack of autecological knowledge

of many of the common-prey species. Important parameters are fecundity, death rates and growth rates. Year-round daily ration estimates are required for the predators as well. There are many demersal predators at both sites, including fishes (Appendix I), echinoderms and carnivorous polychaetes. Communities with a large number of carnivorous invertebrates are poorer fish feeding grounds because a large portion of the available benthic energy flow goes to the invertebrates (Richards 1967; Mills 1975). Fish-benthos interactions are considered below but at this stage it will suffice to say, that while fishes may have an effect on some components of the benthos, the benthos at both sites is held at an early successional, highly productive stage by variable physical conditions. Fluctuating temperatures, and wave and current actions, are almost certainly more important in regulating spatial and temporal benthic species abundance and diversity than are predatory fishes.

4.4 Resource Utilization and Partitioning

Demersal fish in many parts of the world consume fewer polychaetes and more amphipods than would be expected from benthic samples (Fig. 3.3, Appendix VIII, Fig. 3.7, Table 3.5; Arntz 1978 - Kiel Bay; Richards 1963 - Long Island Sound; Moore and Moore 1976a - Severn Estuary). However, the researcher's view of what is apparently available is quite different from what is potentially available to each fish species (Hyatt 1979). A PONAR grab and a fish's mouth are quite different sampling devices. Predator species will respond in a variety of ways to differences in distribution, escape response, degree of concealment and size of prey species.

The efficiency of the predator's digestion characteristics and feeding methods toward each prey type will determine what is observed by the researcher as stomach contents (Steven 1936; Moore and Moore 1976a; Jones 1978; Robb 1981; Appendix II; IV).

Invertebrates that were distributed just below the sediment surface (eg. amphipods, S. scutata, Ampharetidae, Y. sapotilla) are more likely to be fed upon than those that are deeper. Moore and Moore (1976b) speculate that a burrowing polychaete may be difficult for a predator to find and remove. Periploma fragile, a deep-dwelling mollusk, occurred in large numbers at site B but was never consumed by fishes. The shallower Y. sapotilla was consumed in large numbers by most fish species. It was the only mollusk consumed regularly by winter and witch flounder (Fig. 3.10, Appendix VIII). Reading and McGorty (1978) found the sediment depth of Macoma balthica to be the factor that controlled predation rates of wading birds.

Epibenthic invertebrates (mysids, euphausiids, decapods) use underwater vegetation and other obstacles for protection. Nightly vertical migrations by benthic species are probably timed to avoid the peak feeding activity of visual predators. However, early morning and late evening feeding activity by fish may take advantage of vertical migrations by prey species (Arntz 1975; Table 3.1). In the lower Bay of Fundy non-visual feeders (ocean pout) may consume large numbers of Diastylis spp. at this time (Appendices III, IV, VIII).

Much of the food resource partitioning and food "selectivity" observed in demersal fish feeding studies is correlated with

differences in the morphological adaptations and feeding behaviour of each fish species (Brian 1957; DeGroot 1971). Visual feeders such as cod and pleuronectids respond to prey movement and therefore feed on epibenthic and shallow infaunal items (eg. arthropods; Brown 1969; Jones 1978; Ringler 1979; Libey and Cole 1979; Fig. 3.3; Appendix IV). Ocean pout sort mouthfuls of sediment and thus have access to deeper infaunal material (most mollusks). Cod and winter flounder will eat infaunal material, the cod by digging and the flounder by nipping off siphons or crushing the shells (Bishop and Odense 1966; Frame 1974; Appendix IV). Winter flounder mouths are too small to consume large whole objects. Shells must be completely broken down before they can pass through the narrow pyloric sphincter of cod. The extra time required to handle mollusks makes them suboptimal prey to cod, winter flounder and probably witch flounder (Appendices II and IV). Plaice have larger mouths and therefore are able to consume more mollusks than other pleuronectids (Fig. 3.3, Appendix VIII). They eat large quantities of large calcareous prey on the Grand Banks (sand dollars and sea urchins, Macdonald - unpublished) and fish in Kiel Bay (Arntz and Finger 1981).

Calcareous and to a lesser extent chitonous prey were evacuated at a slower rate by most predators and will therefore appear to be eaten in greater numbers than they actually were. Removal of this bias could reduce the degree of food niche overlap that exists between the annelid-arthropod predators and the mollusk predators (Appendix II - Table 4; Fig. 3.9).

4.5 Feeding reactions to spatial and temporal benthic change

Generally the utilization pattern of benthic prey by each demersal fish species is correlated with the abundance of prey in the sediment. This is particularly true when comparing dietary patterns among predator groups that have significantly different available food resources such as site A vs site B (Table 3.2). Many annelids (*Ampharetidae*, *P. praeterrissa*, *H. imbricata*, *S. scutata*), arthropods (*C. bigelowi*, *L. pinguis*, *Unciola* spp., *Diastylis* spp.) and mollusks (*Nucula* spp.) were consumed in greater abundances at the sites and the times that they were more abundant in the sediment (Appendix VIII). However, demersal fishes do not specialize at the species level. Rather they consume food of a general type. For instance, ocean pout eat cumaceans at both sites. At site A they eat *D. quadrispinosa* and *D. sculpta* where they have a higher benthic abundance than site B. At site B they eat *D. cornuifer* which is the more abundant cumacean there. Winter flounder eat amphipods at both sites. At site A they consume the dominant *L. pinguis*, at site B the dominant *C. bigelowi*.

Feeding methods may have a direct effect on predator species' reactions to changes in prey species density. Predators that use visual cues to feed (eg. winter and witch flounder; Appendix IV) are likely to develop search images towards commonly utilized prey species (Tinbergen 1960). The functional responses of one or both of the flounders to high densities of *L. pinguis*, *C. bigelowi* and *Ampharetidae* are explained by search image development (Appendix VIII; Fig. 3.8; Table 3.5). Non-visual feeders (eg. ocean pout) are less likely to develop search images (Ringler 1979). Their

predation rate is likely to remain constant with increasing densities of prey animals.

Some seasonal prey utilization patterns were not related to changes in potential prey species density. Changes in size of benthic animals can also be responsible for dietary shifts (Pearcy 1962; Levings 1974; Moore and Moore 1976a; Arntz 1974; 1978a). According to optimal foraging theory the predator will ignore small prey where the yield in energy per unit foraging time is low. Since energy content increases with size of prey (Kerr 1979) there exists a prey size where the ratio of energy gained to time spent foraging is maximized (MacArthur and Pianka 1966; Krebs 1978). Larger prey will also be more visible. For example, L. pinguis was more heavily utilized by most fishes when it was largest in spring. Yoldia sapotilla is more heavily utilized by winter and witch flounder and ocean pout when it is largest in the summer. Casco bigelowi is more heavily utilized in the summer when it is largest, by plaice and winter flounder (Fig. 3.4, Table 3.5, Appendix VIII). These shifts were not caused by benthic animal density changes. In fact Y. sapotilla and L. pinguis are more abundant during the times of year when predation pressure is minimal. Therefore demersal fishes may play a role in controlling population levels of a few common species, as Levings (1974) found, but predation impact on most benthic species is negligible (Richards 1963 and Arntz 1978b had similar conclusions).

The upper limit to population size of many marine demersal fish species is determined in the first year of life (Jones 1978). It is therefore unlikely that food is a limiting resource for older fish.

If food were limiting, then optimal foraging theory would predict that the fishes on the poorer site (site B), would have more diverse diets (Warner and Hall 1974). Site B had fewer animals and in particular fewer energy rich species such as amphipods. However, there was no difference in the diversity of prey consumed by each predator (Fig. 3.1, 3.3).

Increase in availability of potential prey species has been shown to increase the degree of overlap among predatory fishes (Zaret and Rand 1971; Sedberry and Musick 1978; Pearcy and Hancock 1978; Ringler 1979; Macpherson 1981). In Passamaquoddy Bay the demersal fishes at both sites show significant food resource segregation (Fig. 3.9; Tyler 1972). The greatest diet overlap observed in this study occurred in August (site A) and October (site B) when benthic density and diversity was highest (Fig. 3.1, 3.2, 3.9). Other factors, such as daily feeding times (Appendix III), spatial and temporal variation in predator abundance (Appendix I) and vertical differences in areas of feeding activity (Johansen and Ringler 1980), may serve to reduce niche overlap particularly among winter flounder, plaice and cod in August (site A) and October (site B). However, these three species are found together in large abundances at these sites and times (Appendix I - Table 2). It is likely that food type is the major niche segregating factor. Similar conclusions have been made by Gascon and Leggett (1977), Keast (1978), Kravitz et al (1976) and Macpherson (1981).

5. CONCLUSION

Seasonal movement of the fish species in the lower Bay of Fundy region was largely from an inshore, shallow water locality in summer to an offshore, deep water locality in winter with a reverse movement occurring in spring (Appendix I). The cause of this movement may have a large physiological component related to temperature effects on the osmoregulation of many marine fishes. Juvenile fishes of many species use the shallow water habitat as a nursery area. They are susceptible to coastal impacts from development, degradation, and pollution.

Analyses of systems as complex as this lend themselves well to multivariate statistical modelling techniques where the object is to explore data structure rather than make formal statistical tests at specified probability levels. Discriminant analysis and multi-factor MANOVA are appropriate methods to explore food composition differences among groups of fish species collected at different sites and times. Prey species which contribute most to group differentiation are more easily identified using the variable reduction method developed by Jancey (1979) than by using variable loadings on discriminant functions. Numbers of prey measurements (not weight) were used in the analysis. Additional information gained decreases rapidly as more measurement variables are included (Appendix V).

Differences in diets among fish species is the major niche segregating factor. Other factors, such as daily feeding times (Appendix III) and spatial and temporal variation in predator abundance (Appendix I) are less important.

Fishes do not "prefer" and "select" specific prey in the deliberate sense of the words. Rather, food specialization and dietary niche

separation are a result of evolutionary development of unique feeding behaviours, digestion morphologies and techniques, and mouth structures which interact with the size, behaviour, distribution and abundance characteristics of certain types of available benthic fauna. For instance the development of techniques to feed and process infaunal food efficiently partially explains the predominance of mollusks and sedentary polychaetes in the diet of the ocean pout (Appendices II and IV). Visual feeders (winter flounder, cod, plaice, and witch flounder) are more likely to consume epibenthic prey. As a result many demersal fish species segregate the resource by having somewhat specialized food habits. However, they must also cope with spatially and temporally changing food resources and therefore specialize in general prey types, not prey species.

The perception of the diet composition and consumption rates that fishes have in the natural environment, and our models for describing the digestion processes, are affected by variability in the digestion characteristics of each prey species (Appendix II). Analysis of consumption rates requires that the rate of weight loss by the prey be applied to the model which best describes the digestion process.

It is unlikely that food is a limiting resource to demersal fishes in the lower Bay of Fundy region because: a) the upper limit to population size is probably set in the first year of life, b) only a few prey species show density changes as a result of predation and c) spatial and temporal benthic density changes observed in this study are largely due to physical perturbations.

Further work is required to estimate the production of common benthic species and the daily rations of fishes throughout the year so

that fish production can be expressed as a function of benthic production.

2

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APPENDIX I

Fishes, Fish Assemblages, and Their Seasonal Movements
in the Lower Bay of Fundy and Passamaquoddy Bay, Canada

by

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INTRODUCTION

Although the fish fauna of the Bay of Fundy-Gulf of Maine system is well documented (Bigelow and Schroeder 1953; Richards 1963; Leim and Scott 1966), few studies have examined long-term spatial and temporal changes and interrelationships of the fish assemblages. Previous studies in this region were concerned with the biology and seasonal movements of a single species (McKenzie and Tibbo 1961; McCracken 1963) or the occurrence and composition of communities at a single site (Tyler 1971).

Moore (1977) and Quinn (1980) have emphasized the need for long-term research to establish baseline information and estimates of natural variability for fisheries assessments and pollution impact studies. This is particularly true for inshore regions because of their importance as nurseries and feeding grounds (Warfel and Merriman 1944; Rauck and Zijlstra 1978). The increasing interest in food habits of fishes of an entire community is further reason to document movement, abundance, and co-existence of fishes potentially utilizing the same food resource (Richards 1963; Keast 1970; Tyler 1972; Steiner 1976; Hacunda 1979).

This study examines spatial and temporal variation in fish diversity and abundance over a five year period at two offshore stations within Passamaquoddy Bay, one offshore station in the Bay of Fundy, and at inshore and beach stations in Passamaquoddy Bay. One of the offshore stations sampled had been sampled by Tyler (1971) in 1965-66. An effort was made to determine whether changes have occurred over the intervening years.

METHODS

Three offshore stations in the Bay of Fundy (B) and in Passamaquoddy Bay (A, C) (Fig. 1) were sampled at approximately monthly intervals over a 5-yr period, 1976-81 (Table 1). Station A was the same site sampled by Tyler (1971) during 1965-66. Fish were collected using a 3/4-35 shrimp trawl (3.8-cm stretch mesh nylon; 15.5-m foot rope) towed by the 150-h.p., 14-m stern trawler, Fisheries and Oceans R.V. PANDALUS II. Tows at each station were along a 1.6-km transect at approximately 4 km/h. Sites A and B were sampled once per trip between 1976-79 and site C was sampled sporadically. From 1979-81 tows at A and B were replicated and site C was sampled regularly. Captured fishes were identified as to species. Juveniles and adults were then counted separately. During the final year of collecting, fork length of all fishes was recorded to the nearest centimeter and otoliths were collected from cod, ocean pout, plaice, winter flounder, and witch flounder for age determination. Collections in the final year could not be made in December at site A.

Between June and September 1976, 12 estuarine, intertidal, and inshore marine stations were sampled within Passamaquoddy Bay and Head Harbour Passage (Fig. 1). In addition, station 3 was sampled monthly during the period May 1976-November 1977, station 8 was sampled at approximately weekly intervals from May-September 1981, and stations 1 and 10 were sampled in December 1980 (Table 1). Fish were collected using a 9-m, 1.3-cm mesh beach seine, a 3.7-m shrimp trawl with a 3-mm codend towed behind a 5-m Boston whaler, or bottom-set gillnets with stretched mesh sizes ranging from 7.6-17.8 cm. Standard fishing efforts employed with each gear type were: shore seine hauls of 5 min during the

FIGURE I - 1. Passamaquoddy Bay and the adjacent Bay of Fundy
indicating sampling stations occupied during the study.

TABLE I - 1. Physical and chemical characteristics and sampling history of stations in the study area. Gear: ST = shrimp trawl; S = seine; GN = gillnet. Bottom type: M = mud; Sa = sand; Rk = gravel or rock.

Station	Gear	Max.	Bottom Type	Sampling Temp.	Sampling Salinity	Collection Period	Samp- ling Trips
		Depth		Range	Range		
		(m)		(°C)	(o/oo)		
A	ST	80	M-Rk	0-15	29.5-32.5	1976-81	39
B	ST	80	M	1-12	31.0-32.5	1976-81	37
C	ST	20	M	0-15	-	1978-81	15
1	S	1.5	M-Rk	14.5-20.0	22.1-26.0	06-08/76, 12/80	3
2	S	1.5	M-Rk	15.5-22.5	26.0-29.5	05-08/76	4
3	S	1.5	Sa-Rk	0.0-16.0	21.0-30.0	05/76-11/77	16
4a	S	1.5	Rk	12.5	29.0	06,07/76	2
4b	ST	7.5	Rk	12.5	-	07/76	1
5a	S	1.5	Sa	14.5	30.0	07,08/76	2
5b	GN	33	Sa-M	-	-	08/76	1
6	S	1.5	Sa-M	14.0	28.0-30.0	08-09/76	2
7	GN	30	M	13.5	28.0	06/76	1
8a	S	1.5	M-Sa	11.0-18.5	28.7-30.7	06,07/76	2
						05-09/81	23
8b	ST	12	Rk-Sa	-	-	06,07/76	2
9	S	1.5	Sa	14.0	29.5	06,08/76	2
10	GN	3	M-Rk	13.0	28.0	06,09/76, 12/80	2
11	S	1.5	M	-	-	07/76	1
12a	S	1.5	Sa-Rk	15.0	28.0	07,09/76	2
12b	ST	15	Sa-Rk	-	-	07/76	1

2-h period before and after low water; trawl tows of 10 min; and overnight gillnet sets of 16-h.

Temperature, salinity, and substrate type were recorded for most sampling sites (Table 1). Temperature and salinity data inside and outside Passamaquoddy Bay came from routine monthly sampling by the Department of Fisheries and Oceans at a site opposite the Biological Station (near site A) and at "Prince 5" 2 mi south of Bliss Island in the Bay of Fundy (near site B). Temperatures at deep stations were taken with a reversing thermometer attached to a Nansen bottle and at shallow stations with a hand thermometer. Salinities were determined with a laboratory salinometer from samples collected in the field. Substrate samples at deep stations were obtained with a PONAR grab. At shallow stations, substrate type was assessed visually.

Fishes were identified using Leim and Scott (1966) with the exception of red and white hake, which were determined using Musick (1973).

RESULTS AND DISCUSSION

Station Environmental Characteristics

Temperature and salinity at stations A and B followed the typical yearly cycle of a cold temperate sea (Fig. 2). Annual temperature range in the Bay of Fundy was less than in Passamaquoddy Bay. Summer temperatures at inshore sites were similar to the deep sites but were higher at estuary stations (i.e. 1 and 2) (Table 1). Three notable variations occurred: the early months of 1977 and August 1978 were

FIGURE I - 2. Temperature and salinity at station B in the Bay of Fundy and station A in Passamaquoddy Bay during 1976-1981.

abnormally warm, particularly at station A (J. Hull, pers. comm.); at station B, temperatures increased and decreased earlier than usual during 1980; and throughout the study period there was a generalized cooling trend.

Salinities were highest in late summer-early fall and lowest in early spring at both sites but highest in winter in the Bay of Fundy (B) (Fig. 2). Inshore sites had salinities of 1-2 ppt less than station B and salinities in estuarine sites were as low as 22 ppt during summer (Table 1).

The substrate at stations B and C was mud and at station A mixed mud, gravel, and rock (Table 1). Station A had the steepest slope, approximately 20 m/km. Slopes at stations B and C were 4 m/km and 6 m/km, respectively. Substrate types at coastal intertidal sites were mixed sandy-mud and rock. Slopes were gradual, about 1:100 m. Gillnet collections at stations 5 and 7 were 30-33 m in depth with mud bottom. Estuarine stations (1, 2 and 10) had extremely soft mud bottoms and station 2 had extensive eel grass beds.

