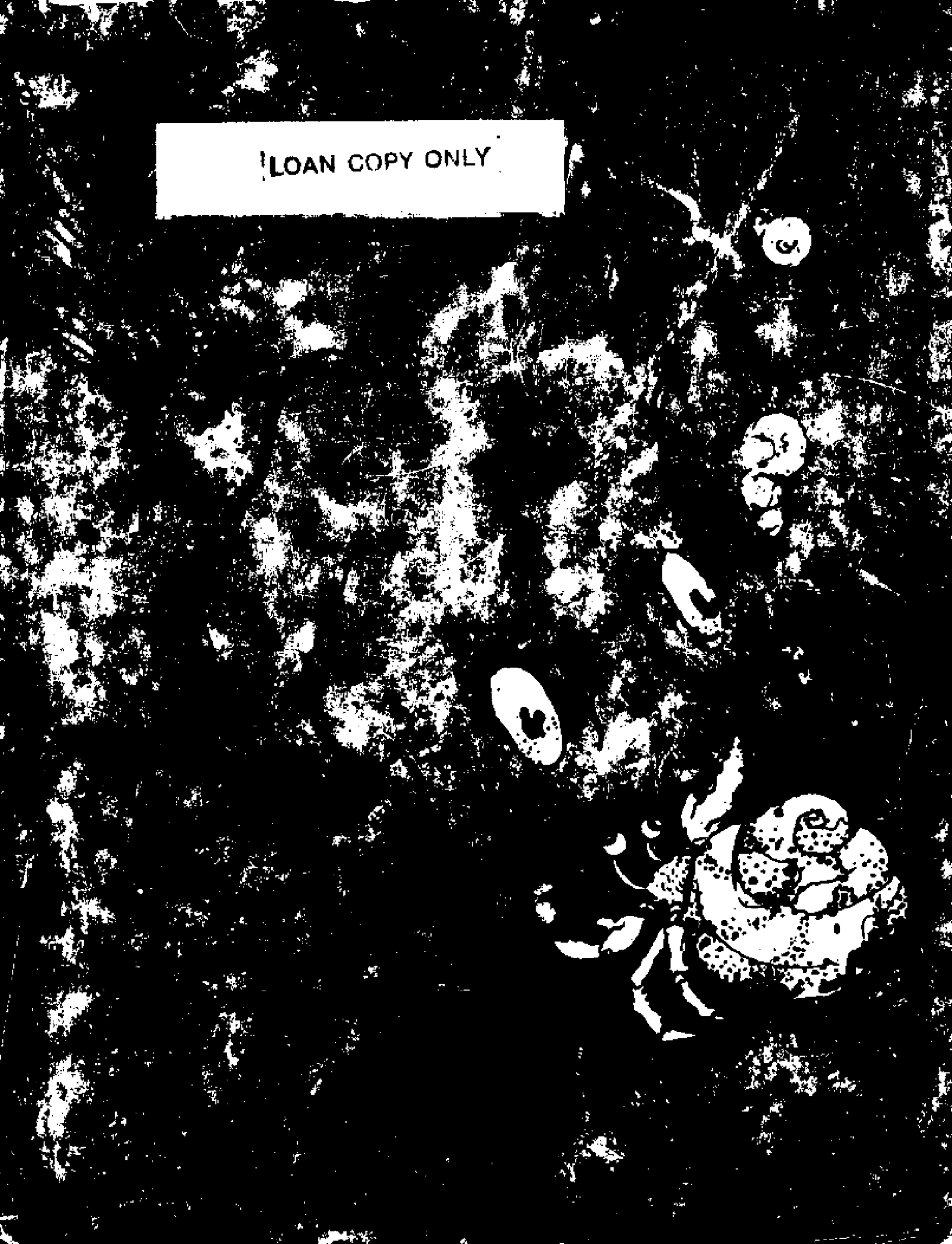
GUTSHOP 81



GUTSHOP '81

Fish Food Habits Studies
Proceedings of the Third Pacific Workshop

December 6-9, 1981
Asilomar Conference Center
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Moss Landing Marine Laboratories, John Martin, Director; Fisheries Research Institute, Robert Burgner, Director; and the Washington Sea Grant Program, William Davis, Director, provided the important sponsorship to the workshop and our own involvement as chairpersons.

The assistance of the staff and students at Moss Landing was particularly essential to the preparation for and smooth operation of the workshop. Linda Kellogg and Signe Lundstrom provided bookkeeping services for our convoluted budget; Rosie Stelow and Deborah Tuel typed the many flyers, forms, and memos; Sandi O'Neill took care of all mailings; and Moss Landing students Mark Carr, Mike Kelly, Linda Martin, Feney Matthews, Lisa Natanson, Ken Nicholson, Mickey Singer, Bruce Welden, Patty Wolf, and Gilbert Van Dykhuizen provided valuable assistance at all phases of the workshop. Bruce Stewart contributed his talented artistry to the flyers, buttons, and other GUTSHOP '81 graphics.

The staff at the Asilomar Conference Center, particularly Oriol Sandwell, was responsible for the pleasant accommodations, fine food, and party and workshop facilities. The generally fun atmosphere and beautiful scenery was enjoyed by all the participants.

Washington Sea Grant Communications coordinated the publication of these proceedings. We also wish to thank the GUTSHOP '81 session leaders for assembling a superb slate of speakers, conducting the sessions within the allocated time constraints, and arranging for reviews of the manuscripts. And to all the participants, we extend our congratulations for a stimulating, educational, and professional workshop.

Key Words 1. Fisheries 2. Fish predation 3. Fish--as prey 4. Food webs 5. Marine biology

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Contents

Introduction

These proceedings document the presentations and discussions which occurred during GUTSHOP '81, the third Fish Food Habits Studies Workshop, held 6-9 December 1981 at the Asilomar Conference Center, Pacific Grove, California. The first GUTSHOP in 1976 and the second GUTSHOP in 1978 were initiated to bring together a diverse group of scientists actively involved in studies of food habits, predation, feeding behavior, competition, and food web structure in fishes. The general purpose of these workshops was to achieve some consensus on sampling design and techniques, analysis and statistical procedures, and interpretive tools available for fish food habits studies. The proceedings of GUTSHOP '76 and GUTSHOP '78 were published in Simenstad and Lipovsky (1977) and Lipovsky and Simenstad (1978), respectively.

While the accomplishments of the first two workshops obviously resolved many of the questions plaguing our studies, the general opinion of the GUTSHOP '78 participants was that a third workshop would be beneficial and should consider both continued discussion of never-ending problems, such as statistical analyses, as well as topics that we had not yet covered, such as the bioenergetics of feeding. Although it took three years for us to assemble again, the wait was rewarded by a highly evolved meeting in which all had something new to discuss and the infusion of new scientists broadened our perspectives. The decision to hold GUTSHOP '81 in California resulted from a survey of the participants at the end of GUTSHOP '78, which suggested that many California scientists who were involved in fish food habits studies were not able to contribute to the workshops held in the Pacific Northwest. Greg Cailliet was asked to act as co-chairman to accomplish efficient workshop arrangements and to ensure contact with California scientists who were not yet familiar with the workshops. The Asilomar Conference Center in Pacific Grove was chosen because it was close to the Moss Landing Marine Laboratories, Greg's institution, and because of its superb location, accommodations, and facilities. The only disadvantage was that we all spent too much time sequestered in darkened rooms attending to the science of fish guts and did not have enough opportunities to spend some time outside enjoying the balmy weather by the beautiful seashore.

We arranged GUTSHOP '81 around five topics:

I. Methodology and Statistical Analysis
II. Bioenergetics of Fish Feeding
III. Competition and Resource Partitioning
IV. Feeding Behavior of Fishes and Prey
V. Fish Feeding as a Structuring Force on Prey Communities

These topics reflected a major evolution in the workshop from methodological and analytical to interpretive concerns. We felt that the first two workshops had brought us to the point that, although we would want to continue to update ourselves on new inovations in methods and statistics, we could start addressing the reason that most of us were conducting fish food habits studies, i.e. to test hypotheses regarding ecological concepts involving predation or feeding behavior and to delve into the role of feeding ecology in the population dynamics of exploited fish populations. Thus, we continued two topics from the previous workshops--methodology and statistical analysis, and competition and resource partitioning--with some change in approach, and added the three new topics which were new to the workshop and reflect more modern ecological subjects of study.

In probably one of the most critical phases of a successful workshop or symposium, we then selected our session leaders who would be responsible for choosing and inviting the participants in their sessions, conducting the session presentations and discussions, and arranging manuscript preparation and review. We cannot stress enough how critical the role of the session leaders was and how much credit for GUTSHOP '81 should go to our six session leaders. Based upon the past participants in the GUTSHOPs and those who had requested the two published proceedings, the call for papers and announcement was circulated and, as you will read in these proceedings, GUTSHOP '81 took form, not unlike a benevolent sphinx once again arising to pose the latest riddles in fish feeding ecology.

Participation in GUTSHOP '81 was, as usual, the most rewarding aspect of the workshops. From 49 participants in GUTSHOP '76 and 65 in GUTSHOP '78, the participants in GUTSHOP '81 increased to 107 registered scientists from even further reaches of North America and from Europe. Given the shift in session topics, there also was a notable change in the composition of the participants from those involved in the technical aspects of fish food habits studies to those designing and conducting experiments to test ecological hypotheses. This also produced a change in the general level and style of discussions, from specific questions and responses of clarification to more theoretical, often esoteric exchanges about the mechanisms and processes which determines why fish eat what they do.

As co-chairpersons, we have partitioned our involvements and responsibilities in arranging and conducting GUTSHOP '81 and assembling the proceedings between us. Greg Cailliet was principally responsible for planning the program and format of the workshop, organizing the session leaders, scheduling the Asilomar Conference Center and its facilities, and for conducting the workshop; Charles Simenstad was principally responsible for compiling the manuscripts, organizing the proceedings, and interacting with Washington Sea Grant through the printing of this volume. Given the mutuality of our contributions, we determined the order of the editorship by the flip of a coin.

The Summary and Recommendations provides our synopsis of GUTSHOP 81's accomplishments, the riddles we left unaddressed, and when, where, and in what form the benevolent GUTSHOP sphinx may rise again.

Gregor Cailliet

Charles Simenstad

July 1982

<u>GUTSHOP Proceedings Publications</u>

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Session I

Methodology and Statistical Analysis

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Variability of the Weight of Stomach Contents Of Fish and Its Implications for Food Studies

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Introduction

Difficulty in determining the optimal sample size to quantitatively describe the diet of fish has received attention in recent years. For example, two workshops on fish food habits studies have included a number of papers that address the problem of determining sample size (Simenstad and Lipovsky, 1976; Lipovsky and Simenstad, 1978). In practice, however, sample sizes are often based on intuition, time constraints, and the number of personnel available for collecting and analyzing the data, especially when a study of fish food and feeding habits is not the sole objective of the cruise (Langton et al., 1980; ICES, Demersal Fish Committee, 1980). The problem with this intuitive or, at least, nonstatistical approach is obvious when designing a survey to quantitatively evaluate predator-prey interactions and estimate the daily ration of fish populations for use in multispecies assessment models. In order to allocate efficiently the available resources, it is necessary to know approximately the magnitudes and sources of stomach content variability. The Northeast Fisheries Center has conducted a large-scale fish feeding habits survey for several years as part of the MARMAP (Marine Resources Monitoring Assessment and Prediction) program. In this paper, the data for Atlantic cod are analyzed to determine the sample sizes needed in future surveys to estimate mean stomach contents at a desired level of precision.

Methods

Beginning in 1973 a systematic attempt was made to collect Atlantic cod stomachs by the Northest Fisheries Center, as part of the MARMAP program. During the period from 1973 through 1976, over 1500 individual cod stomachs were collected and preserved at sea for quantitative laboratory analysis. Scientists and technicians sampled 100 cod stomachs from each of three defined geographic areas per cruise. These 100 stomachs were to be taken from 50 young-of-the-year and 50 adult fish. At each station no more than 10 stomachs were to be collected and collections were not made at consecutive stations. The only exception occurred when it appeared that 50 adult or 50 young-of-the-year would not be taken within a geographic area. For this case, fish were collected as necessary to obtain the desired sample size.

In the laboratory, preserved stomachs were opened and the contents emptied onto a fine mesh screen to permit washing without loss of any food items. The various prey items were sorted, identified and damp dried on bibulous paper. The wet weight of each group was then immediately determined. Further details of field and laboratory procedures are reported in Langton et al. (1980).

To estimate the contribution of various factors to the total variability in stomach content weight, a variance component such as

$$W_{ijkl} = \mu_L + Y_i + S_{ij} + AT_{ijk} + E_{ijkl} \qquad (1)$$

could be fit to the cod data. In equation (1),

W_{ijkl} is the weight of food in the stomach of an individual fish,

μ_L is the general mean stomach contents weight of all fish of lenght L,

Y_i is the effect of the i^{th} year,

S_{ij} is the j^{th} seasonal effect within the i^{th} year,

AT_{ijk} includes factors such as area differences, time of day, etc.,

and

E_{ijkl} is the deviation from the mean not accounted for by the other factors, i.e., the difference in stomach contents between fish of the same length within the same tow.

The estimation of the parameters in a model such as (1) for cod is difficult since the available data are unbalanced with many empty cells. (For a description of variance component analysis for the unbalanced case see, e.g., Searle, 1971.) Furthermore, the distribution of each variable is skewed to the right, and its variance depends on the length of the fish.

In this paper crude estimates are made of the magnitude of the variance components in model (1). The estimates are of sufficient accuracy to provide estimates of the sample sizes required to address various questions at a desired level of certainty.

Since the sample coefficient of variation (cv) appears to be nearly independent of size class (5 cm groupings, Figure 1), it is used as a measure of variability. If two or more fish in the same size class were caught in the same tow, the sample cv is calculated. The average of all such values (over all length classes) is used to estimate $\sqrt{V(E)}/\mu_L$ (which is assumed independent of L). In a similar manner, other quantities such as $\sqrt{V(AT+E)}/\mu_L$ are estimated. From these values rough estimates are made of the relative contribution of each component in model (1) to the total stomach content variability.

Results and Discussion

Table 1 gives the estimated cv for particular subsets of the data. In Table 2 are estimates of the percentage of the total variability due to individual components. The estimates in Table 2 were derived from those in Table 1 by assuming the components in (1) are uncorrelated.

From the tables it can be seen that the data are quite variable. The stomach content weight of Atlantic cod from the same size class, caught in the same place at the same time has a cv of 1; all other factors account for approximately 64 percent of the total variability within a size class.

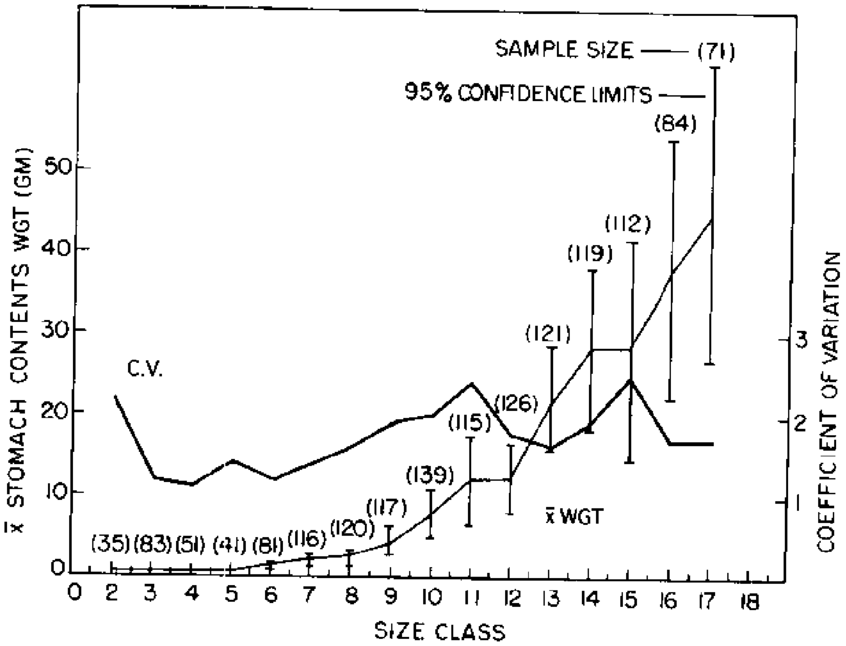

Figure 1. Mean stomach content weight and coefficient of variation versus size for Atlantic cod. Size class are five centimeter groupings: 2 = 6-10 cms, 3 = 11-15 cms, 4 = 16-20 cm, etc.

Table 1. Average over size classes of the coefficient of variation for various levels.

Level	Average c.v.
Within a tow	1.05
Within a season	1.39
Within a year	1.54
Total	1.75

Table 2. Sources of variability of stomach content for fish of the same length.

Source of variability	Percentage of the total
Within tow	36
Due to area, time of day, etc.	27
Seasonal	14
Yearly	23

Table 1 can be used to estimate sample size requirements. Two typical sample size problems are:

(i) the sample size needed to estimate a mean within ± dx100%, with (1-α)x100% certainty

and

(ii) the sample size needed to detect a difference of at least ± dx100% between two areas (or seasons) in mean stomach content (1-β)x100% of the time and claim a difference exists when none actually does only αx100% of the time.

The approximate sizes required are (see e.g., Johnson and Leone, 1977):

$$n \geq [u_{-\alpha/2}/\Delta_d]^2, \text{ for (i)},$$

and

$$n \geq 2\ [(u_{\alpha/2} + u_\beta)/\Delta_d]^2, \text{ for (ii)},$$

where $u_{\alpha/2}$ and u_β are the percentage points of the standard normal distribution, and

$$\Delta_d = d/cv.$$

The approximations above are based on the fact that for large n, the sample mean is approximately normally distributed. As long as the resulting n is large enough so that the sample mean of the stomach content weights has a cv less than .1, the normal approximation should be adequate (Cochran, 1977). For example, to estimate the mean stomach contents for a size class during a season within ± 10% with 95% certainty, then at least (using a cv = 1.4 from Table 1)

$$[-1.96/(.1/1.4)]^2$$
$$= 753$$

fish should be sampled from the size class. It may be noted that for n = 753, the cv for the sample mean will be

$$1.4/\sqrt{753} = .05.$$

Or to detect a difference between two areas of at least 25%, 95% of the time with $\alpha = .1$, then

$$2[(-1.96 - 1.3)/(.25/1)]^2$$

$$= 340$$

fish from the size class should be taken in each area. In the above, the cv is set equal to 1. From Table 1 the cv of fish from the same area, season, and size class is between 1 and 1.4. Figure 2 shows n as a function of k for the two examples.

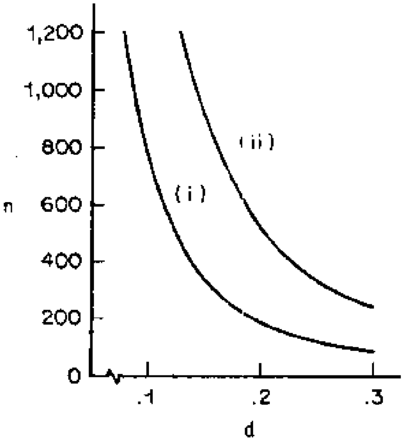

Figure 2. Sample size (n) as a function of d for: (i) $\alpha = .05$, cv = 1.4; (ii) $\alpha = .1$, $\beta = .05$, cv = 1.0.