Fishes and Seasonal Occurrence

Sixty-two species of fish were captured during the study period (Tables 2 and 3). Residency period and abundance are indicated. Fish occurrence is expressed as part of the summer component (July-October), the winter component (November-June), the regular component (caught year round), or the occasional component. Fishes that were occasional components show no seasonal abundance pattern and were collected less than 70 times at stations A, B and C or less than 15 times at stations

TABLE I - 2. Residency and abundance of fishes occurring at deep sampling stations in the Bay of Fundy and Passamaquoddy Bay. Residency is: R (regular; S (summer); W (winter); O (occasional); N (never encountered). Abundance is: a (abundant); c (common); r (rare).

TABLE I - 2.

Species	Station		
	A	B	C
<u>Myxine glutinosa</u>	Oa	N	N
<u>Squalus acanthias</u>	Oc	Sa	Oc
<u>Raja radiata</u>	Rc	Rc	Or
<u>Raja senta</u>	Or	Rc	Or
<u>Raja erinacea</u>	Ra	Rc	Oc
<u>Raja ocellata</u>	Rc	Or	Or
<u>Raja laevis</u>	N	Or	N
<u>Acipenser oxyrhynchus</u>	N	Wc	N
<u>Alosa aestivalis</u>	N	N	Or
<u>Alosa pseudoharengus</u>	Or	Or	Sc
<u>Alosa sapidissima</u>	Or	Sc	N
<u>Clupea harengus</u>	Wa	Wa	Wa
<u>Osmerus mordax</u>	Rc	Or	Sa
<u>Mallotus villosus</u>	N	N	Or
<u>Enchelyopus cimbrius</u>	Oc	Wc	Or
<u>Gadus morhua (adult)</u>	Sc	Wc	Oc
<u>G. morhua (juvenile)</u>	Wa	Wc	Oc
<u>Microgadus tomcod</u>	Or	Or	Oc
<u>Pollachius virens (juvenile)</u>	Wa	Or	N
<u>Melanogrammus aeglefinus (adult)</u>	Sc	Oc	N
<u>M. aeglefinus (juvenile)</u>	Wa	N	N
<u>Merluccius bilinearis</u>	Sa	Sa	Sc
<u>Urophycis tenuis</u>	Sc	Rc	Oc

TABLE I - 2. (Cont'd.)

Species	Station		
	A	B	C
<u>Urophycis chuss</u>	Sr	Sc	Or
<u>Anarhichas lupus</u>	Sr	N	N
<u>Ulvaria subbifurcata</u>	Wr	N	N
<u>Cryptacanthodes maculatus</u>	Or	Or	N
<u>Lumpenus lumpretaeformis</u>	Or	Or	N
<u>Lumpenus maculatus</u>	Or	N	N
<u>Macrozoarces americanus</u>	Ra	Sc	Sc
<u>Nezumia bairdi</u>	N	Or	N
<u>Cyclopterus lumpus</u>	Or	Or	N
<u>Liparis coheni</u>	Wc	Or	N
<u>Liparis inquilinus</u>	Wr	N	N
<u>Sebastes marinus</u>	Wc	N	N
<u>Myoxocephalus octodecemspinosus</u>	Ra	Wc	Oc
<u>Myoxocephalus aeneus</u>	Wc	Or	N
<u>Myoxocephalus scorpius</u>	Wc	Or	N
<u>Hemitripterus americanus</u>	Ra	Rc	Or
<u>Triglops murrayi</u>	Oc	Or	N
<u>Artediiellus uncinatus</u>	Wc	N	N
<u>Aspidophoroides monopterygius</u>	Rc	N	N
<u>Poronotus triacanthus</u>	Oc	Or	Oc
<u>Pseudopleuronectes americanus</u>	Sa	Wa	Sa
<u>P. americanus</u> (juvenile).	Wa	Wr	Sa
<u>Glyptocephalus cynoglossus</u> (adult)	Or	Sc	N

TABLE I - 2. (Cont'd.)

Species	Station		
	A	B	C
<u>G. cynoglossus</u> (juvenile)	Or	Wc	N
<u>Hippoglossoides platessoides</u>	Rc	Ra	Ra
<u>Limanda ferruginea</u>	Sc	Or	Or
<u>Liopsetta putnami</u>	N	N	Wc
<u>Hippoglossus hippoglossus</u> (juvenile)	Wr	N	N
<u>Paralichthys oblongus</u>	Or	N	N
<u>Scophthalmus aquosus</u>	Or	Or	Rc
<u>Lophius americanus</u>	Sc	Or	N

TABLE I - 3. Residency and abundance of fishes occurring at estuarine, intertidal, and shallow marine sites in Passamaquoddy Bay. Residency is: R (regular); S (summer); W (winter); O (occasional). N (never encountered) is used to describe residency at station 3 only because this is the only shallow site that was sampled year round. Abundance is: a (abundant); c (common); r (rare).

TABLE I - 3.

Species	Station											
	1	2	3	4	5	6	7	8	9	10	11	12
<u>Squalus acanthias</u>	-	-	N	-	Sc	-	Sc	-	-	-	-	-
<u>Raja radiata</u> (juvenile)	-	-	Sr	-	Or	-	Or	-	-	-	-	-
<u>Raja erinacea</u>	-	-	Sc	-	Or	-	-	-	-	-	-	-
<u>Raja ocellata</u>	-	-	N	-	Or	-	Or	-	-	-	-	-
<u>Alosa aestivalis</u>	-	-	N	-	-	-	-	Sa	-	Sa	-	-
<u>Alosa pseudoharengus</u>	-	-	Sr	-	-	Or	-	Sa	-	Sa	-	-
<u>Clupea harengus</u>	Sc	Or	Or	Or	-	Or	Or	Sa	-	Sa	Or	-
<u>Salmo salar</u>	-	-	S	-	-	-	-	-	-	Or	Or	-
<u>Osmerus mordax</u>	Or	Sc	Wa	-	-	-	Or	Sa	-	Or	-	-
<u>Mallotus villosus</u>	-	-	N	-	-	-	-	-	-	-	Oc	Oc
<u>Fundulus heteroclitus</u>	Sa	Sc	Wc	-	-	-	-	Or	-	Sc	-	-
<u>Gasterosteus aculeatus</u>	Sc	Sa	Oc	Or	Or	Or	-	Sc	-	Sc	Or	Or
<u>Gasterosteus wheatlandi</u>	Oc	Sa	Sr	-	-	-	-	Sr	-	Sr	-	-
<u>Apeltes quadracus</u>	-	Sc	N	-	-	-	-	-	-	-	-	-
<u>Pungitius pungitius</u>	-	Sa	N	-	-	-	-	-	-	-	-	-
<u>Anguilla rostrata</u>	Or	Sc	N	-	-	-	-	-	-	Sr	-	-
<u>Enchelyopus cimbrius</u> (larvae)	-	-	Sc	-	-	-	-	-	-	-	-	-
<u>Gadus morhua</u> (adult)	-	-	N	-	Or	-	Or	-	-	-	-	-
<u>G. morhua</u> (juvenile)	-	-	Sr	-	Sc	-	Sc	Sr	-	-	-	-
<u>Microgadus tomcod</u>	Wc	Wc	Wc	Or	Or	-	-	Sc	Or	Wc	Or	-
<u>Pollachius virens</u> (juvenile)	Or	Or	Sa	Or	Or	Or	-	Sa	Or	-	-	Or

1-12 during the entire study. We realize that some fish at all sites may have been missed entirely or are listed as rare simply because they were unavailable to the sampling gear used or could avoid capture (eg. mackerel).

The eight species of flatfishes captured (Table 2) represent the most diverse and abundant group of demersal fishes present. Pseudopleuronectes americanus, the winter flounder, was the numerically dominant species (Fig. 3, 5). Juveniles (22 cm, 2+ age group; Fig. 6) were abundant in shallow water during summer (Fig. 5) and at deep stations over hard bottom in Passamaquoddy Bay during winter (Fig. 3). Adult winter flounder were abundant in Passamaquoddy Bay, both inshore and offshore during summer, but rare at the Bay of Fundy site (Fig. 3). During winter they were rare or absent inside Passamaquoddy Bay but common to abundant at the Bay of Fundy station. This pattern reflects the winter movement of this species into deeper water in the northern part of its range (Saila 1961; McCracken 1963; Van Guelpen and Davis 1979), which is probably triggered by temperature. Adults were seldom present in Passamaquoddy Bay when temperatures were below 6°C. During the warm fall of 1977 adult flounder were abundant until late December in Passamaquoddy Bay. During "normal" years adults left Passamaquoddy by late November (Fig. 3). McCracken (1963) found a similar relationship between minimum flounder catch-per-effort and minimum temperature. Surges of adult flounder abundance at offshore sites which coincided with rapid temperature change in spring and fall were evident in most years (Fig. 3 and see Tyler 1971). This is probably related to rapid onshore or offshore movement of the population.

FIGURE I - 3. Seasonal occurrence and abundance of juvenile and adult flatfishes at deep stations in the Bay of Fundy and Passamaquoddy Bay. For witch flounder (Glyptocephalus cynoglossus) dark bars are adults and lined bars are juveniles at site B. Witch flounder were not found at site at site A. For plaice (Hippoglossoides platessoides) open bars are site B and lined bars are site C (all juveniles). Plaice occurred less often at site A.

Pseudopleuronectes americanus

Abundance Per Tow

- -A+C adult means
 ▨ -A+C juvenile means
 □ -B adult means
 ▲ -A+C no catch
 ▼ -B no catch

*Glyptocephalus cynoglossus**Hippoglossoides platessoides*

FIGURE I - 4. Seasonal size distributions of some flatfishes from deep stations in the Bay of Fundy and Passamaquoddy Bay. Shaded area are captures at site B, unshaded site A inside Passamaquoddy Bay.

FIGURE I - 5. Seasonal occurrence and abundance of fishes captured by seine at intertidal site 8 from May to September 1981.

FIGURE I - 6. Mean fish length versus age for five fish species caught
at sites A and B; December 1980 - June 1981.

The witch flounder, Glyptocephalus cynoglossus, was rare or absent at all times inside Passamaquoddy Bay but was a regular component at the soft-bottom Fundy station. Catches from June to October consisted of large adult witch (30-60 cm, 6+ age group) but catches from November to May were 6-25 cm juveniles (0-6 yr) (Fig. 4, 6). Adult witch on the Scotian Shelf also move from intermediate depths (100 m) in summer to deeper water in winter (Powles and Kohler 1970). However, there is no previous record of the abundance of juvenile witch on soft bottom or of their replacement of adults during winter.

Juvenile plaice (Hippoglossoides platessoides) were a major summer component of station C and a regular component of the Fundy station, both soft-bottom habitats, but was only occasional at the hard-bottom station (A). Age 2 plaice (6-14 cm; Fig. 6) were first captured with our shrimp net in April. By the following year recruitment to the gear appears complete at an average size for the age-class of 17 cm (Fig. 4). Juvenile plaice are sedentary, soft-bottom dwellers, that exhibit little seasonal movement, and migration from nursery ground to adult stock is diffusive (Bigelow and Schroeder 1953; Leim and Scott 1966). However, some seasonal movement does occur when plaice leave soft-bottom, mid-depth habitat (30 m) for winter and return in summer (present study). Plaice were a regular, low-density component at station A in 1965 (Tyler 1971) but we found they were almost absent between 1976-81. The difference may be attributable to the general decline of groundfish abundance in the Bay of Fundy after 1970 (Hare 1977).

Among other flatfishes, window-pane, Scophthalmus aquosus, was a regular component at station C and the smooth flounder, Liopsetta putnami, was common among the inshore-estuarine communities during summer

(Table 2, 3). Yellowtail flounder (Limanda ferruginea) was a regular, low-abundant member (4-5/tow) of the summer assemblage at station A and an occasional at the other two deep stations. Juvenile halibut (Hippoglossus hippoglossus) was a regular, low-abundance member (2-3/tow) of the winter assemblage at station A. The four-spot flounder (Paralichthys oblongus) was captured once at station A during the abnormally warm fall of 1978.

Seven species of gadoid fishes were captured during the study (Table 2, 3). Unlike the flatfishes, juveniles of all species except silver hake were found at shallow inshore stations during some period of the year.

Adult cod (Gadus morhua) were an abundant member of the summer component at offshore sites in Passamaquoddy Bay, particularly station A, but were absent in winter and a common member of the early winter assemblage in the Bay of Fundy but rare thereafter (Fig. 7, 8). During summer juvenile cod (10-20 cm) were captured occasionally during seining of beach sites but were more common in gillnet catches at intermediate depth (30 m) inshore (stations 5 and 7; Table 3). The shallow water abundance maxima of young cod (0+, 1+, 17 cm) has not been previously documented in the western North Atlantic but is a well known situation for cod in the North Sea (Daan 1978). During winter juvenile cod were abundant at station A or in colder winters at station B (Fig. 8, 1980-81). Both juvenile and adult cod were more abundant at station A during our study than during 1965 (20-70/tow, Tyler (1971); 1976-81, 50-400/tow).

Haddock (Melanogrammus aeglefinus) were never abundant during our study. Adults were captured only at the hard-bottom station A during

FIGURE I - 7. Seasonal occurrence and abundance of gadoids at deep stations in the Bay of Fundy and Passamaquoddy Bay.

FIGURE I - 8. Seasonal size distributions of cod at deep stations in the Bay of Fundy and Passamaquoddy Bay (Stations A, B and C).¹⁸

Gadus morhua

summer (Fig. 7) and juvenile haddock were occasionally captured at the same site in winter. Catches of haddock declined from a maximum of 25/tow to less than 5/tow during the study period (Fig. 7). However, up to 260 haddock/tow were caught at site A during 1965 (Tyler 1971). Decline in abundance after 1965 might be due to the collapse of the Bay of Fundy haddock stock in 1970 (Hare 1977).

Only juvenile pollock (Pollachius virens) were captured during the study. Pollock of the annual year-class (0+) were either rare or extremely abundant at beach sites (100+/seine haul) in a given year, depending, perhaps, on the overall size of the annual year-class. Pollock dominated beach catches during early summer but disappeared from this region by September (Fig. 5). Pollock of the same year-class were abundant at site A in Passamaquoddy Bay during winter (Fig. 7). In years when 0+ pollock were abundant along the beach in summer they were also abundant the following winter at site A (1976-77) and, in summers of low abundance on the beach, they were correspondingly rare offshore in winter (1977-78; Fig. 7). Larger than usual numbers of pollock larvae were present in the plankton March 1979 (Scott 1980) and we again encountered large numbers of 0+ juveniles at site A in the winter of 1979-80. Present findings suggest there were probably three large year-classes produced during our study period, 1976, 1979, and 1981 in contrast to one large year-class of 1979 reported by Scott (1980).

Adult white and red hake (Urophycis tenuis, U. chuss) were a common summer component at offshore stations A and B. Juvenile white hake (15 cm) were a major component at beach stations especially during early summer (Fig. 5), but were rarely captured at offshore sites in winter. Also in 1965 few small hake were captured after December (Tyler 1971).

Apparently, hake leave Passamaquoddy Bay in winter. The only time hake were observed during winter was at station B in the Bay of Fundy during the abnormally warm winter of 1977-78 (Fig. 7).

The fourbeard rockling (Enchelyopus cimbrius) was present in the winter component at station B in the Bay of Fundy and as a periodic in summer at station A (Fig. 7). The mesh size of our gear was just small enough to capture large individuals of this species and it was probably more abundant than indicated. Larval rockling were a rare but regular component of inshore sites during summer (Table 4). Battle (1930) and Tyler (1971) both considered rockling a summer periodic in Passamaquoddy Bay occurring there during spawning migration. Tyler's catch rate at station A (2-3/tow) was similar to ours at that site. Catch rate at station B (10-50/tow), indicates rockling may concentrate at offshore sites in winter.

Silver hake (Merluccius bilinearis) was often the most abundant gadoid found at offshore stations during summer and juveniles were a regular component at station B year round (Fig. 9). Adult silver hake were present in company with other migratory summer periodics, including shad (Alosa sapidissima), dogfish (Squalus acanthias), and butterfish (Poronotus triacanthus).

The tomcod (Microgadus tomcod) was a regular component of the inshore assemblage and was particularly abundant at beach sites during early summer (Fig. 5) and in estuaries in early winter (Table 3).

Clupeoids and osmerids (Table 2) made up a major portion of the fishes caught at inshore sites. At beach station 8, alewife (Alosa pseudoharengus), herring (Clupea harengus), and smelt (Osmerus mordax) appeared in mid-July and increased in abundance during August, largely

TABLE I - 4. Catch of fishes at intertidal seining site 3 (Brandy Cove) during period May 1976-November 1977. Fish captured during three 5-min seine hauls (100 m x 15 m) ([j] = juvenile; [l] = larvae).

TABLE I - 4.

Fish species	1976							1977						
	15/05	04/06	13/17	18/08	15/09	10/10	08/12	15/02	20/03	10/04	30/05	29/06	15/07	18/09
<u>Raja radiata</u> [j]	-	-	-	-	-	1	-	-	-	-	-	1	-	1
<u>R. erinacea</u> [j]	-	4	-	-	-	-	-	-	-	-	-	1	-	-
<u>Alosa pseudoharengus</u>	-	-	-	-	25	2	-	-	-	-	-	-	-	4
<u>Clupea harengus</u>	-	-	2	2	-	-	-	-	-	-	2	-	15	10
<u>Salmo salar</u> [j]	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<u>Osmerus mordax</u>	3	-	-	11	-	5	1	-	-	4	-	-	3	-
<u>Fundulus heteroclitus</u>	-	-	-	-	-	-	5	3	1	-	-	-	-	-
<u>Gasterosteus aculeatus</u>	-	5	51	5	2	4	-	-	-	5	26	32	5	27
<u>G. wheatlandi</u>	-	-	1	-	-	-	-	-	-	-	-	3	1	-
<u>Enchelyopus cimbrius</u> [1]	-	-	-	2	1	-	-	-	-	-	-	-	-	3
<u>Gadus morhua</u> [j]	-	-	-	1	-	-	-	-	-	-	-	-	2	-
<u>Microgadus tomcod</u>	-	2	3	-	-	-	-	-	4	8	-	3	4	2
<u>Pollachius virens</u> [j]	115	132	15	12	2	-	-	-	-	2	-	-	-	-
<u>Urophycis tenuis</u> [j]	-	1	2	-	-	-	-	-	-	-	3	6	11	-
<u>Scorpaenidae</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Pholis gunnellus</u>	-	1	2	-	-	3	1	1	-	4	-	2	3	1

- observed never captured -

TABLE I - 4. (Cont'd.)