To lessen the burden of sampling within a size class, length could perhaps be used as a covariate. But a change in consumption may not be consistent for all lengths, thus some size specific changes may go undetected. Furthermore, as indicated by the large variability in stomach contents from a single tow, no matter how many 'factors' are taken into account, a relatively extensive sample is needed either to precisely estimate or to detect differences in the quantity of food in fish stomachs.

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Some Statistical Techniques for Analyzing the Stomach Contents of Fish

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It is often desirable to accompany statements of differences in the foraging behavior and stomach contents of fish with statements of statistical significance. This can be difficult for some of the summary statistics commonly used in stomach content analysis (e.g., Index of Relative Importance, Pinkas et al., 1971, and species diversity) because variance estimates are not readily available. Statistical analysis must be done on the raw data (numbers and weight). The multivariate nature of these data has suggested the need for multivariate statistical analyses (Crow, 1979a), but the complexity of both the technique and the assumptions make this extremely cumbersome. A contingency table analysis is suggested for testing for differences, which avoids the elaborate procedures and assumptions of the multivariate tests. Unfortunately, the numerous prey species found in fish stomachs may require that the data be pooled to make the analysis manageable and the results comprehensible. Three criteria for pooling prey species are discussed.

The presence of statistically significant differences in diets does not always yield an ecologically meaningful interpretation. A method for inferring the food habits of predators by grouping predators with similar stomach contents together is presented. Each identifiable group of predators is labeled a feeding mode. This group of predators is then analyzed further by identifying shared characteristics.

Contingency Table Analysis of Stomach Content Data

Contingency tables (Section 16.4, Sokal and Rohlf, 1969) may be used to analyze stomach content data, where the data are arranged in a two-way, R x C, contingency table, where R is the number of prey categories (e.g., prey species), and C is the number of predator categories (e.g., predator species). Each cell in the table (e.g., the ijth cell) should contain the total number of prey of the ith prey category that were found in the stomachs of the jth predator category

The number of individuals of each prey item is the only statistically valid measurement that can be entered into the table. The frequency of occurrence cannot be used, as previously explained in Crow (1979a), because the row and column sums do not represent any real quantity, which violates the assumptions of a chi-square test.

Numerous authors have pointed out that the number of each prey may not be the best indicator of fish food habits, since it contains several biases (Lagler, 1956). However, the purpose of this procedure is to test for differences in food habits and not necessarily to determine what the food habits are or to quantify the differences in food habits. As long as the biases are constant within each prey category, then the differences in the number of prey should reflect differences in food habits.

Sokal and Rohlf (1969) defined two test statistics, X2 and G:

$$X2 = \mathrm{sum}_{i,j} \left(((Xij - (Xi)(Xj)/N)**2)/((Xi)(Xj)/N) \right)$$

and

$$G = 2 * \mathrm{sum}_{i,j}\, Xij \ln(Xij/((Xi)(Xj)/N)$$

where Xij is the number of prey of the ith prey category eaten by predators in the jth category, Xi is the total number of prey of the ith prey category eaten by all predators, Xj is the total number of prey eaten by predators in the jth predator category, and N is the total number of prey eaten by all predators. Both G and X2 are distributed as chi-square random variables (R-1)(C-1) degrees of freedom. Only G will be used in the rest of this paper since it has better additive properties, and is the preferred statistic (Sokal and Rohlf, 1969). If the calculated value for G exceeds the critical value of the chi-square distribution, then there is a statistically significant difference in the proportions of prey species in the diets of the predators. From this we can infer a significant difference in the food habits of the predators. If this is the case then the column sums of G (sums over prey types) can be examined to determine which predator is most different. Then the test can be rerun without that predator in the table (see example in Table 1). This is analogous to *a posteriori* comparisons of ANOVA, but I am unaware of any formal development of this procedure. In fact, any hypothesis concerning either the predator or prey categories can be tested in a manner analogous to the general linear hypothesis using a log-linear model (Bishop et al., 1975). However, these hypotheses appear to introduce more statistical complexity than is necessary for most applications.

Most statistical textbooks suggest that a chi-squared test is not valid if the expected count for any cell is less than five. However, Cochran (1952) showed that if most cells have expected frequencies greater than five, then a few can have expected frequencies even below one without invalidating the analysis (Lindgren, 1968, Page 326; Snedecor and Cochran, 1968, Page 235). More recent work has shown that expected frequencies lower than 0.25 do not seriously affect the results (Koehler and Larntz, 1980). Hence, some expected frequencies less than five should not be a problem.

Pooling Prey Species into Categories

Statistical analysis of stomach content data is often complicated by the presence of a large number of prey species with several prey species present in low numbers, which results in a large number of degrees of freedom in the model and a small number in the residual. This results in a contingency table containing a large number of cells with small expected values. In this situation, a concise, statistically powerful interpretation of the results necessitates the pooling of prey species into broader categories. The goal of pooling is to reduce the number of categories and increase the sample size in the remaining categories. There are no precise limits on the sample size or number of categories, but I have used the following general guidelines: a limit of 25 prey categories, at least 10 stomachs per prey category and 100 stomachs per predator category. Three criteria can be used to pool prey species: first, necessary pooling; second, intuitive pooling; and third, statistical pooling. Necessary pooling occurs where unidentified stomach contents are present. For example, if there are 5 categories of fish species and 1 category of unidentified fish, then the 5 fish species may need to be pooled with unidentified fish before analysis with additional prey can proceed. Alternatively, the unidentified fish can be dropped from the analysis. But an analysis containing both species of fish and unidentified fish would probably be misleading.

Intuitive pooling uses taxonomy and ecology as the basis for pooling. Different species of the same genus are pooled together when the disparity among the species is not believed to be associated with ecological differences that would cause predators to discriminate among them. For example, if 3 species of pelagic copepods are present in the stomachs, and all 3 have similar behavior compared to other species in the diet, then these species could be pooled into a pelagic copepod category. In addition, rare species can be pooled by habitat into categories (i.e., pelagic, hard substrate, soft substrate, etc.).

Statistical pooling implies that procedures for quantitative pooling be used. In quantitative pooling the investigator formulates a hypothesis that two or more categories act as a single resource and should be pooled. This hypothesis can then be tested using pairwise comparisons. A 2x2 contingency table of the presence and absence of two prey species can be formed giving: the number of stomachs without either species, the number of stomachs with one but not the other, and the number of stomachs with both species. If the resulting G statistic is less than the critical value of a chi-square distibution with one degree of freedom, then the predators are taking the prey independently of each other. This means that the prey may be considered two independent resources and should not be pooled. If the G statistic is larger than the critical value, then the prey are either positively or negatively associated. If the prey are positively associated then the cross-product ratio,

$$a = (X11)(X22)/(X12)(X21)$$

will be greater than one. If the prey are negatively associated, the cross-product ratio will be less than one. The prey may only be pooled if they are positively associated, implying that they are acting as a single resource.

Predator Feeding Modes

A fundamental assumption of most parametric statistical methods is that the data are in a normal or multivariate normal distribution. Even most nonparametric procedures assume a unimodal distribution. However, it is highly unlikely that fish have only one mode of feeding and that that the observed variability in stomach contents represents variability around a mean stomach. It is much more likely that fish have several modes of feeding, with a mean diet for each mode. These modes may represent broad feeding categories such as pelagic, hard substrate, and soft substrate, or finer categories such as pelagic fish versus pelagic zooplankton. These modes may arise due to seasonal changes in the environment, choices made by the fish, individual variation in habitat preference, or morphological variability. However, they do appear to exist and statistical procedures need to be developed to analyze multiple feeding modes. Feeding modes can be identified by grouping together fish with similar stomach contents (i.e., prey items which are frequently found together in stomachs probably represent prey that the predator encounters while foraging in the same feeding mode). Crow (1979a,b) discussed methods of identifying feeding modes using cluster analysis and principal component analysis (PCA).

However, quite often neither of these methods are appropriate or necessary. Clustering methods are multivariate methods and assume a multivariate structure of the data, which is not always true for stomach content data. Although fish often eat multiple prey items, their stomachs do not always contain multiple prey items. Of the data that I have examined (black rockfish, *Sebastes melanops*, brown rockfish, *S. auriculatus*, copper rockfish, *S. caurinus*: from Prince et al., in prep.; king mackerel, *Scomberomorus cavalla*, Spanish mackerel, *S. maculatus*, and bluefish, *Pomatomus saltatrix*: from Saloman and Naughton, unpublished data), the majority of the stomachs contained only one or two prey items, and one of the prey items usually dominated the stomach contents. This is not multivariate data, and although the application of multivariate techniques will usually give correct results, their use is unnecessary, since a classification by the dominant prey item will produce the same results. The reason for the absence of multiple prey in fish stomachs may be linked to prey aggregation. If the prey are aggregated, then a foraging predator will probably fill its stomach on the first clump of prey it encounters. Quite often the presence of multiple prey in the stomach may be the result of the incomplete digestion of a previous meal, rather than the predator taking multiple prey during a meal.

The only exception to the above generalization I have encountered has been the kelp greenling (*Hexagrammus decagrammus*, Prince et al., in prep.). The kelp greenling appears to be a hard substrate grazer, and frequently contains multiple prey items in its stomach. Interestingly, no multi-species associations were found in the kelp greenling stomachs. This may result from the greenling's tendency to frequently change foraging locations on a reef (E. Prince, pers. commun.), and hence to randomly sample the hard substrate organisms.