Fish species	1976										1977			
	15/05	04/06	13/07	18/08	15/09	10/10	08/12	15/02	20/03	10/04	30/05	29/06	15/07	18/09
<u>Cyclopterus lumpus</u>	-	1	-	-	-	2	-	-	-	-	-	1	2	-
<u>Myoxocephalus aeneus</u>	1	-	-	-	-	1	-	-	-	-	1	1	-	3
<u>M. scorpius</u> [J]	-	-	-	-	-	-	1	-	-	-	2	-	-	-
<u>M. octodecemspinosus</u> [J]	-	3	-	-	-	2	-	-	1	-	-	-	-	3
<u>Hemitripterus americanus</u>	-	1	-	1	-	1	-	-	-	-	1	-	-	-
<u>Pseudopleuronectes americanus</u>	-	10	9	-	4	-	3	-	-	-	12	22	8	2
<u>Liopsetta putnami</u>	-	-	1	-	-	-	-	-	-	-	-	2	-	-
<u>Menidia menidia</u>	1	-	-	3	-	-	15	4	1	-	-	-	-	-

FIGURE I - 9. Seasonal occurrence and abundance of pelagic fishes and dogfish at deep stations in the Bay of Fundy and Passamaquoddy Bay.

replacing the gadoids (Fig. 5). Herring and smelt were also a regular component in estuaries during spring and fall (Table 3). Adult smelt were present at offshore sites in Passamaquoddy Bay in mid-summer as observed by Tyler (1971). In most winters, juvenile herring (10-20 cm) were abundant at offshore sites, particularly inside Passamaquoddy Bay (Fig. 9). Catches were variable and probably depended on their schooling behaviour. Tagging experiments also indicate herring move from inshore during summer to deeper water in winter (McKenzie and Tibbo 1961).

Six species of sculpin (Table 2) were commonly encountered at deep stations of which two, longhorn sculpin (Myoxocephalus octodecemspinosus) and sea raven (Hemitripterus americanus), were abundant, regular components (Fig. 10). Juveniles of most species were common at beach sites in summer (Table 4) and at station A in winter (Table 2). Increases in abundance of sculpins at station B during winter were observed (Fig. 10) and may be the result of migration out of Passamaquoddy Bay. Two small species, Arctic hooker sculpin (Artediellus uncinatus) and mailed sculpin (Triglops murrayi) were winter periodics at station A. They were perhaps more abundant than catch rates indicated (2-5/tow) because their maximum size range was at the lower limit of catchability for our trawl.

The blennoid-like fishes were represented by seven species (Table 2) of which one, ocean pout (Macrozoarces americanus) was a regular at offshore stations in Passamaquoddy Bay (Fig. 10) and another, rock gunnel (Pholis gunnellus), was a regular component at beach sites (Table 4). Ocean pout abundance was generally highest in Passamaquoddy Bay in early summer and declined thereafter (Tyler 1971; present study). Abundance of ocean pout usually increased at station B in late summer and fall,

FIGURE I - 10. Seasonal occurrence and abundance of sculpins and ocean pout at deep station in the Bay of Fundy and Passamaquoddy Bay.

suggesting movement from Passamaquoddy Bay to the Bay of Fundy. Since this movement was most pronounced during the warm summer of 1977 (Fig. 10), it may be a response to avoid warm temperatures (Olsen and Merriman 1946). Movement of pout is generally thought to cover only short distances (Orach-Meya 1975; Sheehy et al 1977).

Other blennoids occurred infrequently at station A (Table 2). Selectivity of our shrimp trawl may have been a factor in these low catches. One species, radiated shanny (Ulvaria subbifurcata) which was thought to be rare in Passamaquoddy Bay (Leim and Scott 1966), was often captured (5/tow) at station A during winter. SCUBA searches during summer revealed that shanny were abundant inshore, under rocks in 6-9 m of water (Dadswell and Melvin, pers. observation).

Five species of skate were captured during the study (Table 2). Two species, thorny skate (Raja radiata) and smooth skate (R. senta) were common, regular components of the offshore site in the Bay of Fundy. Two other species, little skate (R. erinacea) and winter skate (R. ocellata), were regular components of station A in Passamaquoddy Bay. Some seasonal movement into Passamaquoddy Bay was exhibited. Abundance of smooth and thorny skate at station A increased during summer and declined after late fall. Juveniles of thorny, little, and winter skate were often captured at beach sites during summer (Table 3). Raja laevis was collected occasionally at site B.

Several smaller fishes were captured at inshore sites only but again this may be an artifact of sampling gear. Three-spine stickleback (Gasterosteus aculeatus) was a regular component at most beach sites (Table 4). Other sticklebacks were more or less confined to estuarine areas (Table 3). Mummichog (Fundulus heteroclitus) and silversides

(Menidia menida) occurred mainly in estuaries during summer but were part of the winter community at beach sites (Table 4).

Communities and Diversity

Fish community composition in the study area varied according to site and season. If juveniles and adults of some dominant species are considered as separate taxonomic units (Table 2), coefficients of community similarity show the strongest similarity between habitat types (eg. deep, soft bottom), and between the summer community of one habitat and the winter community of the next seaward habitat (Table 5). In general, movement of assemblages was from inshore in summer to offshore in winter with a return movement in spring (Fig. 11). Some species, however, exhibited a partial reverse of this pattern (tomcod, ocean pout).

Specific groupings of fish were segregated among the available habitats as dictated by season. The "estuarine" assemblage was dominated by warm water, euryhaline species, including sticklebacks, silversides, mummichogs, and juvenile clupeoids. Most of this group moved to adjacent, inshore marine habitat in winter (Table 3, 4), but tomcod and smelt moved in the reverse direction to form a winter estuarine group (Table 3).

The summer "beach" assemblage consisted of regulars such as three-spine stickleback and rock gunnel and periodics including juvenile gadoids, juvenile sculpins, flounders, and juvenile alosoids. Juvenile gadoids (pollock, white hake, and tomcod) dominated this assemblage in early summer but were displaced by steadily increasing numbers of

TABLE I - 5. Coefficients of percent similarity¹ among seasonal fish communities in the lower Bay of Fundy.

TABLE I - 5.

	Seaward											
	Estuarine		Beach		C		A		B		B	
	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer
Estuarine winter	-	10.0	20.0	7.0	0.0	12.5	0.0	2.0	0.0	0.0	0.0	0.0
Estuarine summer	-	-	50.0	12.5	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Beach winter	-	-	-	6.6	14.3	3.8	4.2	0.0	0.0	0.0	0.0	0.0
Beach summer	-	-	-	-	6.6	33.3	36.1	17.3	21.2	0.0	0.0	0.0
C winter	-	-	-	-	-	12.5	4.2	5.7	6.6	0.0	0.0	0.0
C summer	-	-	-	-	-	-	4.8	40.0	40.0	47.0	47.0	47.0
A winter	-	-	-	-	-	-	-	20.9	43.0	26.3	26.3	26.3
A summer	-	-	-	-	-	-	-	-	36.4	42.8	42.8	42.8
B winter	-	-	-	-	-	-	-	-	-	25.8	25.8	25.8

¹ Coefficient of similarity $\frac{C}{A+B-C} \times 100$ where C = # of common species, A = # in community 1,

A+B-C

B = # in community 2.

FIGURE I - 11. Communities of fishes occurring at each site divided into summer component (SC), winter component (WC), and regular component (RC). Arrows indicate direction of seasonal movement.

clupeoids in late summer (Fig. 5). Numerous other postlarval and juvenile fishes, including four-beard rockling and lumpfish, appear in the beach zone during the summer (Table 3). In late fall most of this assemblage left the beaches and occupied deep sites in Passamaquoddy Bay. Herring concentrated at the soft-bottom station C and the gadoids, sculpins, and winter flounder (juveniles) at the hard-bottom station A. Three-spine stickleback and rock gunnel remained at beach sites over winter and were joined by silversides and mummichog to form a winter grouping (Table 4).

During summer an "offshore, hard-bottom" assemblage consisting of adult gadoids (cod, haddock, white hake), adult flounders (winter, yellowtail), ocean pout, adult sculpins, and skates assembled inside Passamaquoddy Bay. Sea raven, longhorn sculpin, ocean pout, and little skate remained at this site over winter to be joined by juvenile fishes from the beach zone. The other species apparently move to offshore sites in the Bay of Fundy and/or to the Scotian Shelf (Edwards 1965; Kulka and Stobo 1981).

The "offshore, soft-bottom" assemblage consisted of plaice, witch flounder, white hake, four-beard rockling, and skates. This group at station B was the most stable assemblage studied and had the largest regular component. Conversely, similar communities which occurred at the shallower, soft-bottom site C were the most seasonally dynamic (Fig. 11). Adult witch and most white hake left station B in winter, possibly for grounds further offshore in the Gulf of Maine (Powles and Kohler 1970; Kulka and Stobo 1981) and were replaced by adult winter flounder and longhorn sculpin, possibly from inside Passamaquoddy Bay or other adjacent inshore sites (McCracken 1963).

Superimposed on the two offshore, essentially benthic fish communities was a seasonal pelagic component. In summer, silver hake was the dominant species. During fall, diversity increased with the arrival of dogfish, butterfish, and shad. In winter, herring dominated the pelagic component of the assemblage at all deep sites (Fig. 11).

Diversity, expressed simply as number of species captured, varied appreciably at beach sites during the year. Diversity was 2-5 species in winter-spring, 9-13 species in summer, and 4-6 species in fall-winter (Fig. 12). Total number of species captured at inshore sites was 35, compared to 51 species captured at offshore sites.

Diversity of communities at deep sites (90+ m) was more stable on an annual basis because of the seasonal influx and departure of species to adjacent habitats (Fig. 13). Species number varied between 7 and 17 fishes at station B and 7 and 20 fishes at station A, fluctuating about a mean of 12/sampling trip. During 1965, Tyler (1971) observed a higher mean diversity of 17 species/trip at station A with a maximum occurrence of 24. The difference between his observations and ours may be accounted for partially by the decline in haddock abundance since 1965 and the recent absence of plaice from this site, and partially by his use of a 0.6-cm codend liner, which would have retained small, occasional species more often than our 2.5-cm codend.

Highest diversities occurred during winter at station B and during summer at station A (Fig. 13) as a result of seasonal exchange between these sites and the arrival of periodics. The highest diversity recorded during the study period occurred at stations A and B during the fall of 1977, coinciding with maximum temperatures recorded at these sites between 1976 and 1981. Similarly, lowest winter diversity recorded at

FIGURE I - 12. Monthly diversity of fishes at intertidal stations 3 and 8 in Passamaquoddy Bay. Species/month for station 3 is mean of 1976 and 1977 samples.

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FIGURE I - 13. Seasonal diversity of fishes at station B (Bay of Fundy) and station A (Passamaquoddy Bay). Vertical bars represent range among replicated collections.

station A occurred in the coldest winter of 1980-81 (Fig. 2). Diversity at station C, the mid-depth site, decreased from 13 species in May 1978 temperature.

GENERAL DISCUSSION

Most authors have related the occurrence and distribution of adult benthic fishes in the North Atlantic to substrate type and temperature (Edwards 1965; Colton 1972; Scott 1976) and have shown there is a marked seasonal variation (Lux and Nichy 1971; Jeffries and Johnson 1974). Our findings agree and indicate yearly differences are influenced mainly by minimum winter and maximum summer temperatures. Species occurrence, abundance, and diversity changed dramatically in response to seemingly small changes in the temperature regime. Jeffries and Johnson (1974) report a similar observation concerning winter flounder abundance over a seven year period in Narragansett Bay. Pelagic and semi-pelagic species (herring, silver hake) demonstrated little or no substrate preference. Occurrence was related to annual migratory behaviour.

Seasonal movements of the various species was largely from an inshore, shallow water locality in summer to an offshore, deepwater locality in winter with a reverse movement occurring in spring. Cause of this movement may have a large physiological component related to temperature effects on the osmoregulation of many marine fishes (Potts and Parry 1964). In the southern part of their range, fish such as winter flounder migrate onshore in winter (Bigelow and Schroeder 1953) in response to availability of preferred temperature but never encounter the low temperatures found at northern latitudes. Tomcod, a species known to

produce an antifreeze in their blood (Fletcher et al 1982), was one of the few fishes exhibiting onshore migration to lower salinities during winter in this area. For many species (pollock, herring, white hake), migration from inshore habitat to offshore is unidirectional for the individual, since each year the beach community consists of the new 0+ year-class. For other species (winter flounder, juvenile sculpins, radiated shanny) the return inshore is an annual occurrence, triggered perhaps as much by resource availability and predator avoidance as by physiology.

Tyler (1971) found that white hake was the only species where large individuals moved independently of small individuals in Passamaquoddy Bay. We found obvious differences in size-class distributions and abundance between summer and winter populations of winter flounder, witch, cod, and pollock at deep sites and a complete lack of most adult fish in shallow water. This suggests marked segregation between juveniles (at least 0+ age group) and adults for these species. The use of shallow water habitat as nursery area by fishes of commercial importance has received little attention in the western North Atlantic. In Europe, this fact has been amply demonstrated for many fish species, including cod and pollock (Zijlstra 1972; Rauck and Zijlstra 1978; Daan 1978; Burd 1978). The extensive use of beach habitat as nursery by these fishes makes them susceptible to coastal pollution impacts and puts their adult fisheries at risk to coastal degradation and development.

Decline in haddock abundance in Passamaquoddy Bay since 1965 coincides with increased numbers of cod. While previous studies indicate little interaction between these two species (Tyler 1972; Jones 1978), competition between cod and haddock may be responsible for the continued

low abundance of haddock in Passamaquoddy Bay.

In the Bay of Fundy region fish assemblages are segregated according to habitat and, although fish movement is influenced by seasonal climatic regime, assemblages are cohesive through time. In summer, fishes were assembled, and exploited the available resources, as members of (1) estuarine; (2) beach; (3) offshore, hard-bottom; (4) offshore, soft-bottom and (5) migratory pelagic assemblages. With winter, movement of species and/or age groups resulted in different seasonal assemblages in each habitat but major groupings remained essentially intact and replaced each other seaward. The reverse movement occurred in spring. A large portion of benthic and pelagic components occurring at the offshore, hard-bottom habitat were migratory. In contrast, the offshore soft-bottom assemblage was more sedentary. More stable water temperature at the Bay of Fundy, soft-bottom site, and the greater seasonal stability of invertebrate food resource production in this type of habitat (Wildish and Dadswell - in press) may also be important. The dynamic nature of the hard-bottom community, particularly among commercially valuable species, emphasizes the need for well designed seasonal sampling programs in order to properly assess the occurrence of species and abundance of fish stocks in a local area.

ACKNOWLEDGEMENTS

We thank Captain Tom Allen and Floyd Johnson, crew of the PANDALUS II for their help. Bill McMullon and Frank Cunningham prepared the figures and Brenda Fawkes and Yvonne Pepper typed the manuscript. J.S. Scott, W.B. Scott, D. Markle and D.J. Scarratt reviewed the manuscript. Thanks also to many of the staff at the Huntsman Marine Laboratory. The work done by J.S. Macdonald was in partial fulfilment of Ph.D. studies supported by NSERC operating and strategic grants to Dr. R.H. Green.

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APPENDIX II

Rates of Digestion of Different Prey in Atlantic Cod (Gadus morhua),

Ocean Pout (Macrozoarces americanus),

Winter Flounder (Pseudopleuronectes americanus), and

and American Plaice (Hippoglossoides platessoides)

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MACDONALD, J.S., K.G. WAIWOOD, AND R.H. GREEN. 1982.

Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus), and American plaice (Hippoglossoides platessoides).

Can. J. Fish. Aquat. Sci. 39: 651-659.

INTRODUCTION

Variation in the digestion pattern of different prey is an important variable in an evaluation of the diet composition, food preference, or consumption rate of wild fish. Estimates of daily ration based on gastric evacuation models require relatively accurate estimates of the rate of stomach emptying which is influenced by many factors, including prey type (reviewed by Windell 1978; Conover 1978). Unfortunately, information about prey-specific variation in digestion patterns is restricted to few predator-prey combinations, and many of these involve non-preferred or processed (eg. dissected or frozen) prey items.

Evaluation of diet composition based on the percentage occurrence of prey in the stomach may be biased by differential rates of prey digestion (Hess and Rainwater 1939; Cailliet 1976; Gaare et al 1977; Berg 1979). Conversion factors have been calculated to compensate for this.

This study was done to investigate the digestion pattern of three common prey (*Yoldia sapotilla*, *Tmetonyx cicada*, and *Nephtys incisa*) in four species of syntopic benthic fish (ocean pout (*Macrozoarces americanus*), Atlantic cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*)). Rate of elimination from the stomach was investigated by visual indexing of digestion stage to calculate the length of time the prey remained identifiable to species and the relationship between prey weight and digestion time.

MATERIALS AND METHODS

Ocean pout (40.5-66 cm), Atlantic cod (32.5-45 cm), winter flounder (21.5-37.1 cm), and American plaice (16.8-31.8 cm) were collected by otter trawl from Passamaquoddy Bay during April-May 1980. They were transported to the St. Andrews Biological Station and held in 300-L-circular holding tanks which were supplied with a constant flow of salt water. The fish were held at ambient temperature (5-10°C) and salinities (28-31 /oo) for a minimum of 3 wk before being introduced to experimental tanks. They were fed a pelleted diet consisting of squid (26%), winter flounder (26%), rock crab (12%), herring meal (29%), herring oil (6%), vitamin package (0.75%), and sodium carboxymethyl cellulose (0.25%). Injured fishes or fishes that did not feed were excluded from subsequent experiments. At the beginning of each experiment, two fish of one species were placed in each of eleven 120-L-circular tanks and kept there for 9 d. A natural photoperiod was adopted and the water temperature was maintained at $6.25 \pm 0.3^\circ\text{C}$ during the experiment. Fishes were given the above diet once daily (09:00-10:00) and were used experimentally once they fed voluntarily.

On the 1st day of a trial, each fish was fed one or more pellets containing one or more of the following prey species: Y. sapotilla (Bivalvia, 0.5-2 cm), T. cicada (Amphipoda, 0.5-1.0 cm), and N. incisa (Polychaeta, 2.0-8.0 cm). Care was taken to incorporate the entire, uncrushed, prey item into the pellet. These prey were collected from Passamaquoddy Bay with a 1.3-m-scallop dredge lined with fine mesh. The food items were frozen and stored at -20°C . The number of prey placed in each pellet varied as a result of differences in the maximum pellet size

that each species could consume. Ocean pout with relatively large mouths could eat large pellets containing three prey species, whereas winter flounder were fed several smaller pellets containing one or two prey items. The prey composition of each pellet consumed by each fish was always recorded. Meal size as a percentage of body weight ranged from 0.5 to 3.3 for ocean pout, 0.96 to 2.14 for cod, 0.66 to 3.10 for plaice, and 0.64 to 3.19 for winter flounder. Five or six fish of each species (92 total) were killed at the following sampling times: 5, 12, 20, and 30 h after feeding. The fish remaining after 24 h were fed prepared food without the prey items, at the normal feeding time.

The alimentary tract was removed from each sampled fish and immediately placed in 5% Formalin saturated with Borax. Gut contents were exposed and prey remains were removed within 48 h of collection. The following data were recorded:

- (1) position of each prey within the gut (stomach or intestine),
- (2) condition of each prey using a four-category visual index,
- (3) prey length for estimating initial prey weight.

Prey remains were placed in aluminum weighing pans and dried to constant weight at 75°C.

In a separate experiment, the effect that frozen prey had on digestion rate was determined by feeding pellets containing freshly killed or live specimens of N. incisa and Y. sapotilla to ocean pout and cod. The fishes were killed 5 and 20 h later. One-way ANOVA was used to test the effect of freezing on the indices of digestion and on the rate of weight loss of the prey with time. Only Y. sapotilla found in cod killed at 5 h showed significantly lower indices of digestion for the fresh as opposed to the frozen specimen ($P < 0.05$). However, both frozen and unfrozen Y.

sapotilla could be keyed to species up to 30 h after feeding. The freezing effect was only significant at the early index categories where recognizability was not a problem. Ocean pout killed at 20 h digested the frozen Y. sapotilla significantly faster than the fresh ones ($P < 0.05$). Previously frozen N. incisa, fed to the cod killed at 20 h after feeding and to the ocean pout killed at 5 h after feeding, also lost weight significantly faster than did fresh ones ($P < 0.05$; ANOVA after arcsine transformation of the data). There were no significant differences between the fresh and frozen prey of any of the other eight predator-prey vs. time combinations. Because freezing has a similar but limited effect on both prey items tested, we believe that our results are valid.

RESULTS

Evacuation rates as described by average indices of digestion

Each category in Table 1 describes a stage in the digestion of a specific taxonomic feature which is required to key the animal to species (Gosner 1971). Digestion of N. incisa followed the same pattern in all predators. Similarly, the digestion pattern of T. cicada differed among predators only in that the viscera was digested and the appendages became detached earlier in the plaice compared with the other predators. Two digestion patterns occurred for Y. sapotilla. Ocean pout digested the viscera with little damage to the shell. The cleared valves could be seen in the rectum. On the other hand, cod digested the entire shell in the stomach, rarely letting any of it pass to the intestine in a recogni-

TABLE II - 1. Indices describing process of digestion from fresh to
unrecognizable for each predator-prey combination.

	<u>Y. sapotilla</u>	<u>T. cicada</u>	<u>N. incisa</u>	Index No.
Pout, cod, flounder, & plaice	Shell fresh, foot and viscera undigested, shell surface unscratched	Fresh animal, color of body and eye intact	Fresh animal, color and setae - distinct	1
Pout, flounder	Foot and mantle digested	Color of body and eyes paled	Setae attached to body but not in orderly rows - disorganized	2
Cod, plaice	Shell surface becoming scratched and opaque	Color of body and eyes paled	Setae attached to body but not in orderly rows - disorganized	2
Pout	Viscera digested	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
Cod	Foot and mantle digested	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
WF	Shell surface becoming scratched and opaque	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
Plaice	Foot and mantle digested	Viscera digested from carapace, carapace brown and clean	Viscera cleared from body leaving clear integument holding patches of setae	3
Pout	Shell broken to unrecognizability	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
Cod	Shell totally opaque, very thin	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
WF	All viscera digested	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
Plaice	All viscera digested, shell very thin, often with holes and ragged edges	Animals broken up	Clumps of setae attached to remnants of integument	4

zable state. Digestion of Y. sapotilla by winter flounder and plaice was similar to that by cod as it involved the decay of the entire shell. However, unlike the cod, the valves were often passed to the intestine before decaying completely.

The average index of digestion at each sacrifice time described the progression towards unidentifiability of the three prey species in each of the four predators (Fig.1). In all four predators N. incisa was digested most rapidly to an unrecognizable state. This occurred after 20 h in the plaice and before 5 h in the three other predators. Yoldia sapotilla was identifiable at least 30 h after consumption in all four predators. Tmetonyx cicada was digested at an intermediate rate in all predators except the cod, where it could be identified 30 h after feeding.

The rate of passage of prey from stomach to intestine varied among predator and prey species (Fig.1). All prey left the ocean pout stomach quickly and in a relatively undigested condition. For example, 50% (by numbers) of Y. sapotilla, T. cicada, and N. incisa were evacuated from the stomach within 15, 8, and 7 h, respectively. For cod, the corresponding values were 30 h for Y. sapotilla, and 17 h for T. cicada and N. incisa. Food left the stomach of plaice and winter flounder at a rate similar to that observed for ocean pout with the exception of the slower passage of N. incisa (Fig.1). There was a tendency for Y. sapotilla to remain in the stomach longer than the other two prey. This was found in all predators but was most noticeable in cod and ocean pout. (Fig.1).

Generally, the rate of passage to the intestine was the most important factor affecting identifiability for Y. sapotilla and T. cicada. Nephtys

FIGURE II - 1. Average index of digestion related to time after feeding for each of the three prey types digested by each of the four predator species. The horizontal lines represent the value of the index beyond which Yoldia, Tmetonyx, and Nephtys, respectively, cannot be identified to species. The vertical lines are the times at which 50% of each prey passes from the stomach to the intestine in each predator. Numbers in parentheses refer to the number of prey recovered at each time.

Incisa tended to decay in the stomach before it passed to the intestine.

Evacuation rates as described by percentage weight loss with time

The length vs. dry weight measurements of the three species of prey were best described by the power function (Table 2). The mean ratio of dry weight of partially digested prey to their initial dry weight (back-calculated from the power functions) decreases with time for all predator-prey combinations (Fig.2). Linear, logarithmic, and logistic models applied to the data emphasize this (Fig.3). Two-parameter models with no specified Y-intercept were originally fitted. Subsequently, better estimates of evacuation rate were found by fitting one-parameter models with percentage recovery at time zero set at 100. These were linear, $Y = 100 - bt$; logarithmic, $Y = 100e^{-bt}$; and the logistic, $Y = \frac{100}{1 + e^{-b(t - t_0)}}$ 99.9

$$Y = \frac{100}{1 + e^{-b(t - t_0)}}$$

Deviations of Y-observed from Y-predicted, as back-calculated from the models, were tested against a null hypothesis of the linear equation passing through 100%. This gave a more meaningful test than with a null hypothesis of zero slope (Table 3). Negative values for all predator-prey combinations, except for N. incisa in the ocean pout, suggest that the logistic curve gave a poorer fit than the null hypothesis (the linear model). Similarly the logarithmic model gives negative or low positive r^2 values when fitted to the Y. sapotilla decay curves of the four predators. Possibly in these situations, the linear model gives at least as good a fit as the logarithmic model. In all other predator-prey

TABLE II - 2. Relationships used to convert length measurements (L in mm) of partially digested prey into original prey dry weight (W in g).

Prey	Measurement	Power function	Multiple correlation coefficient (r^2)
<u>Yoldia sapotilla</u>	Length of valve	$W = 0.03101(L)^{2.821}$	0.99
<u>Tmetonyx cicada</u>	Length of notch in last pleon.	$W = 0.00991(L)^{2.77}$	0.87
<u>Nephtys incisa</u>	Length of body	$W = 0.00130(L)^{2.2628}$	0.81

FIGURE II - 2. Relation between percent by weight of prey recovered and time after feeding, for different predator-prey combinations. Lines represent 95% confidence intervals about the mean.

TABLE II - 3. Squared multiple correlation coefficients (r^2) representing unexplained deviations of the actual Y value (percentage of prey weight recovered) divided by the total deviations from the corresponding value representing the null hypothesis, all subtracted from one. In this case, the null hypothesis is the linear model passing through a Y-intercept of 100%. Negative values result where the fit is poorer than the linear model. Positive values result when the fit is better.

	Log	Logistic
Ocean pout		
Yoldia	-2.815	-59.520
<u>Tmetonyx</u>	0.886	-2.240
<u>Nephtys</u>	0.880	0.920
Cod		
Yoldia	0.445	-4.060
<u>Tmetonyx</u>	0.245	-1.320
<u>Nephtys</u>	0.500	-0.486
Winter flounder		
Yoldia	-0.066	-2.070
<u>Tmetonyx</u>	0.814	-0.681
<u>Nephtys</u>	0.594	0.707
Plaice		
Yoldia	0.153	-1.150
<u>Tmetonyx</u>	0.595	-0.852
<u>Nephtys</u>	0.478	0.525

situations the logarithmic model gives a higher r^2 .

The r^2 values for the data from all predator-prey combinations, for each model, were tested using a paired t-test after they were transformed by the ranking method described by Fisher and Yates (1973). The only significant difference in fit was between the logarithmic and logistic models, with the logarithmic model giving the best fit ($P < 0.05$).

The slopes from the logarithmic model fitted to each of the 12 predator-prey evacuation curves (Fig. 3) were compared using a two-way ANOVA. There was no significant predator effect, but there was significant difference between the evacuation rates of Y. sapotilla and the other two prey species ($P < 0.05$). When slope values of all four predators are combined for each prey, the 95% confidence limits express the difference in evacuation rates between Y. sapotilla and the combined rates of N. incisa and T. cicada (Fig. 4).

DISCUSSION

Evacuation rates as described by average indices of digestion

Ocean pout and cod have different patterns of food passage from the stomach. These patterns can be related to morphological differences in their alimentary tracts. The heavily muscularized cod stomach (Tyler 1973) breaks whole food and digests it before it is passed to the intestine. Ocean pout stomachs appear to be less muscularized and are primarily for storage. Molluscan valves and chitin are partially broken by the flattened pharyngeal teeth, are passed through the pyloric sphincter sooner, and are less digested than in cod.

FIGURE II - 3. Linear, logarithmic, and logistic models fitted to the data presented in Fig. 2 (the r^2 values are given in Table 3).

FIGURE II - 4. Evacuation rates, using the logarithmic model, for Yoldia sapotilla and the combined decay of Tmetonyx cicada and Nephtys incisa for all fish. Shaded areas represent 95% confidence limits of the model. The vertical lines to the 5.1- and 17.6-h marks show the time taken to achieve 50% evacuation by the N. incisa-T. cicada combination and Y. sapotilla, respectively.

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The large-diameter intestine of the pout accepts larger and less-digested objects from the stomach than in the other species of fish examined. Experiments with plaice (Edwards 1971), cottids (Western 1971), and trout (Kionka and Windell 1972) suggest that narrow sphincters and intestines restrict the passage of large undigested objects from the stomach. This may also explain why large indigestible objects such as Y. sapotilla were expelled slower than other prey. A shorter, larger-diameter intestine may be an adaptation to retain large food longer and to allow more time for absorption. Longer retention in many herbivores and polychaete feeders results from increased intestine length (DeGroot 1971; Tyler 1973).

Increased absorptive area is achieved with pyloric ceca in the gadids and the pleuronectids. The thickened wall of the pout intestine may act in the same way in the absence of pyloric ceca. If larger objects pass into the pout intestine, pyloric ceca may be too constrictive to work efficiently.

Differences in rates of food passage among the four predators accounted for the major differences in decay pattern of the prey. From indices of digestion (Table 1), it appears that Y. sapotilla valves in cod and pleuronectids were retained in the stomach, having been broken more than those in pout. The stomach is more acidic than the intestine (Wilson 1972; Western 1971) and will digest a shell given sufficient time. Even though the gadids and pleuronectids appear to consume bivalves in nature (Fråme 1974; Arntz 1974, 1977), this long retention time may make them a suboptimal food. Any factor that slows evacuation rates slows food uptake rates and therefore prevents maximum growth (Vahl 1979). Yoldia sapotilla was not reported as a major food item for winter

flounder or cod by Tyler (1972). Cod and pleuronectids have been observed by us and by Bishop and Odense (1966) to shake mollusks from their shells.

The change in physical condition of various food items as digestion proceeds has been reported (Hess and Rainwater 1939; Hunt 1960; Western 1971; Tyler 1973, Jones 1974). Generally, their observations agree with our results. The greater the percentage of chitin or shell in a food item, the longer it remains recognizable, i.e. bivalves were digested slower than amphipods which were digested slower than polychaetes. Many polychaetes have cuticles that resist digestion (Tyler 1973). Although many empty N. incisa skins were found in the stomachs, they do not have sufficient taxonomic detail to permit identification to the species level.

Hess and Rainwater (1939) demonstrated that diet analysis can be biased by the differential digestion rate of prey. Their method of calculating factors to correct for different digestion rates was modified to include correction for different food passage rates of the prey (Table 4). We found that many prey items passed from the stomach before digestion rendered them unrecognizable (Fig.1). The length of time each prey species could be recognized in the stomach of each predator species was divided into the time required for the slowest prey item (Y. sapotilla) to disappear from the stomach. The actual number of prey species found in the stomach can be multiplied by the correction factor to give an unbiased estimate of diet composition.

TABLE II - 4. Correction factors for comparing the number of each of the three prey species within a single species of predator based on differential rates of evacuation or digestion (whichever causes the prey to disappear the fastest). Similarly, values in parentheses compare number of any one of the prey species among the four predators. Multiplication of the number of each prey observed in a particular predator's stomach by their correction factors will give comparable values of numbers of each species of prey eaten between prey species or between predator species.

	Prey		
	<u>Y. sapotilla</u>	<u>T. cicada</u>	<u>N. incisa</u>
Ocean pout	1.00 (2.14)	1.75 (2.06)	3.10 (4.33)
Cod	1.00 (1.00)	1.82 (1.00)	6.70 (4.33)
Winter flounder	1.00 (1.82)	2.20 (2.06)	3.67 (4.33)
Plaice	1.00 (1.50)	5.63 (4.71)	1.08 (1.00)

Evacuation rates as described by percentage of original prey weight, lost over time

Percentage weight loss of food items over time is often used to describe digestion and to predict daily rations for fish (reviewed by Elliott and Persson 1978). Some researchers found no difference in depletion rate among different prey (e.g. Persson (1979) using zooplankton, amphipods, and chironomids; Windell (1966) using the natural prey of Lepomis macrochirus). Others, such as Jones (1974) using Nereis, Nephtys, and Crangon in cod and haddock, and Kitchell and Windell (1968) using damselfly naiads and mealworm larvae in pumpkinseed sunfish, found that prey type did affect rates of food depletion.

Many models have been fitted to evacuation data (Elliott and Persson 1978; Fänge and Grove 1979). There is difficulty in choosing the best one because several biological forces shape evacuation rate curves. First, a lag occurs when the food enters the stomach (Y. sapotilla in ocean pout and cod, Fig. 2). Enzyme reactions are exponential and therefore start slowly (Jennings 1972). In experiments where a starvation period precedes the experiment, the digestive juices are not present when the food enters the stomach (Elliott 1972). The lag time also depends on the resistance of the food's surface and on the ratio of the food's surface area to volume (Windell 1967). Second, there is a period after the lag time when the digestive rate is maximal. The slope and shape of the line at this point is at least partially controlled by fat content of the food (Quigley and Meschan 1941; Windell 1967). Third, the rate of evacuation will level off at a point determined by the percentage of indigestible material within the food, e.g. chitin (Battle

1935). Even when data are fitted to linear models, leveling off is often observed after 80 or 90% of the material is digested (Fig. 3; Daan 1973). Finally, it has not been considered that food may enter the intestine before it is fully digested. The stomach may act as a holding facility, emptying material to the intestine at a constant rate as intestinal space permits (e.g. ocean pout). Alternatively, the stomach may retain food until it has sufficiently mixed or broken down before passing it to the intestine (e.g. cod). One model may not fit all digestive relationships well, given the many fish species and the many foods eaten.

The linear relation fits as well or better than the other two models when the prey is composed of a high degree of digestion-resistant material as in Y. sapotilla (Table 3). Despite its inherent ability to accommodate lag time, a steep rate of descent, and a leveling off with time, the logistic curve poorly described the gastric process; in some cases, lag times were not long enough and food items did not decay close enough to 0% to accept such a model (Fig. 3, Table 3). The exponential curve seemed to give a good fit for the faster digesting prey where there was less delay in commencement of digestion when the food entered the stomach (Table 3). For this reason, it successfully fitted data where prepared food or dissected natural food was used (Tyler 1970; Elliott 1972; Jones 1974). Cutting natural food, such as shrimp or fish, exposes the centre of the food to the action of digestive enzymes and could potentially increase the rate of digestion.

The results of the visual index and weight loss over time methods of evaluating digestion time partially support each other. The visual method indicates differences between all prey and some predators. The

weight loss method shows differences between Y. sapotilla and the other two prey only (Fig. 4). However, the visual index method was not comparable to the weight-loss technique. The visual index is qualitative and true confidence limits cannot be applied. Also, digestion or weight loss of a prey item need not have any bearing on recognizability if the digestion has occurred to a portion of the animal that is not required to identify it.

The perception of the diet composition and consumption rates that fish have in the natural environment, and our models for describing the digestion processes, are affected by variability in the digestion characteristics of each prey species. Analysis of consumption rates requires that the rate of weight loss by the prey be applied to the model which best describes the digestion process.

ACKNOWLEDGEMENTS

We are grateful to many of the staff at the St. Andrews Biological Station and the Huntsman Marine Laboratory, including Dr. M.J. Dadswell and Mr. R. Gowan for their assistance during this study. Thanks also go to Dr. D. Ankney and Dr. R.W. Langton for their critical review of this paper. Ms. R. Garnett made numerous suggestions to improve the manuscript. Messrs. W. McMullon and C.F. Cunningham prepared the figures. The work done by J.S. Macdonald was in partial fulfillment of Ph.D. studies supported by NSERC operating and strategic grants to R.H. Green.

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APPENDIX III

Feeding Chronology and Daily Ration Calculations
for Winter Flounder (Pseudopleuronectes americanus),
Plaice (Hippoglossoides platessoides), Cod (Gadus morhua),
and Ocean Pout (Macrozoarces americanus) with Consideration
of Prey Type.