Once the stomachs have been classified into feeding modes, *a priori* groupings of predators can be tested for a significant difference in the selection of feeding modes with a chi-squared test for independence. If the predators are preying on aggregations, then this test compares the frequency with which a foraging predator encounters an aggregation of a certain type of prey. The frequency is dependent on when, where, and how the predator is foraging (i.e., its feeding mode). A contingency table can be constructed using R feeding modes and C groups of predators. A significant difference in the predators' selection of feeding modes exists if the resulting G statistic is larger than the critical value from a chi-square distribution with (R-1)(C-1) degrees of freedom. The most significantly different group can be identified by looking at the column sums of G and eliminating the group with the largest column sum, and retesting the remaining groups until a homogeneous group of foragers is found. This is analogous to the contingency test presented in table 1, replacing prey species with feeding modes, and Xij is now the number of fish in a mode.

Table 1
Example of Contingency Table Analysis of Stomach Content Data

1) Make a table of the number of each prey found in each predator

	Predator A	Predator B	Predator C	Ni	X2i	Gi
Prey 1	254	15	67	336	3.37	3.19
Prey 2	110	2	10	122	9.48	11.40
Prey 3	33	4	13	50	4.96	4.41
Prey 4	88	9	10	107	6.04	6.12
Nj	485	30	100	615		
X2j	3.63	6.48	13.74		23.85	
Gj	3.61	6.75	14.77			25.13

3 Predators x 4 prey = 2x3 = 6 degrees of freedom

The critical values for a chi-square distribution with 6 degrees of freedom at the 0.05 and 0.005 levels are 12.6 and 18.6, respectively. Since the values of both X2, 23.85, and G, 25.13, are greater than these critical values, there is a significant difference in the stomach contents of the three species. Predator A dominates the expected values due to its large sample size (Na=485). Predator C is very different from Predator A (G2=14.77). Prey 2 is the source of the difference (G2=11.4). Subsequent analysis showed that Predator B was not different form either Predator A or C (Gab=7.7,GBc=6.77). This lack of difference could have been due to the small sample sizes involved, particularly in the bc comparison. The ab comparison is shown below.

	Predator A	Predator B	Total
Nj	485	30	515
X2j	0.42	6.73	7.15
Gj	0.42	7.28	7.70

2 Predators with 4 prey = 3 degrees of freedom

There is no significant difference in the stomach contents of the two species (i.e., G=7.7, and the critical value of a chi-square distribution with 3 degrees of freedom at the 0.05 significance level is 7.82).

Predator Characteristics

The interpretation of feeding modes is dependent on information known about the individual fish, in addition to their stomach contents. Several predator characteristics that can be measured to provide this information include: predator morphology, percent of empty stomachs, gut volume, number of items in stomach, size of prey, number of species per stomach, and when, where, and how the fish were caught. Common morphological measurements include length, condition factor, mouth gape, eye size, eye location, gill raker size and number, and fin position. These predator characteristics can be summarized for each group of predators to aid in the interpretation of group differences. Predator characteristics can also be summarized for each feeding mode, and differences tested using appropriate statistical procedures (e.g., a Kruskal-Wallis test or a contingency table of fish classified by feeding mode and level of a predator characteristic provide simple tests). This approach can be used to determine if different types of predators are using different feeding modes, and thereby identify guilds of different types of predators that forage in similar ways. Examples of the use of predator characteristics are presented in Tables 2 and 3.

Table 2

Testing for Seasonality in Feeding Modes

Feeding Mode	Winter	Spring	Summer	Fall	N	G
1	2 (7.3)*	6 (10.5)	15 (15)	21 (10)	44	16.23
2	18 (8.3)	13 (12)	14 (18)	5 (12)	50	13.08
3	6	7	13	5	31	1.31
4	0	9	12	7	28	5.85
5	1	4	4	1	10	2.21
	27	39	58	39	163	38.68

5 modes X 4 seasons = 4x3 = 12 d.f.

The critical values for a chi-square distribution with 12 degrees of freedom at the 0.05 and 0.01 levels are 21.0 and 26.2, respectively. Since the value of G, 38.68, is greater than these critical values, there is a strong seasonal component in the abundance of feeding modes in species A. The difference arises from mode 1 (G1=16.23) being underrepresented in winter and spring and overrepresented in the fall, and mode 2 (G2=13.08) being overrepresented in winter and underrepresented in summer and fall.

A separate test of feeding modes 3, 4, and 5 showed no significant difference in seasonal abundance among these 3 feeding modes (i.e., G=9.8, and the critical value of a chi-square distribution with 6 degrees of freedom at the 0.05 significance level is 12.6).

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* Numbers in parentheses are expected values

Summary

It appears that most stomach content data are not true multivariate data. Despite the presence of the numerous prey species found in stomachs, individual stomachs often contain few categories of prey and are usually dominated by one prey category. This makes sophisticated multivariate analysis unncessary.

The feeding modes of predators can be indentified by grouping together predators with similar stomach contents. Feeding modes can be infered from the repeated occurrence of similar stomach contents. Different a priori groupings of predators can be examined to see if they differ in their foraging behavior either by comparing their frequency of occurance in different feeding modes, or by the numerical abundance of prey in their stomachs. Either comparison can be made in a contingency table, and any statistical hypothesis can be tested using a log-linear model. Contingency tables can also be used to aid in making decisions concerning the pooling of prey species into broader prey categories.

After the predator feeding modes have been identified, the characteristics of the predators using a mode can be examined, and feeding guilds of predators can be identified if differences in the predator characteristics occur between feeding modes. This approach should aid in making ecological inferences concerning the feeding and competitive relationships of the various types of predators in a system.

Table 3

Testing for Feeding Modes Varying by Length

Feeding Mode	Length (cm) <17.5	17.5 - 22.5	>22.5	N	G
1	14	17	13	44	0.7
2	21	20	9	50	2.2
3	17	10	4	31	5.8
4	1	14	13	28	17.2
5	3	7	0	10	6.2
NJ	56	68	39	163	32.4

5 modes and 3 sizes = 4x2 = 8 d.f.

The critical value for a chi-square distribution with 8 degrees of freedom at the 0.05 level is 15.5. Since the value of g, 32.4, is greater than the critical value, different size fish use different feeding modes. Feeding mode 4 is the most different (G4=17.2), and is overrepresented by large fish.

A separate analysis of feeding modes 1, 2, 3, and 5 showed no significant difference with respect to size among these fish (i.e., G=11.68, d.f.=6, and the critical vlaue at 0.05 is 12.6).

Acknowledgments

This research was conducted under the predator-prey model project of the coastal pelagics program of the Southeast Fisheries Center. I am indebted to Eric Prince, Carl Saloman, and Steve Naughton for the generous use of their data to test out my ideas for analysis. I also thank Patty Phares, Ray Conser, Joe Powers, Lee Trent, Mark Williams, Carl Saloman, and especially Eric Prince and Steve Naughton for their comments on an earlier draft of this manuscript.

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Graphical Methods for Fish Stomach Analysis

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Introduction

Statistical analysis of predator stomach content data is required for two basic purposes: hypothesis testing and description. While many specific hypotheses can be addressed with existing parametric (e.g. t-test, ANOVA) and non-parametric (e.g. chi-squared, runs test) statistical tests, most stomach content data sets are difficult to describe.

As an adjunct to statistical hypothesis testing, a graphical technique has been found effective for descriptive purposes. Prey types are ranked according to an Index of Relative Importance (Pinkas et al., 1971; Cailliet, 1975) and then arrayed in a trophic spectrum diagram (Darnell, 1961; Cailliet et al., 1978). When stomach analysis results are portrayed graphically, trends are easily understandable and easily communicated.

The objective of this paper is to describe the methodology for graphical analysis, and show, by way of example, how the technique can be effectively utilized.

The Graphical Approach

Rather than reiterate procedures commonly used during field, laboratory and data analyses, we have chosen to focus on specific problems that we have encountered during our work, and possible solutions to them. Much of the ensuing discussion can be related to the flow chart diagram (Fig. 1).

1) Sample collection: it is important to obtain and preserve subsamples in an unbiased fashion if meaningful analyses are to follow.

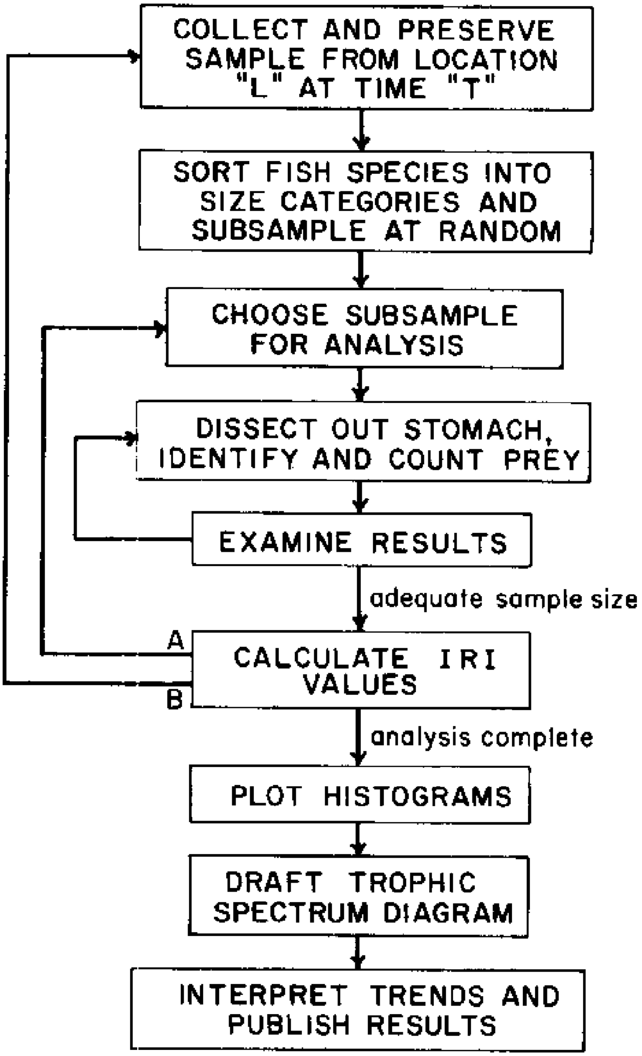

Fig. 1. Flow chart diagram illustrating sequence of steps for graphical analysis of fish stomach content data.