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INTRODUCTION

Several researchers have emphasized the importance of feeding chronology (time of daily feeding activity) and daily ration studies in the examination of interspecific competition and predator-prey interaction studies (Darnell and Meierotto 1962; Keast and Welsh, 1968; Doble and Eggers 1979). Recently there has been increased interest in daily feeding times and ration of northwest Atlantic fishes.

Feeding chronology of winter flounder was observed by Olla et al (1969), winter flounder and cod by Hacunda (1980), and ocean pout by Edwards and Bowman (1979). Unfortunately, few statistical techniques have been used to analyze feeding periodicity data and it has never been expressed in terms of ration (amount consumed corrected for amount evacuated).

Ration estimates of haddock have been made by Jones (1978), and of winter flounder by Tyler and Dunn (1976) and Huebner and Langton (1982) in laboratory studies. Daily rations have not been calculated for any other northwestern Atlantic fishes. Estimates have not considered the evacuation rate differences that occur among prey types (Macdonald et al 1982). The daily ration of slow evacuating prey (eg. bivalves) will be over estimated and the ration of fast evacuating prey (eg. polychaetes and amphipods) will be under estimated. If the evacuation rates do not differ among all predator species considered in the study (as is the case in this study) rations calculated for predators that consume a large portion of slow evacuating prey will be over estimated.

This field study investigates the feeding chronology of 4 syntopic species of demersal fish (ocean pout - Macrozoarces americanus, winter

flounder - Pseudopleuronectes americanus, American plaice - Hippoglossoides platessoides and cod - Gadus morhua) using 3 methods.

a) Mean volume of food found in the stomachs of each species of fish collected at 4 times during a 24h day are compared using analysis of covariance (ANCOVA) where total fish lengths was the covariate. b) Estimates of food volume consumed between each collection time are made using Elliott and Persson's (1978) ration model with evacuation rates that are specific to prey type. c) Visual indices of digested prey condition (Macdonald et al 1982) are used to estimate the numbers of common prey species eaten during the sampling period. The last 2 methods also provide estimates of daily ration. The two ration estimates are compared by converting number of prey of each collection interval to volume of prey using estimates of average prey weight in the predator's stomachs, from unpublished data.

MATERIALS AND METHODS

The study was carried out in Passamaquoddy Bay, N.B., based on one 24h period of otter trawling on May 15, 1981. The study site was 30 fathoms (56 m) deep and had a bottom temperature during the collection period of $5.8 \pm 0.3^{\circ}\text{C}$. Four half-hour tows were made at 5 to 7h intervals at 1:00, 7:00, 14:00, and 20:00. There was no evidence of regurgitation of stomach contents during the collection.

Since fish size has an effect on food uptake rates and on rates of gastric evacuation, collections of each species were restricted to the commonest size class. The total lengths, mean weights and sample sizes were: ocean pout (Macrozoarces americanus) 42-56 cm, 560 gms, $n = 36$;

winter flounder (Pseudopleuronectes americanus) 27-34 cm, 370 gms, n = 40; American plaice (Hippoglossoides platessoides) 14-31 cm, 90 gms, n = 25; cod (Gadus morhua) 16-27 cm, 100 gms, n = 25.

On the boat, the fish were measured, weighed, and their stomachs and intestines were preserved separately in numbered jars of 10% formalin saturated with borax. Gut contents were exposed and prey remains were removed within 48h of collection. The following data were recorded: 1) volume of stomach contents, including mucus and all prey remains were measured as water displaced in a graduated cylinder after excess water was blotted from sample (empty stomachs were included when estimating mean volume of stomach contents); 2) prey were identified to the lowest possible taxonomic level; 3) condition of most prey items in the stomachs and intestines were noted using a four category visual index proposed by Macdonald et al (1982).

Times of daily peak feeding activity were expressed in three ways. Numbers of common prey items eaten during each collection time were estimated using indices of digestion. The indices describe stages in the digestion of specific taxonomic features which are required to key prey to species. At temperatures close to 5.5°C, an index value can be used to estimate the length of time each prey item has been in the stomach and thus the time of day it was consumed. The indices were calculated for Yoldia sapotilla (Bivalvia), Nephtys incisa (Polychaeta), and all species of amphipods. This assumes all amphipod species follow the digestion patterns described by Macdonald et al (1982) for Tmetonyx cicada. The bivalves consisted of 98% Y. sapotilla, the polychaetes 60% N. incisa. Ninety-seven percent of the total diet of all fish was described by indices.

A second estimate of feeding periodicity was made by plotting mean food volume consumed during each sampling interval by each predator species vs time of day. A two-way ANCOVA was used to examine the consumption of food with respect to predator species and time effects controlling for the covariate fish length. In this way, variation in volume due to larger fish having larger stomachs was examined and corrected. Tests for interaction between main effects investigate the hypothesis that fish species feed at different times of day. When significant interaction occurs, main effects can only be tested by partitioning the data matrix by predator species and doing four one-way ANCOVA's. Data were analysed using the MANOVA procedure in SPSS on the University of Western Ontario's CYBER 170.

The third estimate of feeding periodicity involved the calculation of volume of food consumed over each collection interval after the food evacuation rate is taken into consideration (food ration). Food evacuation in the stomach of the four species of fish was described by an exponential decay function with a rate (R) of -0.03865 for bivalves and -0.1346 for the combined rates of amphipods and polychaetes (Macdonald, unpublished data; for the same fish and prey species used by Macdonald et al (1982) found no significant evacuation rate differences among predators or between amphipods and polychaetes). The mean of the two rates agrees closely with the winter flounder evacuation rates described by Huebner (1982). Huebner's study used a diet of squid and was carried out at approximately the same temperature. When evacuation occurs exponentially and feeding is constant, the best model to calculate the volume (C_t) of each of the two prey categories consumed over a given time (t) is described as: $C_t = (S_t - S_0 e^{-Rt}) R_t / (1 - e^{-Rt})$ by Eggers (1977),

Elliott and Persson (1978), Cochran (1979), and Jobling (1981). S and S are mean relative stomach volumes at the end and beginning of the interval between catches. The equation corrects for food volume loss due to digestion. Estimates were made for the two prey categories over each of the four sampling intervals for each predator species.

Daily ration estimates for each predator species were calculated by combining volumes of each prey type eaten at each sampling interval. They are expressed as volume per fish per day and as volume as a percent of body weight per day. Estimates of volume of food consumed calculated in this manner (Vol/fish/day) were compared to estimates of number of prey consumed daily after numbers were converted to volumes by multiplying by the average weight of each prey species. Volume estimates (% body wt/day) were also compared to weight estimates of winter flounder daily ration made by Tyler and Dunn (1976) and Huebner and Langton (1982).

RESULTS

There are differences in the time of day each fish species consumes the maximum volume of food (significant fish species x time interactions - $P < 0.05$). Three of the predators contained maximum food volumes in early evening (20:00 - Figure 1; $P < 0.05$ after partitioning by fish species to do four one-way ANOVAs). A fourth predator, cod, displays no significant feeding periodicity ($P > 0.05$). The period of most intense feeding, occurs between 7:00 and 14:00 for winter flounder and ocean pout. This is the period when ration (volume corrected for evacuation rate) is highest (Fig. 2). Plaice tended to have a higher ration later in the day. The winter flounder was the only predator species to show

FIGURE III - 1. Mean volume of food in the stomachs of each predator species at each of the four collection times (vertical bars are 95% confidence limits on the means). The horizontal axis is shaded to show times of darkness. Probabilities that collection time has an effect on food volume are also presented (N/S - not significant).

FIGURE III - 2. Amount of food consumed per gram of fish (ration) per hour vs time of day. The horizontal axis is shaded to show times of darkness. Bivalve rations are separated from amphipod and polychaetes because their evacuation rates differ. Negative values have no biological meaning. They are probably the result of the large number of empty stomachs collected during the evening sampling.

an increase in the volume of food consumed with increasing fish size (covariate $P < 0.10$).

The greatest number of prey were consumed at midday by winter flounder, at midday, dawn and dusk by ocean pout, and later in the day by plaice (Fig. 3). Ocean pout and winter flounder consume a greater number of prey per fish than plaice or cod. Yoldia sapotilla was the primary food of ocean pout and plaice while amphipods were heavily utilized by winter flounder. Digestive indices could not be calculated for many of the prey consumed by cod (eg. Pandalus sp.). This may be the cause of the gaps and the apparent feeding periodicity for cod on Fig. 3.

The type of food consumed by each predator species did not change among collection times (Fig. 2, 3). The slower evacuating prey species (Y. sapotilla) remain identifiable longer and, therefore, make up a larger proportion of the prey eaten the day before the collection (Fig. 3).

Daily ration estimates indicate that both winter flounder and ocean pout consume more food per fish than the other predators. However, when volume is expressed as a percentage of body weight per day (ie. corrected for interspecific size differences), winter flounder and cod have the highest consumption rate followed by ocean pout and plaice (Table 1; Fig. 2). A large portion of the ocean pout daily ration is amphipods and polychaetes despite the fact that bivalves are the major component of their stomach contents (Table 1). The negative ration values in the late evening for ocean pout and plaice have no biological meaning (Fig. 2). Food evacuation rate alone does not account for the large decrease in volume from the preceding collection. There were a large number of empty stomachs encountered in the late evening and therefore food volume

TABLE III - 1. Three types of daily ration estimates, and percent composition, of each prey type consumed by each predator species. Daily ration as number of prey per day is calculated from Figure 3. Daily rations in volume per fish per day are calculated in two ways: (1) by multiplying number of each prey type per day times the average volume of one item and (2) from Elliott and Persson's model-figure 2. Daily ration is also presented as a percentage of body weight to allow comparisons with literature values.

Predator	Prey Type	% of Stomach Composition	DAILY RATION			
			No. of Prey/Day	mL/fish/day (1)	mL/fish/day (2)	% body wt./day
Winter Flounder	Bivalvia	24	1.8	1.08	.093	.025
	Polychaeta	15	1.1			
	Amphipoda	61	4.6	.15	6.01	1.62
	Total		7.5	1.23	6.11	1.65
Ocean Pout	Bivalvia	95	37.8	1.58	2.09	.37
	Polychaeta	3	1.0			
	Amphipoda	2	.9	.12	4.91	.88
	Total		39.7	1.70	7.00	1.25
Cod	Bivalvia	0	-	-	.0047	.0047
	Polychaeta	0	-	-		
	Amphipoda	100	2.2	.02	1.66	1.66
	Total		2.2	.02	1.66	1.66
Plaice	Bivalvia	77	2.0	.08	.024	.027
	Polychaeta	4	.1			
	Amphipoda	19	.5	.015	.6	.67
	Total		2.6	.095	.62	.69

FIGURE III - 3. Plot of number of prey eaten per fish vs time of day consumed (times of darkness are shaded). Consumption time was estimated using state-of-digestion indices.

estimates are low. Possibly larger sample sizes are required to reduce the chance of getting large numbers of fish with empty stomachs.

DISCUSSION

Feeding Periodicity

Two basic problems often face researchers when analyzing feeding periodicity studies. Sample size often differs among collection times and larger fish eat more food than smaller fish causing fish size to be confounded with the effect time has on volume (Diana 1979; Edwards and Bowman 1979). Unequal sample sizes can be dealt with by choosing among various weighted ANOVAs or regressions in many statistical computer packages followed by plots of mean measures of amount consumed at each collection time (Windell 1978). Correction for fish size variation has been treated many ways. Some researchers choose to avoid this problem by stratifying the fish into sufficiently small length groups such that the length effect is insignificant (Doble and Eggers 1978; Windell 1978). This will work when sample sizes are large. All size categories can be pooled if analysis shows length effect to be insignificant.

Others ignore the problem altogether by plotting a food quantity measure from all sizes of fish vs collection time (Najim et al. 1977). This method becomes less acceptable with increasing fish size variation. Catfish collected by Najim et al (1977) range from 105-185 mm. Volume of food required to fill the stomach probably changes within this range.

The most common length correction method involves the calculation of a ratio of stomach quantity (volume, number, or weight) to some measure

of fish size. Windell (1968) and Hureau (in Berg 1979) have developed "fullness indices" that are food weight divided by fish weight. Keast and Webb (1968), Foltz and Norden (1977), Clarke (1978), Nakashima and Leggett (1978), Cordes and Page (1979), Hacunda (1980), Godin (1981) and others have plotted a fullness index, or some modification of it vs collection time to estimate peak feeding activity. Edwards and Bowman (1979) and Bowman and Bowman (1980) use the ratio of stomach quantity to intestinal quantity (S/I ratio) as a means of estimating feeding periodicity for some northwestern Atlantic fish, including the ocean pout. The S/I ratio is plotted for each sampled fish at different times of day. Unfortunately this ratio will be biased if, as in the ocean pout, the size proportion between stomach and intestine changes as the fish grows (Edwards and Bowman 1979). Additionally, it does not consider the differences in food passage rates from stomach to intestine that have been shown to occur among fish species (Macdonald et al 1982). The ocean pout passes food to the intestine faster than other species. A large amount of food in the intestine in the afternoon may have been consumed during the morning, not during the night as Edwards and Bowman concluded. Ocean pout in Passamaquoddy Bay are diurnal feeders with the greatest activity at dawn (Fig. 1).

Green (1979) has reviewed many of the problems associated with using two variables to create a ratio index. Ratios tend to increase the variability of the original variables, bias the estimation of the true mean of the ratio, lead to nonnormal distributions and obscure intervariable relationships (Sokal and Rohlf 1973). While the results of many of the feeding chronology studies that use ratio variables are valid, there are better ways of approaching this problem, particularly if

one intends to use statistical analyses. For instance, this study used a two-way ANCOVA to test the main effects (time and fish species) with fish length as a covariate. Had the size range of fish in this study been larger, the covariate would have probably been significant for more of the predator species. Interaction between the main effects indicates different times of peak feeding among the predator species (Fig. 1).

When evacuation rates are available the information from Figure 1 can be used to calculate amount of food consumed at different times of day (Fig. 2). This presents time of most intense feeding rather than time when food volume is greatest. Another advantage to this method is that it allows calculation of daily ration of each predator species. (Further discussion in the next section).

Many researchers have found a variety of flatfish species to depend on light for feeding (eg. Percy (1962), Olla et al (1969), and Hacunda (1980) using winter flounder and Olla et al (1972) using summer flounder (Paralichthys dentatus)). Others such as Tyler (1971) using winter flounder and Gibson (1980) using plaice (Pleuronectes platessa) describe patterns of movement and feeding that depend on the tidal rhythm. They do not mention the effects of interaction between tidal rhythm and daylight on feeding behaviour. Brawn (1969) has described methods by which cod can capture food during day (sight) or night (taste). This supports the findings of this study and Hacunda's (1980) where no distinct diurnal pattern is seen. Different feeding times among fish species may serve to reduce interspecific competition. Future studies will be done at different times of year to see if feeding patterns change with different seasonal conditions. However, Doble and Eggers (1978) found no seasonal effect with sockeye salmon.

The digested condition of prey has been used previously to estimate consumption time (Darnell and Meierotto 1962; Olla et al 1969; Diana 1979). Feeding periodicity calculated using digestion indices considers relative evacuation rates of different food items. If indices are known for a large percentage of the prey species in the diet, this method will also provide a rough estimate of daily ration in number of prey (Fig. 3, Table 1). However, there are three disadvantages: 1) digestion indices are difficult to calculate and hence have not been developed for many prey species; 2) their subjective nature prevents the use of confidence limits; 3) prey that have been consumed and evacuated within the sampling interval will not be tallied. This problem is reduced by considering both stomach and intestinal contents. (Further discussion in the next section).

Daily Ration

Published methods for quantifying daily ration depend on measurements of metabolic requirements (Gerking 1972; Jones 1978), cyclic changes in the quantity of food in the stomach (Keast and Welsh 1968; Nakashima and Leggett 1978) or knowledge of the digestive rate equation of the fish and prey being digested (Darnell and Meierotto 1962; Tyler and Dunn 1978; Doble and Eggers 1978; Elliott and Persson 1978; Huebner and Langton 1982). Metabolic methods and methods that depend on discontinuous feeding assume that all prey species show similar evacuation characteristics. Incorporating evacuation rate differences among prey into daily ration models provides a more exact estimate of daily consumption, and allows a quantitative description of predation

pressure exerted by a predator on specific prey types (Huebner and Langton 1982, Fig. 2). Figure 2 clearly shows that, despite a heavy utilization of Y. sapotilla by ocean pout (95% by number/fish) and a moderate utilization (24% by number/fish) by winter flounder (Table 1), the volume of bivalves consumed by both species is proportionally small. If the slow evacuating prey are not considered separately, they will be over emphasized in the results. Calculating daily rations based on prey type permits the researcher to consider the amount of each prey type utilized after evacuation rates have been corrected for. It also allows for a more accurate food ration estimate as prey composition changes.

Comparisons of daily ration estimates (mL/fish/day) between Figure 2 (Elliott and Persson's model, 1978) and Figure 3 (stage-of-digestion indices) show that over a 24h period only the slow evacuating prey species (bivalves) remain in the stomach long enough to assess accurately the ration from indices of digestion (Table 1). Most predators digest amphipods and polychaetes so rapidly that their numbers and therefore volumes are drastically underestimated. Indices of digestion should only be used to estimate ration over very short intervals (probably 5h). Indices of digestion are of more value to estimate time than rate of feeding (see previous section of the discussion).

The winter flounder daily ration estimate (1.65% body wt/day) was lower but similar to the estimates of Tyler and Dunn (2% for daily fed fish) and Huebner and Langton (1.8-2.4%) for laboratory studies at a similar temperature (Table 1). The Elliott and Persson (1978) model used has a tendency to underestimate amount of food consumed as length of time between sampling periods increases. Sample intervals will be minimized in the future.

Winter flounder and cod had higher daily rations (per gram of fish) of food that has higher caloric value than food of the other fish (Tyler 1973). This suggests that they have higher rates of growth or higher metabolic activities. Laboratory observations suggest that winter flounder and cod are more active than ocean pout. Plaice feed throughout the year and therefore require less per season. Future work should consider the effects season and bottom temperature have on daily ration so that a yearly ration can be calculated.

It is impossible to apply confidence limits or statistical tests to ration estimates collected from field data. Knowledge of stomach content quantity at the beginning and end of each collection interval for each fish is required to obtain an estimate of variance about the mean ration. Such information can be collected only by following the progress of individual fish in the laboratory.

Our perception of feeding periodicity and daily ration of fishes in the natural environment is affected by the variation in digestion rates among predator and prey species. Knowledge of the nature of this variation and the correct analysis techniques are required in the design of future studies on the interaction among fishes and their environment.

ACKNOWLEDGEMENTS

We are grateful to many of the staff at the St. Andrews Biological Station and the Huntsman Marine Laboratory, including Dr. M.J. Dadswell, Mr. D. Beattie and Ms. C. Carver for their assistance during this study. Thanks also to Dr. R.H. Green and Dr. G. Wells for their critical review of this paper. The work done by J.S. Macdonald was in partial fulfillment of Ph.D. studies supported by NSERC operating and strategic grants to Dr. R.H. Green.

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APPENDIX IV

Laboratory Observations of Feeding Behaviour
of the Ocean Pout (Macrozoarces americanus)
and Winter Flounder (Pseudopleuronectes americanus)

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INTRODUCTION

Attempts have recently been made to isolate some of the factors involved in the choice of food by fish, including descriptions of prey organisms available to the fish while they are feeding (Frame, 1976; Hacunda, 1980; Hyatt, 1979). However, prey availability is only one of the many factors involved in prey choice. Moore and Moore (1976) also cite search image development, escape response and degree of concealment of prey and, most significantly for the purposes of this paper, hunting efficiency of the fish. Tyler (1972) and Hyatt (1979) suggest that differences between predators in hunting efficiency for different prey may be responsible for resource division.

The feeding behaviour of many benthic fish is well documented. The foraging behaviour of cod has been studied by Brawn (1969), the gurnard, the dragonet and some flounders by Stevens (1930) and many other flatfish by Olla et al (1969, 1972), de Groot (1969, 1971) and Stickney et al (1973). However, with the exception of Brawn's work and field observations by Olla on the winter flounder, there is little published information about methods of foraging on natural prey by common fishes of the northwestern Atlantic.

Many diet studies have provided insight into food selection by benthic feeding fish in the northwestern Atlantic. Tyler (1971b, 1972) and the author (unpublished observations) have found that ocean pout (Macrozoarces americanus, Zoarcidae) eat large numbers of sedentary polychaetes (eg. Sternaspis scutata) and molluscs (eg., Yoldia sapotilla) from the environment. The winter flounder (Pseudopleuronectes americanus, Pleuronectidae) consumes fewer bivalves in favour of

polychaetes (eg., Nephtys incisa) and amphipods (eg., Casco bigelowi). In this paper the behaviour of the ocean pout and the winter flounder in searching, detection, capture and ingestion of prey was studied under a variety of laboratory conditions. The influence of feeding methods on the type of prey taken was considered.

MATERIALS AND METHODS

Feeding observations were made on nine winter flounders (18-35 cm total length, T.L.) and eight ocean pout (45-60 cm T.L.) that were collected in a shrimp trawl in the spring of 1980 in Passamaquoddy Bay, N.B., Canada. They were fed five prey species that were collected in a fine mesh-lined scallop dredge: the amphipod Casco bigelowi (.85 - 1.10 cm T.L.), the bivalve Yoldia sapotilla (.4 - .5 cm T.L.), the scaphopod Dentalium entale (1.5 - 3.0 cm T.L.) and the polychaetes Sternaspis scutata (.52 - 1.0 T.L.) and Nephtys incisa (4.3 - 6.5 cm T.L.; Table 1).

Fishes were kept together in a 2 x 5 x 2 m deep 20,000 L tank at the Huntsman Marine Laboratory Public Aquarium. Seven cm of fine sand covered the bottom of the tank. Several rocks, shells, logs and plants (Ascophyllum sp.) provided shelter for the fishes and the prey species. During a one month acclimation period fish were held at ambient temperatures (12°C) and salinities (28-31‰) and under a natural photoperiod (12L/12D). They fed on several species of mollusks and crustaceans that were present in the tank before the experiment started, and on a supplemented diet of sliced herring. No herring was fed to the fishes for a period of 72 h before the experiment commenced.

Three plastic pipes (15 cm x 1.5 m) were placed on end in the bottom

sediment of the study tank. They were attached to supports above the tank. One end of each pipe cleared the surface of the water, allowing different prey species to be introduced onto the substrate through each pipe. Several individuals of each prey species were placed in each pipe before each observation period. The prey were allowed to acclimate in the sand for 1 h before the pipes were removed. This presentation method permitted the prey items to assume natural positions in the habitat before being exposed to the predators.

Observations were made for a period of 1 h after removal of the pipes. This was repeated during the morning and afternoon for 6 consecutive days (12 h observation time). Times between first feeding response and successful consumption of the prey were recorded with a stopwatch. The positions of the pipes within the tank and therefore the positions where prey were presented were randomized to prevent the fish from developing a searching pattern. During the course of the experiment the fishes did not orient to the prey introduction pipes. When searching for prey the fishes divided their time among the many types of substrates available.

Both species of fish were also fed boluses of prepared food (7 mm to 14 mm in diameter) to assess the importance that movement of the food had on feeding response and handling methods. The prepared food consisted of 32% ground-up winter flounder, squid and crab, 53% herring meal, 12% herring oil, 3% vitamins and a binding agent. On seven occasions with each predator species, boluses were attached to the end of a long piece of fine wire and pulled slowly along the bottom of the tank. The responses of each fish were observed. The responses of all fishes as they fed on herring and prepared food dropped from the water surface was also observed.

To assess the sensory functions of the large lips of ocean pout, 60 histological cross sections, 7 microns thick, were taken from the ventral surface of the upper lips and dorsal surface of the lower lips of one fish. The sections were stained with Ehrlich's alum haematoxylin and Bowie's eosin, dehydrated in a technicon automatic tissue processor and embedded in tissue prep.

RESULTS

(a) Winter flounder: The winter flounder crawled and shambled (Kruuk, 1963) across the bottom with their heads raised during times of feeding on live and prepared food. Shambling has been described by Kruuk (1963) as a combination of swimming close to the sand and crawling at speeds of approximately 40 cm/sec. The eyes projected from the head and moved independently to give the fish a field of vision wider than 180° . Once a potential prey object was sighted, the fish shambled toward it until the prey was 2-3 cm from the mouth. The head was then pointed toward the prey at an angle of approximately 30° below the horizontal. The body was arched downward with the dorsal and anal fins braced in the sand. A short lunge or peck secured the food item (Fig. 1). During this sequence the eyes appeared to be continuously focused on the prey. Suction created from the expansion of the opercula was used in conjunction with the lunge to capture all prey. This method was particularly important when capturing mobile amphipods and errantid polychaetes. In all cases the flounder took single items with each peck and were never observed taking mouthfuls of sand to sort in their mouths.

In most cases the flounder were more likely to respond to moving than

FIGURE IV - 1. Feeding response of winter flounder as it searches (a) and lunges (b) at a benthic prey item.

a

b

stationary prey. This applied to swimming amphipods, crawling polychaetes and foot or siphon movements of molluscs. On two occasions, two flounders were observed to peck at the tips of moving fin rays of other buried flounders. Flounders that did not feed voluntarily on natural or stationary prepared food could be stimulated to feed on a bolus of prepared food bounced gently along the bottom on the end of a fine wire.

Food was usually taken in one or two pecks. This was followed by a few seconds of pharyngeo-esophageal activity, presumably to break up and swallow the prey (described as chewing by Gibson, 1980). Judging from stomach contents, the pharyngeal teeth flattened or partially crushed the exoskeletons of amphipods and shells of mollusks (unpublished observations). However, larger items that did not fit into a flounder's mouth (eg. large mollusks) were bitten many times, held in the jaws by the viscera and then shaken up and down rapidly. It is assumed that this food was too large to fit through the flounders' relatively small mouths. This served to break a portion of flesh off or to crack the shell. Four individual flounders were observed to do this to eight Y. sapotilla and two D. entale. One 18-cm flounder spent 11 min pulverizing one mollusk although the average handling time for all bivalves was approximately one min. The average handling time for all other natural prey did not exceed eight sec. (Table 1). Unfortunately no quantitative information on the effect of fish size on handling time was collected. Only small flounder shook mollusks in this manner.

Similarly, the flounder responded to larger boluses of prepared food even though they required shaking and biting before they would fit into their mouths. It took 10-25 sec for a bolus to be chewed by the

TABLE IV - 1. Handling time (in seconds) for each of the prey by both predators. Values record time between first feeding response (ie. peck or lunge) and successful consumption of prey. Handling time of prey acquired by sorting mouthfuls of sediment was not recorded.

TABLE IV - 1.

Winter flounder						Ocean Pout			
<u>N.</u> <u>incisa</u>	<u>S.</u> <u>scutata</u>	<u>D.</u> <u>entale</u>	<u>Y.</u> <u>sapotilla</u>	<u>C.</u> <u>bigelowi</u>	<u>N.</u> <u>incisa</u>	<u>S.</u> <u>scutata</u>	<u>D.</u> <u>entale</u>	<u>Y.</u> <u>sapotilla</u>	<u>C.</u> <u>bigelowi</u>
3	23	5	10	10	1	1		1	
3	3	3	15	3	1	1		1	
3	3	3	20					1	
3	3		3					1	
3			3					1	
3			60						
3			20						
3			33						
3			3						
			3						
			60						
			3						
			700						
n	9	4	3	17	2	2	-	4	-
$\bar{X}$	3	8	3.7	55.6	6.5	1	-	1	-

pharyngeal teeth before swallowing. During chewing, portions of the food were expelled through the gill aperture.

(b) Ocean pout: When foraging, the ocean pout swam a few centimeters from the bottom, then settled on the sediment. While on the sediment, the tail was coiled and the head and eyes pivoted to scan the environment. The coiled tail acted as a base from which the head was extended to capture prey. Food was consumed by a rapid scooping motion of the lower jaw in conjunction with opercular suction. However, potential prey (eg. amphipods or polychaetes) were often not seen by a feeding fish even when they were swimming or crawling a few centimeters from the fish's head. A large or small bolus of prepared food was as likely to be responded to when stationary as it was while in motion. When moving food was lunged at, it was often missed. Handling times were difficult to collect because it was often difficult to see which prey the ocean pout were feeding on. Mean time taken to handle all prey species was one sec.

A disturbance of the sediment, such as a flounder burying itself, quickly attracted one or more ocean pout from at least a meter away. This was observed eight times in three different fish. No potential food was ever exposed by these disturbances, so the fish were not observed feeding.

Three ocean pouts were seen filling their mouths with sediment. To collect the sediment, the head was tilted downwards and the lower jaw scooped a trench 2-3 cm long and 3-5 mm deep. The head was held at an angle that allowed both the lower and upper lips to come in contact with the substrate. The sediment was mixed in the mouth for 10-30 sec and

then spit out, a bit at a time (Fig. 2). This behaviour was observed 17 times, often at the same location. It did not always result in the discovery of food because ocean pout sampled throughout the tank, not only in areas where food had been placed. It was difficult to see how many items were eaten and when they were swallowed.

An alternative type of digging behaviour was observed on two occasions when an ocean pout used its upper lip to overturn a large shell.

The ocean pout rarely left the bottom to feed. They maneuvered very poorly when off the bottom, often snapping at but missing prepared food that was dropped from the water's surface.

Observations of the histological sections revealed both taste bud organs and pressure sensitive tactile papillae or ridges on the ventral surface of the upper lip (pers. comm. Mr. R. Harris, U.W.O.). The lower lip had taste bud organs and mucus glands in the epidermal layer. Sections also revealed unattached longitudinal bone or cartilage that may act to stiffen the lower lip. Both longitudinal and cross sectional voluntary muscles were attached to the bone and could be used to roll the lip backwards and forwards or draw it into a scoop shape.

DISCUSSION

Some of the observations made during this experiment have been described for other species of flounders. The shambling movements while seeking food were originally described by Kruuk (1963) for Solea vulgaris, and have since been used to describe the movements of Pleuronectes platessa by Gibson (1980). They have also been described as cephalocaudal movements for Paralichthys dentatus by Olla et al (1972).

FIGURE IV - 2. Feeding response of ocean pout as it scoops (a) and sorts (b) mouthfuls of gravel.

a

b

This study serves to re-emphasize the importance of sight for feeding in winter flounders (Olla et al 1969). Their wide field of vision is well suited for the detection of moving food (natural or prepared). Each feeding advance is directed at an individual prey and not at a portion of the substrate. Other flounder, including Platichthys flesus (Moore and Moore, 1967), Paralichthys dentatus (Olla et al 1972), and Pleuronectes microcephalus (Steven, 1930) also rely to a great extent on eyesight for feeding. This has been used to explain their greater activity during the day and their attraction to moving objects.

In contrast, ocean pout showed no stronger response or ability to detect moving than stationary food. Prey detected on the bottom were consumed but many potential prey were missed. Slow swimming speeds (Beamish, 1966) and apparent poor maneuverability when the tail is not coiled while on the bottom indicate that ocean pout are not adapted to pursue moving prey, a process that requires good sight. An alternate strategy, employed by 37% of the ocean pout observed, involved folding the lower lip outwards to permit the fish to scoop up mouthfuls of sediment. Zoarces viviparus (Zoaridae) takes mouthfuls of vegetation and sand in a similar manner (Blegvad) while seeking mollusks. The subsequent sorting of benthos within the mouth probably requires sensory structures on the lips and in the mouth. Iwai (1963) reports the presence of taste buds and other sensory structures on the lips, barbels and gill rakers of Plotosus anguillaris. He suspects they play a major role in selecting food after it has entered the mouth.

Using sight or hearing, ocean pout detected disturbances in the sediment caused by flounder digging in. Although the ocean pout were never observed feeding during this activity, they may be attracted to any

disturbance at the bottom that might expose benthic prey.

Direct comparison between the natural diet of the two predator species and the relative utilization of food in the laboratory was impossible because there was no accurate way of estimating what prey items were consumed by the ocean pout when they took mouthfuls of benthos.

The development of techniques to feed more efficiently on non-mobile prey within the sediment may partially explain the predominance of bivalves and sedentary polychaetes in the natural diet of the ocean pout. (Fig. 2; Table 1). Visual feeders that respond to moving prey, including the winter flounder, are more efficient at eating polychaetes, amphipods and the common epibenthic fauna (decapods and nekton) than on bivalves (Tyler, 1972). This may explain observed interspecific resource partitioning. However, if winter flounder take a significant number of bivalves by removing the viscera from the shell before swallowing, a count of shells in the stomach will underestimate the total number of animals consumed. In this case a viscera count would be more accurate than a shell count, if the viscera could be keyed to the required taxonomic level reliably. Several researchers have observed nipped off bivalve siphons in the stomach contents of winter flounders (Tyler 1971; Woodin pers. comm.). Presumably this behaviour is a method for handling prey too large to be consumed whole. The extra handling time would, however, reduce the prey's overall value as a food source. Future work should consider the effect of fish size and food size on handling time.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. B. Driedzic for the food habit information, Dr. K. Waiwood for use of his research facilities and R. Harris for histological assistance. Thanks also goes to Dr. R. Green whose NSERC strategic grant supported this research, and the staff of the Huntsman Marine Lab Aquarium where much of this work was done. Dr. B. Seghers, Dr. W.B. Scott, and Dr. M.H.A. Keenleyside made numerous suggestions to improve the manuscript. These data will partially fulfill the requirements for a Ph.D. at the University of Western Ontario.

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APPENDIX V

Redundancy in Environmental Variables

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INTRODUCTION

In an effort to identify dominant or important prey species, researchers of animal diet have used several types of measurements. They include numerical abundance, volumes or weights, percent frequency of occurrence and caloric value (reviewed by Hynes 1950; Berg 1979; Hyslop 1980). Each measure was developed to fulfill a different purpose.

Numerical abundance measures reflect the process of density-dependent prey acquisition by predators and thus provide insight into feeding behaviour. They may have an advantage if data are being collected in an environment where weigh scales won't work (eg. some research vessels) or if the researcher is not back-calculating original weights or volumes from taxonomic measures of digested prey (Windell and Bowen 1978).

Volume or weight measures reflect prey species nutritional value and should be used when prey species are too numerous to be counted (Richards 1963). Ellison (1978) has noted the importance of using actual caloric value as a measure of importance. Caloric values were not available for the prey species in this study but we suspect they would be highly correlated with the other measurement types. Feinsinger et al (1981) has found caloric methods to be the least appropriate in availability vs. use studies as consumers do not choose resources joule by joule but rather item by item.

Percent frequency of occurrence gives an indication of prey species variability in predator diets. Frost (1977) has found percent occurrence measures to be particularly appropriate when there are few food categories.

Different measurement types are usually assumed to contain information independent of each other (Hyslop 1980). To avoid information loss several methods have been developed to combine two or more measures. Hynes (1950 - points method) and Hureau (1969 - in Berg 1979) create indices that combine numerical and volumetric measures. Pinkas (1971) and Prince (1975) combine percent numbers, volumes, and occurrence into a single index (index of relative importance - IRI). These indices are based on an equal contribution by each type of measure. Cailliet (1976), Hulberg and Oliver (1978) and Hacunda (1980) have used Pinkas' IRI successfully. Cailliet, Hulberg and Oliver use the three measurement types to define rectangular areas which are compared among prey species and among predator species.

Compound indices are not exclusive to dietary research. Numbers and weight have been used to describe numerically dominant species in marine benthic samples by Ellis and Conlan (1979). Curtis and McIntosh (1951) combine density, frequency and dominance estimates to measure plant species importance in an upland forest in Wisconsin.

This note addresses the question of data redundancy that may occur among three measurements that are often applied to rank prey species importance. It may not be necessary to combine all measures into one index. One measure may describe most of the information in a data matrix.

MATERIALS AND METHODS

The data were collected as part of a study of spatial and temporal variation in fish diet in the lower Bay of Fundy region, N.B., Canada

(45°N, 67°W). This is now being prepared for publication. Three hundred and ninety seven stomachs from five species of fish (Pseudopleuronectes americanus - winter flounder, Hippoglossoides platessoides - plaice, Gadus morhua - cod, Macrozoarces americanus - ocean pout and Glyptocephalus cynoglossus - witch flounder) were collected from two sites at seven times over a period of one year (1979-80). Stomachs were removed immediately after capture and immersed in 10% formalin. They were later transferred to 70% ethanol. Two hundred and seventeen prey species were identified. Numerical abundances and blotted wet weights of each prey in each stomach were stored in matrix format on a CDC-Cyber 170 computer at the University of Western Ontario. A FORTRAN program created a data file of mean number, mean weight and percent occurrence of three prey species (Ninoe nigripes - polychaete, Leptocheirus pinguis - amphipod, Yoldia sapotilla - bivalve) in each fish species caught at each site and time. The program also performed Taylor's power law (Elliott 1977) on the numbers and weights to transform them in a way that best removed the dependence of the variance on the mean. The percent occurrence data were treated using an arcsine transformation for the same reason (Sokal and Rohlf 1973). The transformed data were analysed separately for each prey species using principal component analysis (FACTOR - SPSS) to determine the amount of variation in the data that was shared among the measurement variables. This process was repeated after removal of the added correlation caused by cases (fish at each site and time) where all three measures were zero.