2) Subsample collection: when a fish species (within a sample) is highly variable in length or weight, size categories can be arbitrarily assigned by the investigator. Subsequently, ontogenetic shifts in feeding associated with changes in body size can be analyzed.

3) Subsample choice: a decision must be made at the outset of a study as to how many samples to consider. This decision should reflect

time and budget constraints. After the subsamples are defined, it is important to prioritize the collection so that the overall research goals are met. Frequently, fish species of economic or ecological importance are included for analysis as a high priority.

4) Laboratory analysis: there are three major departures of our methods with those commonly used by other investigators. Firstly, concerning the level of taxonomic detail required for the analysis, we frequently find it unnecessary to identify prey items down to the species level. Sorting prey into higher level classes (e.g. insect larvae, insect adults, fish larvae) can generate an adequate number of categories for representation in a trophic spectrum diagram. Secondly, when dealing with small fish predators (less than 100mm FL), volumetric data have been estimated visually (to the closest 5%). Lastly, occurrence data are scaled by the total number of occurrences of all prey classes so that the histograms plotted in step 7 are comparable.

5) Preliminary data examination: the purpose here is to reach a decision concerning the adequacy of the sample size. As an alternative to a statistical procedure, we arbitrarily assume a sample size of 10 individuals (with food in their stomachs) to be adequate. This assumption can be evaluated at the beginning of a research program by independently analyzing several subsamples of 10 fish from the same sample. If differences are apparent, a sample size greater than 10 is warranted.

6) Calculate index of relative importance (IRI) values: these are calculated across prey categories using average % occurrence, average % volume, and average % frequency data in the formula

$$\text{IRI} = \%\ \text{occurrence}\ (\%\ \text{volume} + \%\ \text{frequency}).$$

7) Plot histograms: after all samples have been processed and all prey categories defined, histograms showing the numerical data can be plotted. Some redefinition of prey categories may be necessary at this step (to reduce the number of categories) so that the data can be arrayed graphically in a legible manner.

8) Draft trophic spectrum diagram: the services of a draftsperson are required to diagram the prey and predator types. After diagrams have been drafted, they can be reproduced photographically at relatively low cost.

Examples of the Graphical Approach

During 4 years of research on fish feeding habits in tidal channels within the Fraser River estuary marshes, we have investigated the following sources of variability:

i) species variability - descriptions of the food habits of dominant fish species (Levy *et al.*, 1979).

ii) temporal variability - daily and seasonal differences in juvenile salmon feeding (Levy *et al.*, 1979).

iii) spatial variability - differences in juvenile salmon feeding within tidal channels (Levy *et al.*, 1979), between neighbouring tidal channels (Levy and Northcote, 1981), and between neighboring marshes (Levy *et al.*, in press).

During 1980 and 1981, field studies were conducted to detect the effects of intertidal log storage on fish populations in the Fraser estuary. One component of the study examined the differences in juvenile salmon feeding in the Point Grey log storage area and the neighbouring Musqueam Marsh. The results of the study serve as an example of the graphical approach we have developed. The details of the experimental procedures are described in a technical report (Levy *et al.*, in press). Briefly, the experiment involved releasing groups of fin-clipped, starved chinook fry simultaneously in the log storage area and the marsh for a short (4-12h) foraging period. On the following low tide, a fraction of the marked fish were recaptured as the tidal channels dewatered, and then preserved for stomach analysis in the laboratory. In addition to analyzing the stomachs of 10 marked chinook fry from each release group, wild (unmarked) chinook fry were obtained and included for comparison of feeding habits.

Results from this experiment showed a clear difference in the feeding of chinook fry in the log storage area and the marsh. The size of the histograms, representing % volume, % occurrence and % frequency results (Fig. 2), indicate the relative importance of the prey types arrayed on the abscissa. A histogram plot (Fig. 2) can be usefully included as an appendix of a report. The IRI values calculated from the data (Fig. 2) are ranked and serve as a basis for a graphical plot (Fig. 3). Thus, both Fig. 2 and Fig. 3 portray identical results.

Spatial and temporal differences in feeding can be explained in reference to the graphical plot (Fig. 3). Chinook fry recaptured at the two release sites had markedly different diets. The proportion of insects (adults, pupae and larvae) was greater in the stomachs of fish recaptured in the Musqueam Marsh than in the stomachs of fish recaptured in the log storage area. Marked chinook fry in the Point Grey log storage area acquired high proportions of epibenthic invertebrates during all of the releases. In particular, the proportion of *E. confervicolus*, *Corophium* sp., *N. mercedis*, and fish larvae was higher in the stomachs of chinoook fry from the log storage area. As a result of this analysis, we concluded that insect production in Fraser estuary marshes is very closely linked with the presence of marsh plants.

In this example, the diet of chinook fry was portrayed at different times in 2 separate locations. This type of analysis can be extended to graphically portray results for a combination of fish species, locations, and sampling times. When many fish species are considered, the results represent a trophic spectrum diagram (Fig. 4). A considerable amount of information can be effectively represented in a relatively small space. Here again, it is important to have the raw data accessible, either in an appendix or a data repository.

Conclusion

Graphical representation of fish stomach content data is relatively inexpensive, easily performed and easily understood. Large data sets can be described and simplified for effective communication. For management purposes, qualitative data are frequently sufficient to

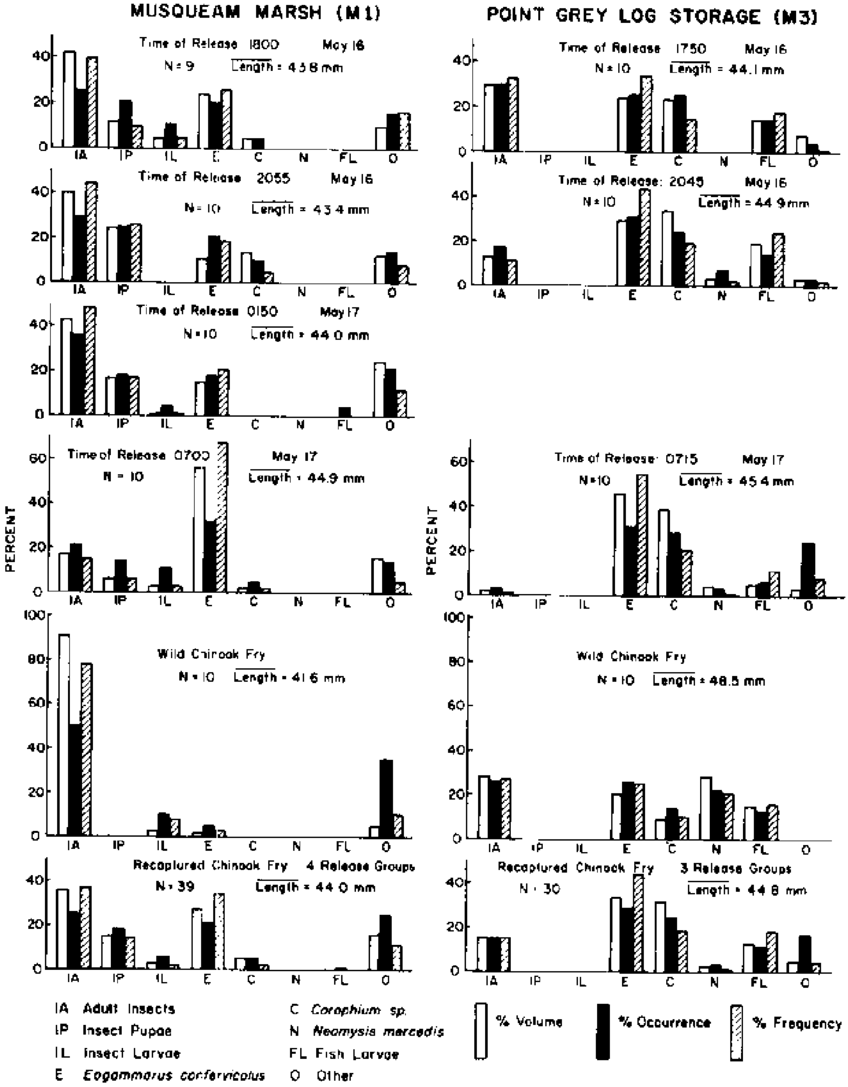

Fig. 2. Results of chinook fry mark-recapture feeding experiment in the intertidal areas of the North Fraser estuary, May 16-17, 1980.

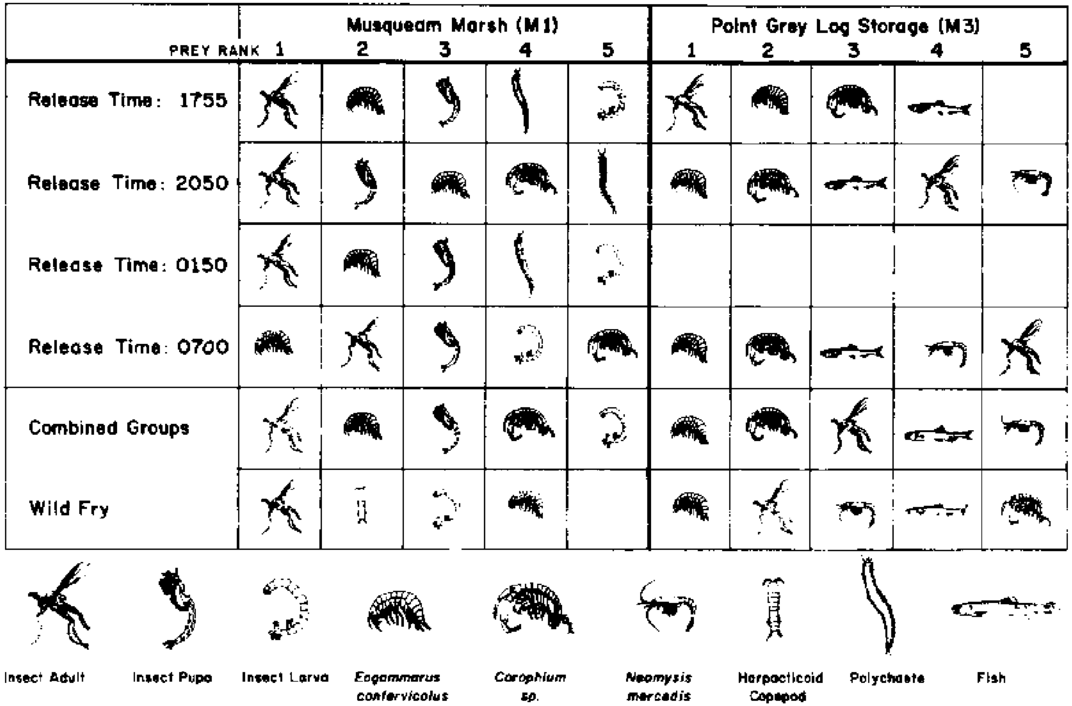

Fig. 3. Graphical portrayal of the rank importance of prey items acquired by chinook fry during the May 16-17, 1980 mark-recapture feeding experiment. Diagram not drawn to scale.

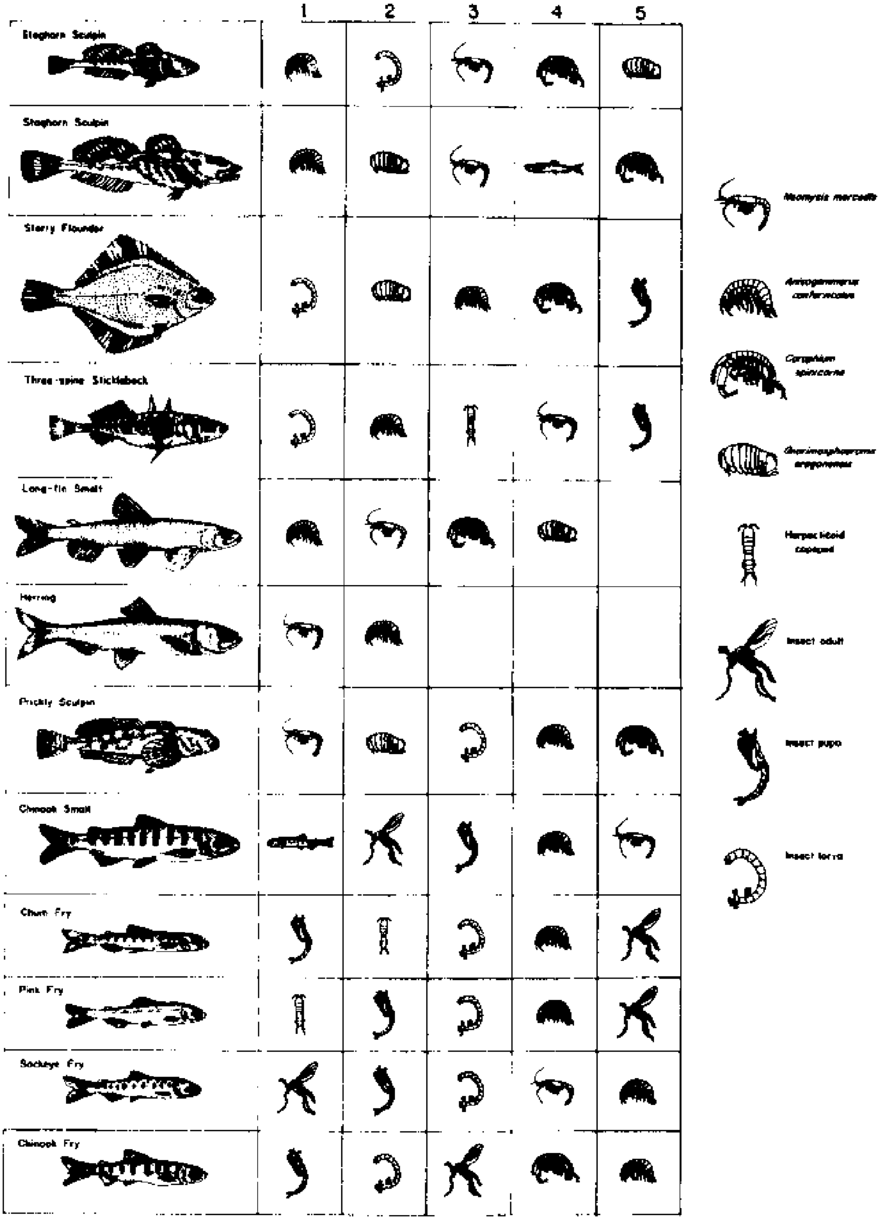

Fig. 4. Trophic spectrum showing rank importance of prey in stomachs of dominant fish species of a Woodward Island tidal channel during 1977-78. Diagram not drawn to scale. Modified from Levy et al. (1979).

represent the prey organisms that fish acquire in the aquatic environment. When patterns or differences emerge, meaningful hypotheses can be formulated and tested during subsequent research.

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Constraints of the Laboratory Environment On Predator-Prey Systems in Fishes

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Introduction

The performance of fishes is commonly studied under experimental conditions by isolating behavioral mechanisms that structure their predator-prey relationships (Ivlev 1961; Ware 1972; Werner and Hall 1974; Stein 1977). Many types of methodological bias, however, can influence results of laboratory predator-prey studies (Lewis and Helms 1964; Espinosa and Deacon 1973). The goal of this paper is to improve the understanding of the frequent disparity between results of laboratory and field predator-prey studies.

The importance of predator-prey studies in solving real-world problems is exemplified in the Snake River where harvest of salmon and steelhead is a major economic consideraton. Predation upon juvenile anadromous salmonids (smolts) in the Snake River by several piscivorous fishes is one factor that has severely reduced chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Salmo gairdneri) populations of that system (Bennett et al. 1981). Smallmouth bass (Micropterus dolomieui) are reported to eat mainly crayfish (Procambarus spp.) and few smolts, while channel catfish (Ictalurus punctatus) eat mostly smolts and a few crayfish during the smolt migration (Bennett et al. 1981). I designed a laboratory predator-prey study with the objective of determining what mechanisms governed prey selection by smallmouth bass and channel catfish when they were offered chinook and steelhead smolts and crayfish. The disparity between my results and those collected in the Snake River, however, was considerable. Resolution of this disparity leads to the objectives of this paper, which are: 1) briefly assess potential sources of methodological bias affecting laboratory and field predator-prey studies in fishes; and 2) analyze possible factors responsible for the disparity between laboratory and field data on prey selection by smallmouth bass and channel catfish in the Snake River.

Laboratory Predator-Prey Study

Two smallmouth bass (269 and 455mm) and two channel catfish (530 and 610mm) were collected by trapnet in the Little Goose Pool, Snake River. Their lengths approximated the medium and larger-sized individuals of their respective populations. Chinook and steelhead smolts were taken from stocks at the University of Idaho, and their length ranges (70-120mm and 120-360mm, respectively) approximated those of the downstream smolt migrants in the Snake River. As a result of a shortage of steelhead smolts, they were only used in the first experiment with smallmouth bass. Crayfish were collected in the Palouse River, Idaho, by minnow trap. All predators and prey were held in separate 665 l circular aquaria prior to experimentation. All prey species were fed Oregon Moist Pellets® four times daily, and predators were starved 1-2 days before each experiment.

Prey selection experiments were conducted in a 1,640 l aquarium with gravel and angular rubble substrate. Each test of predator selectivity was one experimental trial. Two and three trials, respectively were conducted for channel catfish and smallmouth bass. Two predators of the same species were introduced into the test aquarium. Prey, which had been measured several hours earlier (smolts total length and crayfish carapace length) and allowed to recover from handling stress, were then added to the test aquarium in various ratios (Tables 1 and 2). The test aquarium was maintained in total darkness during prey introduction and for several hours following to allow for their acclimation to the test environment (Stein and Magnuson 1976). During the experiments, light intensity varied from total darkness to midday conditions approximating the prevailing photoperiod. Prey in the experiments were fed Oregon Moist Pellets® four times daily and each experiment was terminated when at least 30 percent of one prey item had been eaten.

Results

Trends of prey selection by smallmouth bass and channel catfish in my laboratory trials were consistent. Six smolts and no crayfish were eaten during the first smallmouth bass prey selection trial (Table 1). Two of the 5 chinook smolts were eaten by smallmouth bass during the second trial; again no crayfish were selected. Crayfish were both vulnerable and available to smallmouth bass during the trials since 8 were eaten when crayfish alone were introduced in the third trial. Channel catfish ate 3 crayfish and no smolts during the first trial (Table 2). Five crayfish were eaten and no smolts were consumed during the second trial. Experiment duration ranged from 72 to 168 hours.

Problems in the interpretation of these data stem from several factors. Sample sizes are very small; since only two individuals of each predator species were used in trials, the lack of data on variation in individual behavior and preference is obvious. Although my laboratory results are consistent in revealing trends in predation by smallmouth bass and channel catfish, they differ substantially from results of prey selection for these predators in the Snake River. Here the contribution of smolts to the diet of smallmouth bass was relatively minor; smolts were found in 16 percent of the stomachs analyzed; smolts contributed more significantly to the diet of channel

Table 1. Number of prey selected by two smallmouth bass (TL-269 and 455mm) in a laboratory aquarium, May 1980.