RESULTS

Numerical abundance data required either a square root or a log ($X+1$) transformation. This is consistent with the literature (Marriott 1974, Green 1980). Transformations for weight data were less predictable as each prey species required a different treatment under Taylor's power law (Table 1). The first principal (PC) component described a large portion of the variation whether or not groups with zero values were included (Table 2). All three measurement variables loaded heavily on the first principal component axis and were highly correlated with each other (Table 3).

DISCUSSION

It is often desirable to reduce numbers of variables (see discussion in Green 1979). Large numbers of variables require extra work to collect and analyse, and they increase sensitivity to violations of assumptions in multivariate analyses. In many cases the additional information gained decreased rapidly as more variables are included (Kaesler et al 1974). The high positive loadings on the first PC demonstrate that any one of the three variables in this study will adequately describe prey species importance regardless of the definition of importance. This avoids the difficulties involved in interpretation and statistical analysis of compound indices (Green 1979).

TABLE V - 1. Transformations required by each variable type for each invertebrate species to remove the variance associated with the mean. Transformations were calculated using Taylor's power law.

Prey	<u>Ninoe nigripes</u>	<u>Leptocheirus pinguis</u>	<u>Yoldia sapotilla</u>
No.	$Z^* = \sqrt{X}$	$Z = \ln (X+1)$	$Z = \ln (X+1)$
Wt.	$Z = X .8695$	$Z = X .285$	$Z = X$
Occ	$Z = \arcsin X$	$Z = \arcsin X$	$Z = \arcsin X$

TABLE V - 2. Amount of variation accounted for by the first principal component of the analysis on each species. Runs were made with and without the added correlation caused by cases where all 3 measures were zero.

Prey	<u>Ninoe nigripes</u>	<u>Leptocheirus pinguis</u>	<u>Yoldia Sapotilla</u>
Percent	All		
Varia-	Grps . 95.5%	95.5%	90.5%
tion			
Associated	No		
with First	Zeros 91.4%	91.4%	89.0%
PC			

TABLE V - 3. Variable loadings on the first 3 principal components of each species. Correlation coefficients associated with each species are also included.

Prey	<u>Ninoe nigripes</u>			<u>Leptocheirus pinguis</u>			<u>Yoldia sapotilla</u>		
	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>
Regression Coefficients (Loadings)	No. .986	-.042	-.163	.975	-.220	.043	.986	-.111	-.124
	Wt. .970	.24	.058	.996	-.055	-.063	.956	-.278	.098
	Occ. .976	-.192	.107	.960	.281	.021	.910	.413	.032
Correlation Matrices (with zeros in data)	<u>No.</u>	<u>Wt.</u>	<u>Occ.</u>	<u>No.</u>	<u>Wt.</u>	<u>Occ.</u>	<u>No.</u>	<u>Wt.</u>	<u>Occ.</u>
	No. 1			1			1		
	Wt. .937	1		.981	1		.961	1	
	Occ. .952	.907	1	.857	.939	1	.847	.758	1

ACKNOWLEDGEMENTS

We are grateful to Dr. M.H.A. Keenleyside and Mr. G.S. Sudbury for their critical review of this paper. The work done by J.S. Macdonald was in partial fulfillment of Ph.D. studies supported by NSERC operating and strategic grants to R.H. Green.

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APPENDIX VI

List of the 217 variables (prey or potential prey) collected using all sampler types at both sites and all times. Each item is categorized by phylum. Numbers in brackets indicate number of those items collected during the entire sampling period. A total of 23,534 prey were collected and identified. Species marked with an '*' are variables of the reduced data matrix used for the multivariate statistical analysis of food habits.

Classification is based on Gosner (1971) for the phyla Cnidaria, Rhynchocoela and Echinodermata, Gosner and Leim and Scott (1966) for phylum Chordata, Brinkhurst et al. (1970), Dadswell (pers. comm.), Roff (1978) and Smith (1964) for phylum Arthropoda, Gosner and Abbott (1974) for phylum Mollusca and Appy (1980) and Linkletter (pers. comm.) for phylum Annelida.

Phylum Cnidaria (498)

Class Hydrozoa

Corymorpha perdula
Peachia parasitica

Class Anthozoa

Edwardsia elegans
Bunadactis stella

Phylum Rhynchocoela (45)

Class Anopla

* Micura affinis
Cerebratulus lacteus

Class Enopla

Amphiporus spp.
Tetrastemma spp.
Ototyphlonemertes pellucida

Phylum Mollusca (4,664)

Class Aplacophora

Chaetoderma nitidulum

Class Polyplacophora

Ischnochiton ruber

Class Gastropoda

Subclass Prosobranchia

Puncturella noachina
 * Lunatia heros
L. pallida
L. triseriata
Colus stimpsoni
Colus obesus
Colus pygmaea
Crucibulum striatum
Propebela turricula
Trichotropis borealis
 * Alvania pelagica
Natica pusilla
Natica clausa
Mitrella dissimilis
Neptunea decemcostata
Oenopota decussata
Solariella lamellosa
 unidentified gastropod

Subclass Opisthobranchia

Diaphana minuta
 * Cylichna alba

Class Scaphopoda

* Dentalium entale

Class Pelecypoda

Subclass Protobranchia

* Nucula proxima
 * N. tenuis
 * N. delphinodonta
 * Yoldia sapotilla
 * Nuculana tenuisulcata

Subclass Lamellibranchia Mytilus edulis
 * Musculus niger
Modiolus modiolus
Mya arenaria
M. truncata
Crenella spp.
 * Cardita borealis
Astarte subaequilatera
A. undata
 * A. borealis
A. montagui
Placopecten magellanicus
Pitar morrhuana
Lyonsia hyalina
Pandora gouldiana
 * Cerastoderma pinnulatum
Arctica islandica
 * Thyasira flexuosa
 * Periploma fragile
Macoma balthica
Aequipecten glyptus
 unidentified bivalve

Subclass Septibranchia Cuspidaria glacialis

Class Cephalopoda Ilex illacebrosus

Phylum Annelida (8,274)

Class Polychaeta

Subclass Errantia
 * Nephtys incisa
 * Lumbrineris fragilis
L. tenuis
L. latreilli
Lumbrinidae family
Drilonereis magna
 * Ninoë nigripes
 * Goniada maculata
 * Phyllodoce groenlandica
P. maculata
Neris virens
 * Harmothoe extenuata
 * H. imbricata
Harmothoe spp.
Eteone trilineata
 * E. longa
E. flava
Eteone spp.
Paranaitis speciosa
 * Ammotrypane aulogaster
Goniada norvegica
Ophioglycera gigantea
Glycera spp.

Subclass Sedentaria

- * Sternaspis scutata
- * Terebellides stroemii
- Capitella capitata
- * Rhodine loveni
- * Melinna cristata
- * Owenia fusiformis
- * Tharynx acutus
- * Potamilla neglecta
- * P. reniformis
- * Praxillella praetermisa
- P. gracilis
- * Scalibregma inflatum
- * Brada villosa
- * Euchone rubrocincta
- * Ampharetidae family
- Pherusa plumosa
- * Syllis cornuta
- Trichobranchus glacialis
- Laonice cirrata
- Cossura longocirrata
- Clymonella zonalis
- * Aricidea quadrilobata
- * Chaetozone setosa
- * Aphrodita hasata
- Sabellaria vulgaris
- * Pherusa affinis
- Pherusa aspera
- Spirorbis spp.
- Brada villosa
- Brada granosa
- Nicolea venustula
- Heteromastus filiformis
- Cistena granulata
- Diplocirrus hirsutes
- * Maldanidae family
- Unidentified worm

Phylum Arthropoda (9814)

Subphylum Pycnogonida

Nymphon grossipes

Subphylum Mandibulata

Subclass Copepoda

Order Cumacea

- Eudorella emarginata
- E. truncatula
- * E. pusilla
- E. hispida
- Diastylis rathkei
- * D. quadrispinosa
- * D. cornuifer
- * D. sculpta
- D. polita
- Diastylis sp.
- * Leptostylis longimana

- Order Cumacea (Cont'd.) * Petalosarsia dedidis
 * Campylaspis rubicunda
C. affinis
Leucon americanus
- Order Isopoda * Edotea montosa
Idotea phosphorea
 * Synidotea nodulosa
Chiridotea laevis
Ptilanthura tenuis
Munna fabricii
Calathura branchiata
- Order Amphipoda * Leptocheirus pinguis
 * Haploops fundiensis
Casco bigelowi
Aeginina longicornus
Erichthonius rubricornis
 * E. difformis
 * Unciola leucopis
 * U. irrorata
 * U. inermis
Unciola spp.
 * Stenopleustes inermis
 * Orchomonella minuta
Calliopius laeviusculus
Byblis gaimardi
 * Maera danae
M. loveni
 * Syrrhoe crenulata
Argissa hamatipes
Hippomedon serratus
 * H. propinquus
Anonyx sarsi
 * A. lilljeborgi
Oedicerotidae family
 * Westwoodilla caecula
Monoculodes edwardsi
Ampelisca aequicornus
A. macrocephala
Pontogeneia inermis
 * Dyopedos monocanthus
 * D. porrectus
Protomedia fasiata
Parathemisto compressa
Paroedicerus lynceus
Photis macrocoxa
 * Tmetonyx cicada
Aceroides latipes
Phoxocephalus holbolli
Phoxichilidium femoratum
Acanthonotozoma serratum
 * Harpina propinqua

Order Amphipoda
(Cont'd.)

Ischyroceros anguipes
Stenopleustes gracilis
Paradulichia typica
Gammaropsis melanops
Metopella angusta
Caprella septemtrionalis
Melita dentata
Mayerella limicola
Pleurogonium spinosissimum
Corophium bonelli
 unidentified amphipod

Order Mysidacea

Erythrope erythrophthalma
Neomysis americana
Mysis stenolepis

Order Euphausiacea

Meganyctiphanes norvegica

Order Decapoda

Pandalus borealis
P. montagui
Cancer irroratus
Pagurus spp.
Crangon septemspinosa
Eualus pusiulus

Phylum Echinodermata (155)

Class Holothuroidea

Molpadia oolithica

Class stelleroidea

Gtenodiscus crispatus
Ophiura sarsi
 * Amphipholis squamata

Phylum Chordata (83)

Class Ascidiacea

Boltenia ovifera
 * Mogula spp.

Class Osteichthyes *

Merluccius bilinearis
Clupea harengus
Pseudopleuronectes
americanus
Osmerus mordax
 * unidentified fish remains

Additional Variables

inorganic sediment

APPENDIX VII

FORTRAN[®] program to calculate percent frequency of occurrence and mean prey abundance data for each sampler type. Program also calculates Ivlevs' and Shorigins' electivity indices.

C FORTRAN PROGRAM TO RUN ON THE CYBER 170 THAT CALCULATES SHORIGINS AND
 C IVLEVS ELECTIVITY INDICES. PROGRAM ALSO CALCULATES MEAN NO. OF EACH PREY
 C ITEM THAT WAS FOUND IN EACH PREDATOR SPECIES STOMACH AND PERCENT FREQ.
 C OF OCCUR ENCES. DATA IS ENTERED FROM SEPERATE FILES; EACH FILE CONTAINS
 C DATA FROM A SEPERATE PREDATOR SPECIES OR BOTTOM GRAB. INFORMATION ABOUT
 C THE NO. OF FISH IN EACH FILE AND THE NO. OF VARIABLES IN ALL FILES IS
 C ENTERED ON A SEPERATE CARD AT THE END OF THE PROGRAM.

C
 C
 C

```

PROGRAM NAME(INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT,TAPE11,TAPE12,
*TAPE13,TAPE14,TAPE15,TAPE16)
  DIMENSION X(10,217,6),SUM(217),N(6),GSUM(6),SUM1(6),OCC(217),
  *PSUM(217),PSUM1(217),E(217),C(217),MOC(217),MN(217),F(217)
  REAL SUM,PSUM,SUM1,MN,MOC,GSUM,X,E,C,F,OCC
  INTEGER P,I,J,O,N,K,IU,M
  READ *,P,N,L
  DO 500 K=1,L
    IF(N(K).EQ.0) GO TO 500
    IF(K.EQ.1)PRINT 11
11  FORMAT (" GRAB",/)
    IF(K.EQ.2)PRINT 12
12  FORMAT (" COD",/)
    IF(K.EQ.3)PRINT 13
13  FORMAT (" OP",/)
    IF(K.EQ.4)PRINT 14
14  FORMAT (" WF",/)
    IF(K.EQ.5)PRINT 15
15  FORMAT (" PLAICE",/)
    IF(K.EQ.6)PRINT 17
17  FORMAT (" WITCH",/)
    IU=K+10
    M=N(K)
    DO 10 I=1,M
      READ(IU,16)(X(I,J,K),J=1,P)
16  FORMAT (30(7F10.5/),7F10.5)
10  CONTINUE
      GSUM(K)=0
      SUM1(K)=0
      DO 30 J=1,P
        SUM(J)=0.0
        OCC(J)=0.0
        MN(J)=0.0
        MOC(J)=0.0
        DO 40 I=1,M
          SUM(J)=SUM(J)+X(I,J,K)
          IF (X(I,J,K).GT.0)OCC(J)=OCC(J)+1
40  CONTINUE
          SUM1(K)=SUM(J)+SUM1(K)
          O=J+19
          MN(J)=SUM(J)/N(K)
          MOC(J)=OCC(J)/N(K)*100
          WRITE(6,50)O,SUM(J),MN(J),OCC(J),MOC(J)
50  FORMAT (" SUM,MEAN SUM,# OCCURING AND % OCCURANCES OF VARIABLE ",
  *I3,2X,F5.1,2X,F7.3,2X,F3.0,2X,F7.3)

```



```

30 CONTINUE
   GSUM(K)=SUM1(K)
   IF (GSUM(K).NE.0.0) GO TO 95
   PRINT 65
65  FORMAT(" GRAND SUM = 0,CANT CALCULATE INDICES")
   GO TO 500
95  DO 60 J=1,P
   PSUM(J)=0
   E(J)=0.0
   C(J)=0.0
   O=0
   O=J+19
   IF (K.NE.1)GO TO 100
   PSUM1(J)=(SUM(J)/GSUM(K))*100
   WRITE(6,75)O,PSUM1(J)
75  FORMAT(" % OF VARIABLE ",I3," IN ALL GRAB SAMPLES ",F7.3)
   GO TO 60
100 PSUM(J)=(SUM(J)/GSUM(K))*100
   WRITE(6,70)O,PSUM(J)
70  FORMAT(" % OF VARIABLE ",I3," IN ALL SAMPLES ",F7.3)
   F(J)=PSUM(J)+PSUM1(J)
   IF (F(J).EQ.0)GO TO 58
   E(J)=(PSUM(J)-PSUM1(J))/F(J)
   WRITE(6,83)E(J),O
83  FORMAT(" IVLEVS INDEX IS ",F5.2," FOR VARIABLE",I3)
   IF (PSUM1(J).EQ.1)GO TO 58
   C(J)=PSUM(J)/PSUM1(J)
   WRITE(6,80)C(J),O
80  FORMAT(" SHORIGINS INDEX IS ",F8.3," FOR VARIABLE",I3 /)
   GO TO 60
58  PRINT 59
59  FORMAT(" INDEX CANT BE CALCULATED",/)
60  CONTINUE
500 CONTINUE
   END

```

APPENDIX VIII

Densities (mean number of prey) of 60 of the 74 variables of the reduced data matrix in all sampler-types at each time and site. All principle prey recorded by Tyler (1972) are also included.

The areas of the circles represent the following mean number of prey/fish or grab sample.