	Prey Introduced				Number of Prey Eaten		
Trial	Steelhead	Chinook	Crayfish	Experiment Duration (hr)	Steelhead	Chinook	Crayfish
1	5	5	10	120	2	4	0
2		5	10	72		2	0
3			10	168			8

Table 2. Number of prey selected by two channel catfish (TL-530 and 610mm) in a laboratory aquarium, June 1980.

	Prey Introduced			Number of Prey Eaten	
Trial	Chinook	Crayfish	Experiment Duration (hr)	Chinook	Crayfish
1	10	10	72	0	3
2	10	10	72	0	5

catfish, however, and they occurred in over 30 percent of the stomachs analyzed (Bennett et al. 1981).

Discussion

Based on my tenatative laboratory results, I was unable to isolate factors influencing predator-prey interactions between smallmouth bass, channel catfish, chinook and steelhead smolts, and crayfish in the Snake River.

In the laboratory environment, bias from several potential sources can change performance of predator and prey from that of their natural surroundings. An obvious and major problem with laboratory studies lies in the contrast between the natural environment and the aquarium (Warren et al. 1979). Aquaria used in laboratory studies are usually characterized by small size and very low habitat complexity. Aquarium size alone can affect fish behavior (Andorfer 1980); both foraging behavior of predators, and escape behavior of prey are influenced by restricted space. The natural distribution and availability of prey may be difficult to simulate in aquaria because of the lack of habitat heterogeneity.

The level of structural complexity in an environment has a significant effect on predator-prey interation (Cooper and Crowder 1979). Physical structure in the environment (habitat heterogeneity) leads to spatial patchiness in prey distribution (Werner and Hall 1974) and affects foraging strategy of predators (MacArthur and Pianka 1966). The level of structural complexity in the environment affects predator diet breadth, energy expenditure per attack on prey, and search and pursuit components of foraging in response to patterns of prey distribution associated with that particular level of complexity. Vulnerability of prey often depends on how they use physical structure in the habitat, and their vulnerability in aquaria (homogeneous habitat) may not reflect that in the natural environment (Stein 1977 and Gillen et al. 1981).

The stress on predator and prey due to handling as well as chronic stress related to their confinement is difficult to control and is a characteristic problem of experiments in aquarium conditions. Stressed fish are more suceptible to predation than non-stressed individuals under natural and experimental conditions (Herting and Witt 1967). A seldom addressed source of bias related to stress deals with the acclimation of predators and prey to the test aquarium. Should predator and prey be acclimated simultaneously? If not, which should be acclimated first? The ramifications of this situation are obvious and the problem deserves further treatment.

Variation in the behavior of individual predators and prey should be considered as a potential source of bias. Although this source of bias is not inherent in the experimental system itself, it should be considered in the study design. The use of small numbers of predators in particular could bias results of predator-prey studies conducted in experimental systems.

Studies of predator-prey systems in the natural environment are also subject to error. The abundance and distribution of prey (availability) is difficult to assess accurately. The effect of physical habitat structure on the temporal and spatial scope of interaction of predator and potential prey is often hard to define. The situations we observe in the field and try to simulate in the laboratory may not accurately reflect actual conditions due to shortcomings in our experimental design and biases in sampling gear.

The performance of predator-prey systems (manifested prey selection) is dependent upon the interrelationships among several variables. Bias from the previously mentioned sources can influence relationships between these variables, resulting in changes in system performance (Figure 1).

Laboratory predator-prey study

Controlled experiments of prey selection by smallmouth bass have been documented in the literature (Lewis et al. 1961; Lewis and Helms 1964; Stein 1975; 1977; Stein and Magnuson 1976 and Paragamian 1976). The selection of smolts over crayfish by smallmouth bass in my laboratory experiments is not entirely surprising. Lewis et al. (1961) and Lewis and Helms (1964) documented prey selection between fish and crayfish by smallmouth bass in aquaria and ponds. Smallmouth bass selected fish over crayfish in aquaria, however, they reversed this trend in the pond environment, selecting crayfish over fish. Smolts in my laboratory trials often displayed erratic movements and exhibited behavioral characteristics much different from those in holding tanks; this probably resulted from the combined effects of confinement and predator presence (Beyerle and Williams 1968). Vulnerability of smolts was probably increased in the aquarium due to their modified behavior and inability to escape the predator (Lewis and Helms 1964).

At the approach of a predator, larger crayfish flee before making a defense stance of chelae display; their vulnerability increases dramatically with the distance of their flight as they become exhausted (Stein 1977). Since larger crayfish in my laboratory trials would never swim more than one meter before chelae display, their vulnerability in the aquarium was probably lower than that of those in the natural environment (Stein 1977). Vulnerability of smaller life stages of crayfish in my trials was probably reduced or similar to that of those in the natural environment. Their use of the angular rubble substrate and corners of the aquarium as cover agree with observations by Stein (1975; 1977 and 1979) and Stein and Magnuson (1976).

The relative vulnerabilities of smolts and crayfish were probably reversed in the aquarium due to their modified behavioral patterns. Since smallmouth bass forage optimally (Stein 1977), they may have switched their prey selection from crayfish to smolts to minimize their cost-benefit ratio of feeding, which is the premise of optimal foraging theory (Werner and Hall 1974); and since the predators were large, they were probably able to easily handle all sizes of prey offered in the experimental trials (Werner 1974). Abundance of prey was apparently not as important as their relative vulnerabilities since smolts were selected even when crayfish were twice as abundant (Ware 1972).

The piscivorous nature of channel catfish has been well documented in the literature (Bailey and Harrison 1948; Busbee 1968; and Starostka and Nelson 1974). Busbee (1968) suggested that channel catfish larger

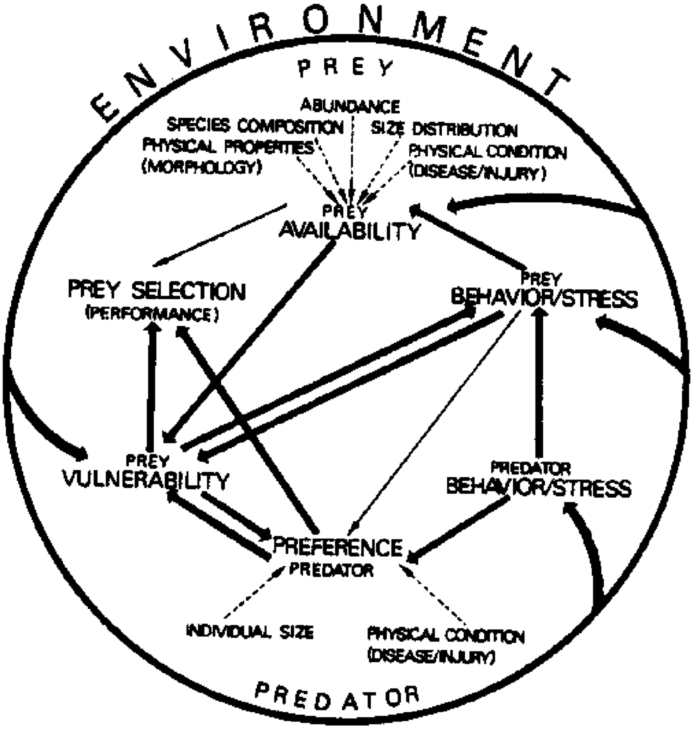

Figure 1. Conceptual model of relationships between variables determining performance (manifested prey selection) of a predator-prey system, demonstrating how relationships are affected by changes in environment.

┈┈► Relationships between variables affecting predator preference and prey availability, which are relatively independent of changes in environment and can be controlled to some degree under experimental conditions.

——→ An indirect relationship between variables determining system performance, which changes with alteration of environment and cannot be controlled under experimental conditions.

━━➡ Direct relationships between variables determining system performance, which change with alteration of environment and cannot be controlled under experimental conditions.

than 40cm should be considered mainly carnivorous, and Bailey and Harrison (1948) revealed that the utilization of forage fish by channel catfish was positively correlated with water clarity and forage fish abundance; no marked preference or selection of specific fish foods was evident. Channel catfish appear to be opportunistic in their feeding. It is unclear, however, whether channel catfish are aggressive pursuit predators or simply feed on dead and dying fish from the bottom (Swingle 1950). Bailey and Harrison (1948) observed parts of forage fish in the stomachs of channel catfish and determined that they feed mostly at night. Since active pursuit would be difficult in total darkness, this evidence suggests that one of their modes of forage fish utilization may be scavenging.

Smolt mortality associated with dams on the Snake River is signficant, and has been estimated at 15 to 20 percent at each dam. Assuming that channel catfish are opportunistic feeders, the high smolt mortality associated with each dam could conceivably provide large numbers of dead and stressed fish for their consumption. Though I was unable to analyze the utilization of dead and moribund fish in the laboratory, my results suggest that channel catfish may not be active pursuit predators of smolts. It must be remembered, however, that the foraging behavior of channel catfish may have been influenced by the aquarium environment, and that no firm statement can be made about their modes of smolt utilization.

Summary

Smolts were consumed in preference over crayfish by smallmouth bass, and channel catfish ate crayfish and no smolts in my laboratory trials. My data are very tentative and conflict with those collected on smallmouth bass and channel catfish prey selection in the Snake River. My results were influenced by several types of methodological bias in the laboratory environment and no generalizations can be made about factors governing predator-prey interactions between smallmouth bass, channel catfish, chinook and steelhead smolts, and crayfish in the Snake River.