—	-	no sampler type collected
○	-	0.1 - 0.29
○	-	0.3 - 0.59
○	-	0.6 - 1.0
○	-	1.1 - 2.0
○	-	2.1 - 4.0
○	-	4.1 - 8.0
○	-	8.1 - 15.0
○	-	15.1 - 25.0
○	-	25.1 - 50.0
○	-	50.1 - 100.0
○	-	100.0 +

PREY SPECIES	SITE	GRAB 33 35 36 37 38 39 40 41 42 43 44 45	COD	OCEAN POUT	WINTER FL.	PLAICE	WITCH FL.
<i>Sternaspis</i> <i>scutata</i>	A	ooo-oo	—	ooo-oo	ooo- o	- o	- o —
	B	oooooooo	- o	ooo o	ooo- oo	oo oo	oooooooo
<i>Nephtys</i> <i>incisa</i>	A	ooo-ooo	— o	o o —	ooo- o	oo-ooo	— —
	B	oooooooo	—		ooo- oo	ooo ooo	ooo - o
<i>Lumbrineris</i> <i>fragilis</i>	A	ooo ooo	— o	—	ooo- o	-	- o —
	B	oooo oo	-		ooo o	oo oo	oooooooo- o
<i>Praxillella</i> <i>praetermissa</i>	A	ooo-ooo	—	—	ooo- o	-	— —
	B	ooooooo	-		oo	-	- o
<i>Scalibragma</i> <i>inflatum</i>	A	ooo-ooo	—	—	- -	-	— —
	B	ooooo	-		- o	-	- -
<i>Harmothoe</i> <i>imbicata</i>	A	ooo-ooo	—	— o	oo - o	-	— —
	B	oo oo	-	-	-	-	- -
<i>Eteone</i> <i>trilineata</i>	A	ooo-ooo	—	—	ooo- o	-	— —
	B		-	-	o	-	o - o
<i>Aphrodita</i> <i>hasata</i>	A	oo- oo	o —	o — o	- o	-	— —
	B		- o	o	-	-	-
<i>Heteromastus</i> <i>filiformis</i>	A	o-ooo	—	—	-	-	— —
	B	oooo	-	-	-	-	-
<i>Astarte</i> <i>borealis</i>	A	ooo-ooo	—	o o —	-	-	— —
	B	oo oo	-	o o	-	-	-
<i>Cylichna</i> <i>alba</i>	A	o o- oo	—	ooo- o	oo- o	-	— —
	B	oo ooo	-	ooo	o	-	-
<i>Yoldia</i> <i>sapotiilla</i>	A	ooo-oo	—	ooo-oo	ooo- oo	ooo- oo	— —
	B	oooooooo	-	ooo o	oo	oo o	oooo o

PREY SPECIES		GRAB	COD	OCEAN POUT	WINTER FL.	PLAICE	WITCH FL.
<i>Ninoe nigripes</i>	A	○○○-○○	—	—	○○○-○	—	—○—
	B	○○○○○○	—	—	○○○	○	○○○○-○
<i>Rhodine loveni</i>	A	○○○-○○	—	—	○○○-○	—○	—
	B	○○○○○○	—	—	○○○	○	○○○
<i>Melinna cristata</i>	A	○○○-○○	—	—	○○○-○	○	+ —
	B	○○○-○○	—	—	○○○	○	○○-
<i>Owenia fusiformis</i>	A	○○○-○○	—	—	○○○	—	—
	B	○○○○○○	—	—	○○○	○	○○-
<i>Tharyx acutus</i>	A	○○○-○○	—	—	○○○	○	—
	B	○○○○○○	—	—	○○○	○	○○○○-○
<i>Potamilla neglecta</i>	A	○○-○○	—	—	○○○	—	—
	B	○○○○○	—	—	○○○	○	○○-
<i>Goniada maculata</i>	A	○○○-○○	—	—	—	—	—
	B	○○○-○○	—	—	—	—	—
<i>Phyllodoce groenlandica</i>	A	○-○○○	—	—	—	—	—
	B	○○○○○	—	—	○○○	○	○○-○
<i>Harmothoe exeluvata</i>	A	○○-○○○	—	—	○○○	—	—
	B	○○○○○○	—	—	—	—	—
<i>Brada villosa</i>	A	○○○-○○○	—	—	○○○-○○	○	—
	B	○○○○○○	—	—	—	○○○	○○-
<i>Euchone rubrocincta</i>	A	○○○-○○○	—	—	○○○	—	—
	B	○○○○○○	—	—	—	○○○	—
<i>Terebellides stroemii</i>	A	○○○-○○○	—	—	○○○	—	—
	B	○○○○○○	—	—	—	—	—

PREY SPECIES	SITE	GRAB	COD	OCEAN POUT	WINTER FL.	PLAICE	WITCH FL.
<u>Ampharetidae</u>	A	○○○-○○○	—	—	○○○-○	○○-○○○	— — —
	B	○○○○○○○	—	—	○ ○	○	○ ○ ○ - ○
<u>Periploma fragile</u>	A	○○ - ○○	—	—	—	—	— — —
	B	○○○○○○○	—	—	—	—	— — —
<u>Dentalium entale</u>	A	○ ○ - ○○	—	—	—	—	— — —
	B	○○○ ○○○	—	○	—	—	○
<u>Thyasira flexuosa</u>	A	○○○-○○○	—	○ ○ — ○	○ -	—	— — —
	B	○○○○○○○	—	—	—	—	— — —
<u>Alvania pelagica</u>	A	○ ○ - ○	—	○ ○ —	—	—	— — —
	B	○○○○○○○	—	○ ○	—	—	— — —
<u>Haploopsis fundiensis</u>	A	○○○-○○○	—	○○ —	○○○-○	○ -	— — —
	B	○○○○○○○	—	○	—	○ ○	○○ ○
<u>Orchomonella minuta</u>	A	○○○-○○○	○ - ○	— ○	○○○-○	—	— — —
	B	○	—	○○	○	○	○ -
<u>Hippomedon propinquus</u>	A	○○-○○○	—	— — ○	○ -	—	— — —
	B	○○○○○○○	—	○ ○	—	○	○○ ○ - ○
<u>Nucula tenuis</u>	A	○○○-○	—	○○ — ○	○ - ○	—	— — —
	B	○○○○○○○	—	○○○ ○	○ ○ ○	—	— — —
<u>Diastylis quadrispinosa</u>	A	○○○-○○○	—	○○○-○○○	○○○-○	○ - ○	— — —
	B	○○○○○○○	—	○○○	—	○	— — —
<u>Diastylis sculpta</u>	A	○○○-○ ○	—	○○○-○	—	—	— ○ —
	B	○○ ○	—	—	—	—	○
<u>Diastylis cornuifer</u>	A	○ - ○ ○	○ — ○	○○ —	○○ -	—	— ○ —
	B	○○○○○○○	—	○○○	—	○	○

PREY SPECIES	SITE	GRAB	COD	OCEAN POUT	WINTER FL.	PLAICE	WITCH FL.
		Jul Aug Sep Oct Nov Dec					
<u>Nucula proxima</u>	A	oo- oo	—	.oo—	oo o	oo -	— —
	B	o o o o	-	oo			-o
<u>Arctica islandica</u>	A	ooo- oo	—	oo — o	o	o -	— —
	B	o oo	-	oo		o	-
<u>Cerastoderma pinnulatum</u>	A	ooo-ooo	—	ooo— O	o	o -	— —
	B	oooo oo	-	ooo			-
<u>Nuculana tenuisulcata</u>	A	ooo- oo	—	O o— o		- o	— —
	B	oooooo	-	ooo	o	oo	o -
<u>Musculus niger</u>	A	o o-o o	—	o — o o		-	— —
	B	o	-	o o			-
<u>Cardita borealis</u>	A	oo-oo	—	o —		-	— —
	B		-				-
<u>Leptocheirus pinguis</u>	A	ooo-ooo	oo—oo	ooo—oo	ooo O	- o	— —
	B	oo o	-	o		oo	-o
<u>Casco bigelowi</u>	A	oo -oo	— o o	o o— o	ooo	o - o	-O—
	B	ooo-oo	-	ooo o	oo oo	ooo ooo	oooooO
<u>Erichthonius rubricornis</u>	A	O o-o	—	—	o	-	— —
	B	o	-			o	-
<u>Unciola leucopis</u>	A	ooo-ooo	oo— O	—oo o	O	o	— —
	B		-		o		-
<u>Unciola irrorata</u>	A	ooo-oo	O-o-O	o-o-oo	o O	- o	— —
	B	o	-			o	-
<u>Unciola inermis</u>	A	O -oo	o —	— o		-	— —
	B		-				-

PREY SPECIES	SITE	GRAB	COD	OCEAN POUT	WINTER FL.	PLAICE	WITCH FL.
<u>M. norvegica</u>	A	00-	0-0	-	-	-0	-
	B		00-				-
<u>Pandalus montagu</u>	A	-	0-	-	-	-0	-
	B		-				-
<u>Maera loveni</u>	A	00-	-	-	-	0-	-
	B	00	-				-
<u>Dyopetos monacanthus</u>	A	00-00	-	-	-	-0	-
	B	00	-		0		-
<u>Eudornella pusilla</u>	A	0-00	-	-	-	-	-
	B	00	-				-
<u>Maldanidae family</u>	A	0-0	-	-	0	0-	-
	B	0	-		0	0	0-
<u>Amphipolis squamata</u>	A	000-00	0-	00-	00-0	0-000	-
	B	0000	-	0		0	-
<u>Nucula delphinodonta</u>	A	0-0	-	00-	-	-	-
	B	000000	-	00			-
<u>Harpina propinqua</u>	A	00-000	-	-	-0	-	-
	B	0000	-		0	000-	-
<u>Syrrhoë crenulata</u>	A	000-0	0-	-	0-	00-	-
	B	0	-				-
<u>Chaetozone setosa</u>	A	0-	-	-	-	-	-
	B	000	-				-
<u>Mogula spp.</u>	A	-0	-	00-0	00-0	-	-
	B		-			00	-

APPENDIX IX

* FORTRAN program to calculate 95% confidence ellipses around centroids of any bivariate data. Comment statements (marked "C" in the left column) have been left in to aid future error searches.

C THIS PROGRAM CALCULATES 95% CL ELIPSES AROUND THE CENTROIDS
 C CALCULATED IN DISCRIMINANT ANALYSIS. THE DATA (THE DISCRIMINANT
 C SCORES) ARE INPUT FROM UNIT=1. THE DATA NEEDNT BE GROUPED. THE
 C USER MAY ENTER THE DATA IN RANDOM ORDER AND THEN SPECIFY WHICH
 C LINES ARE ASSOCIATED WITH EACH CENTROID. HOWEVER THE DATA MUST BE
 C IN TWO COLUMNS (ONE FOR EACH DISCRIMINANT FUNCTION). K(I) IS DIMENSIONED
 C FOR THE NO. OF DISCRIMINANT SCORES. IF THE DATA IS IN GRPS IT CAN
 C BE DIMENSIONED TO THE NO. OF GRPS. M(I) AND N ARE DIMENSIONED TO THE
 C NO. OF CENTROIDS. CENT1(I), CENT2(I) ARE DIMENSIONED TO CENTROID NO.
 C THIS PROGRAM WORKS WELL WITH ANY BIVARIATE DATA AS WELL!

```

C
C
C
    INTEGER J,O,P,S,U,J1
    REAL DCRIM2,DCRIM1,CENT2,CHI
    DIMENSION K(20),M(10),N(30),CENT1(6),CENT2(6),CLX(6),CLY(6)
    N1 = 0
    TYPE 10
10  FORMAT (' FTN PROGRAM TO CALCULATE 95% ELIPSES IN DCRIM ANALYSIS')
    OPEN(UNIT=1,DEVICE='DSK',ACCESS='SEQIN',FILE='DSDECW.DAT')
    OPEN(UNIT=2,DEVICE='DSK',ACCESS='SEQOUT',FILE='ELDECW.DAT')
    OPEN(UNIT=20,DEVICE='DSK',ACCESS='SEQOUT',FILE='WF.DAT')
    OPEN(UNIT=21,DEVICE='DSK',ACCESS='SEQOUT',FILE='OP.DAT')
    OPEN(UNIT=22,DEVICE='DSK',ACCESS='SEQOUT',FILE='C.DAT')
    OPEN(UNIT=23,DEVICE='DSK',ACCESS='SEQOUT',FILE='P.DAT')
    OPEN(UNIT=24,DEVICE='DSK',ACCESS='SEQOUT',FILE='W.DAT')
    OPEN(UNIT=25,DEVICE='DSK',ACCESS='SEQOUT',FILE='G.DAT')
    TYPE 15
15  FORMAT(' HOW MANY CENTROIDS ARE THERE, 6 MAX. ')
    ACCEPT *,J1
    C
    TYPE 17
C17  FORMAT(' ENTER CHI X2 VALUE...FOR 2 DFS,95% CL X2=5.991')
    C
    ACCEPT *,CHI
    TYPE 20
20  FORMAT(' HOW MANY GRPS IS THE DATA ARRANGED IN? ')
    ACCEPT *,J
    TYPE 30
30  FORMAT(' INPUT VECTOR OF GRP SIZES')
    DO 40 I=1,J
    READ(5,32)K(I)
32  FORMAT(I2)
    U=U+K(I)
40  CONTINUE
    WRITE(6,44)U
44  FORMAT(' TOTAL NO. OF DCRIM SCORES FOR EACH DF EQUALS ' I4)
    TYPE 50
50  FORMAT(' INPUT GRP ID VECTOR WF=20 OP=21 C=22 P=23 W=24 G=25')
    DO 60 I=1,J
    READ(5,32)M(I)
60  CONTINUE
    C
    WRITE(6,61)M(1),M(2),M(3)
C61  FORMAT(' ',I2,1X,I2,1X,I2)
    DO 55 I=1,30
    N(I)=0
55  CONTINUE
  
```

```

DO 70 I=1,J
DO 80 L=1,K(I)
READ (1,90)DCRIM1,DCRIM2
90  FORMAT(1X,F8.4,2X,F8.4)
    IF (M(I).EQ.20) N(20)=N(20)+1
    IF (M(I).EQ.21) N(21)=N(21)+1
    IF (M(I).EQ.22) N(22)=N(22)+1
    IF (M(I).EQ.23) N(23)=N(23)+1
    IF (M(I).EQ.24) N(24)=N(24)+1
    IF (M(I).EQ.25) N(25)=N(25)+1
100  WRITE (M(I),100)DCRIM1,DCRIM2
80  FORMAT(1X,F8.4,2X,F8.4)
70  CONTINUE
    CONTINUE
    CLOSE(UNIT=1)
    CLOSE(UNIT=20)
    CLOSE(UNIT=21)
    CLOSE(UNIT=22)
    CLOSE(UNIT=23)
    CLOSE(UNIT=24)
    CLOSE(UNIT=25)
    OPEN(UNIT=20,DEVICE='DSK',ACCESS='SEQIN',FILE='WF.DAT')
    OPEN(UNIT=21,DEVICE='DSK',ACCESS='SEQIN',FILE='OP.DAT')
    OPEN(UNIT=22,DEVICE='DSK',ACCESS='SEQIN',FILE='C.DAT')
    OPEN(UNIT=23,DEVICE='DSK',ACCESS='SEQIN',FILE='P.DAT')
    OPEN(UNIT=24,DEVICE='DSK',ACCESS='SEQIN',FILE='W.DAT')
    OPEN(UNIT=25,DEVICE='DSK',ACCESS='SEQIN',FILE='G.DAT')
C   TYPE 75
C75  FORMAT(' THE PROGRAM READS AS FAR AS THE 2ND OPEN GRP')
    DO 110 I=1,J1
    D1=0
    D2=0.0
    DCRIM1=0
    DCRIM2=0.0
    P=M(I)
C   WRITE(6,133)N(20),N(21),N(23)
C133  FORMAT(' I2,1X,I2,1X,I2)
    WRITE(6,134) M(I)
134  FORMAT(' SUMMATION OF DISCRIMINANT SCORES FOR GRP. 'I3)
    DO 120 L=1,N(P)
    READ (M(I),130)DCRIM1,DCRIM2
130  FORMAT(1X,F8.4,2X,F8.4)
    D1=D1+DCRIM1
    D2=D2+DCRIM2
    WRITE(6,135)D1,D2
135  FORMAT(1X,F8.4,2X,F8.4)
120  CONTINUE
    CENT1(I)=D1/N(P)
    CENT2(I)=D2/N(P)
    REWIND M(I)
110  CONTINUE
C   TYPE 122
C122  FORMAT(' PAST 2ND READ')
    DO 250 I=1,J1
    A=0

```

```

B=0.0
C=0.0
X=0.0
A1=0
B1=0
A2=0.0
B2=0.0
A3=0.0
B3=0.0
Y1=0
Y2=0.0
XY=0.0
P=M(I)
DO 140 L=1,N(P)
150 READ(M(I),150)DCRIM1,DCRIM2
   FORMAT(1X,F8.4,2X,F8.4)
   A1=(DCRIM1-CENT1(I))**2
   B1=B1+A1
   A2=(DCRIM2-CENT2(I))**2
   B2=B2+A2
   A3=(DCRIM1-CENT1(I))*(DCRIM2-CENT2(I))
   B3=B3+A3
140 CONTINUE
   Y1=B1/(N(P)-1)
   Y2=B2/(N(P)-1)
   XY=B3/(N(P)-1)
   IF (M(I).EQ.20) TYPE 190
190  FORMAT(' WINTER FLOUNDER')
   IF (M(I).EQ.21) TYPE 200
200  FORMAT(' OCEAN POUT')
   IF (M(I).EQ.22) TYPE 210
210  FORMAT(' COD')
   IF (M(I).EQ.23) TYPE 220
220  FORMAT(' PLAICE')
   IF (M(I).EQ.24) TYPE 230
230  FORMAT(' WITCH')
   IF (M(I).EQ.25) TYPE 240
240  FORMAT(' GRAB')
   WRITE(6,160)CENT1(I),CENT2(I)
160  FORMAT(' CENTROID IS 'F10.6,4X,F10.6)
   WRITE(2,161)CENT1(I),CENT2(I)
161  FORMAT(F12.6,4X,F12.6)
   WRITE(6,170)Y1,Y2,XY
170  FORMAT(' DF1 VARIANCE'F12.5' DF2 VARIANCE'F9.5' COVARIANCE'F9.5)
   IF (Y1.NE.0) GO TO 173
   TYPE 172
172  FORMAT(' VARIANCE DF1=0 CALCULATIONS FOR THIS GRP CEASE')
   GO TO 250
   IF (Y2.EQ.0) GO TO 174
173  TYPE 311
311  FORMAT(' ENTER F-VALUE FOR THIS GRP.,F.05,NUM DF=2,DEN DF=N-2')
      ACCEPT *,F
      F1=XY**2
      D=SQRT(((Y1+Y2)**2)-(4*(Y1*Y2-F1)))
      EIGEN1=(Y1+Y2+D)/2

```

```

EIGEN2=(Y1+Y2-D)/2
SLOPE1=XY/(EIGEN1-Y1)
SLOPE2=-1/SLOPE1
EIGEN3=EIGEN1*EIGEN2
N3=(N(P)-1)*2
N4=N(P)*(N(P)-2)
C1=(EIGEN3*N3)/N4
C=F*C1
C WRITE(6,7) C,N(P),EIGEN1,EIGEN2
C7 FORMAT(' C AND N(P)',F14.5,2X,I4,2X,F14.5,2X,F14.5)
CLX(1)=SQRT(C/Y2)+CENT1(I)
CLY(1)=CENT2(I)
CLX(2)=CENT1(I)-SQRT(C/Y2)
CLY(2)=CENT2(I)
CLX(3)=CENT1(I)
CLY(3)=SQRT(C/Y1)+CENT2(I)
CLX(4)=CENT1(I)
CLY(4)=CENT2(I)-SQRT(C/Y1)
G=EIGEN2*(1+(SLOPE1**2))
G1=C/G
G2=SQRT(G1)
CLY(5)=G2+CENT2(I)
CLX(5)=CENT1(I)+SLOPE1*(ABS(CLY(5)-CENT2(I)))
G3=EIGEN2*(1+(SLOPE1**2))
G4=C/G3
G5=SQRT(G4)
CLY(6)=CENT2(I)-G5
CLX(6)=CENT1(I)-SLOPE1*(ABS(CLY(6)-CENT2(I)))
DO 300 L=1,6
WRITE (6,310) CLX(L),CLY(L)
WRITE(2,400)CLX(L),CLY(L)
900 FORMAT(F12.6,4X,F12.6)

310 FORMAT(' COORDINATES OF ELIPSE=',F9.3,2X,F9.3)
300 CONTINUE
GO TO 250
174 TYPE 175
175 FORMAT(' VARIANCE DCRIM SCORES 2=0,95% CL FOR 2ND DIMENSION 2=0')
250 CONTINUE
END

```

END

1 | 6 | 0 | 9 | 8 | 3

FIN