Methodological bias from several sources can affect the results of laboratory predator-prey studies. The size of the test environment and its associated habitat complexity is of primary consideration. Handling of predators and prey should be minimized in controlling stress factors which can affect their behavior and performance. Relevant problems of determining prey availability in the field should be addressed when trying to simulate these conditions in the laboratory environment.

Acknowledgments

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Beyond Guts

The Powers and Pitfalls of Experimentally Documenting Functional Aspects of Fish Foraging Behavior

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Introduction

Most studies of the feeding ecology of fishes usually result in the rediscovery of fish diets and further documentation of the prey assemblages potentially susceptible to predation (Sibert and Kask 1978). It is at this point that a well designed descriptive approach based upon divergently contrasting dependent variables usually lacks the ability to explain why fish eat what they do. For example, we usually find a degree of "selectivity" or "electivity" in fish diets, where the fish have fed upon prey which were neither numerically nor spatially prominent. Obviously, we need to step beyond the descriptive stomach contents data in order to adequately explain fish feeding behavior. A desirable solution to this dilemma is to experimentally or observationally dissect the behavioral interactions between the fish and their potential and actual prey organisms.

Microcosm studies of the behavioral interactions between fish and prey have been a major part of our research on the estuarine carrying capacity for juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal, a fjord extension of Puget Sound. Based upon our documentation of the stomach contents of juvenile chum salmon migrating through Hood Canal and the structure of the epibenthic and neritic zooplnakton assemblages they encountered, we hypothesized that the growth and residence times of the juvenile salmon in estuarine and nearshore habitats was determined by foraging success (Simenstad and Salo 1982). But, in order to test this hypothesis we needed to develop a model of prey ingestion, growth, and behavior based upon composition and standing stock of preferred prey. Apparent prey selection for large, relatively rare epibenthic (harpacticoid copepods, gammarid amphipods) and neritic zooplankters (calanoid copepods) was evident in our descriptive data (Simenstad et al. 1980). Thus, we needed to design laboratory and field experiments to elucidate the causal mechanisms of the prey selection process, particularly to discriminate between passive (encounter rate) and active (behavioral) selection (Eggers 1982), which would greatly influence our ability to make predictions about foraging success under known prey assemblages.

Research Perspective

Holling (1959) developed a functional components model which allows the predation process to be experimentally defined on the basis of six components: 1) search, 2) encounter, 3) pursuit, 4) capture, 5) eating, and 6) digestion. These can be redefined functionally into three components: 1) the rate of encounter (search + encounter), 2) the handling time (pursuit + capture + eating + digestion), and 3) the capture success. The relationship of these components to the rate of ingestion, I, may be expressed as:

$$I = \frac{\lambda S}{1 + \lambda H}$$

where λ is the rate of prey encounter, S is the capture success, and H is the handling time. The rate of encounter is dependent upon prey visibility, fish swimming speed, and prey density. Prey visibility varies as a function of the reactive distance (the minimum distance at which the fish can locate a specific prey), prey size, shape, color and contrast, and motion; light intensity and turbidity affect the effective prey visibility. Capture success is determined by prey size and avoidance behavior and fish mouth gape; handling time similarly depends upon prey size and behavior, fish mouth gape, and fish hunger.

Since about 1970, a number of investigators have studied these components by testing hypotheses about optimal foraging theory (Ware 1972; Werner 1974; Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Vinyard and O'Brien 1976; Durbin 1979; Furnass 1979; O'Brien 1979; Gibson 1980; Gardner 1981) and the methodology is well documented. To test the encounter rate model and examine the prey selection process in multispecies prey assemblages, we designed experiments dimilar to Ivlev's (1961), wherein fish were offered dichotomous prey assemblages under a spectrum of prey density ratios. We extended this approach by inclusion of treatments on the estimated visual field and encounter rate. We also examined the bioenergetic cost, in terms of somatic growth, of fish upon different prey taxa and ration levels over the normal period of estuarine residence of the juvenile chum salmon. Acknowledging the many biases inherent in quantifying feeding behavior via experiments in aquaria, we extended our controlled experiments to more complex habitats where the cryptic and behavioral escape responses of the prey and the fish foraging behavior were not as compromised. These microcosm experiments expanded upon past studies of fish predator-prey interactions (Vince et al. 1976; Virnstein 1977, 1979; Nelson 1979) by examining the effect of differential foraging success upon the growth and survival of the fish (Pardue 1973; Cooper and Crowder 1979).

Our objectives were to conduct controlled laboratory and microcosm experiments to: 1) cocument reactive distance, handling time, and capture success as a function of fish size, prey taxa and size, and light intensity; 2) test feeding selectivity by different sizes of fish upon different density ratios of dichotomous prey taxa and size assemblages; 3) monitor long-term fish growth and survival under differing ration levels of different prey taxa; and, 4) measure growth of different densities of fish introduced into relatively equivalent, structurally complex microcosm systems representative of shallow sublittoral, estuarine habitats. The organization of these experiments permits the utilization of results of each experiment for model development and design of subsequent experiments (Fig. 1). The following describes our methodological approach to these experiments and the results in terms of our ability to successfully quantify functional relationships between fish and prey.

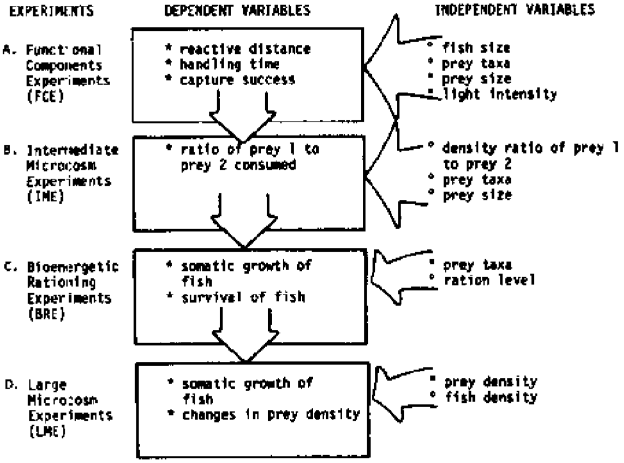

Fig. 1. Organization of laboratory and microcosm experiments to document functional aspects of juvenile chum salmon foraging behavior.

Methods and Materials

All experiments were performed at the University of Washington's Friday Harbor Laboratories, located on San Juan Island in northern Puget Sound, between February and May 1981. Juvenile ("button-up") chum salmon (30-50 mm initial fork length) were obtained from two sources: 1) two groups of fish, resulting from the early and late spawning runs in Hood Canal, were transported from Washington Department of Fisheries's Hoodsport Hatchery via Fisheries Research Institute's Big Beef Research Station to Friday Harbor in early February and late March, respectively; and 2) fish from eggs transported from the Washington Department of Fisheries's Nooksack Hatchery and incubated in egg-boxes located in Beverton Creek, immediately adjacent to the Friday Harbor Laboratories, in early December 1980 to early March 1981. After transport in freshwater, all fish were acclimated over 18-24 hours then introduced directly into full-strength (32°/₀₀ salinity) seawater. Fish for use in experiments were maintained in flow-through holding aquaria where water temperatures ranged between 7.6° C and 10.2°C and salinities ranged between 11.0°/₀₀ and 33.4°/₀₀. Fish in the holding aquaria were fed varying sizes of Oregon Moist Pellets to excess three times per day. Natural mortality rate in the holding aquaria was low, less than 1% per day. Three separate groups of juvenile chums allowed us to experimentally test three size intervals:

1) 35-45 mm fork length (FL); 2) 45-55 mm FL; and, 3) greater than 55 mm FL.

Three divergent classes of representative prey of juvenile chums were used in the experiments: 1) harpacticoid copepods; 2) gammarid amphipods; and 3) calanoid copepods. Review of the literature on culturing these organisms and some initial attempts at culturing endemic species at Friday Harbor illustrated that culturing could not supply the high numbers of test organisms we required within the short period of our experiments. We were thus forced to select taxa which could be routinely obtained in relatively monospecific, high density collections in the vicinity of Friday Harbor. *Tigriopus californicus*, a large, orange-colored harpacticoid copepod, was chosen because of its availability in high densities in high tidal splash pools; although its non-cryptic coloration and behavior of swimming throughout the water column suggest that they are not adapted to avoid fish predation (Dethier 1980), they do represent the size range of the epibenthic harpacticoids naturally consumed by juvenile chum salmon (Simenstad et al. 1980). *Tigriopus* were pumped from tidal pools using hand or electric bilge pumps and retained on 350 μm mesh sieves. At the laboratory the *Tigriopus* were held in shallow, 500 liter tanks and fed commercial hamster food. The harpacticoids were separated into four life history stage categories for the functional components experiments, including: 1) juveniles ($\bar{x}$ = 69 μm total length[1]); 2) non-ovigerous adults and later-stage copepodites ($\bar{x}$ = 107 μm); 3) mating pairs ($\bar{x}$ = 137 μm); and 4) ovigerous females ($\bar{x}$ = 129 μm).

Paramoera mohri, a large eusrid, was chosen as a representative gammarid amphipod due to its availability in the mid-littoral region of exposed gravel beaches on San Juan Island and its known appearance in the diet of juvenile salmon. *Paramoera* were collected by washing large quantities of beach gravel through 2.0 mm sieves and sieving the wash water through 1.0 mm and 0.5 mm sieves. *Paramoera* were held in the laboratory in 10 cm deep water tables and fed hamster food.

Two size classes of calanoid copepods were utilized in the experiments: small calanoids represented by *Pseudocalanus* spp. ($\bar{x}$ = 136 m) and large calanoids represented by *Calanus* spp. and *Epilabidocera longipedata* (5 to 15 mm). *Pseudocalanus*, primarily *P. minutus* were sampled by hand-towing a 0.5-m ringnet equiped with a 225 μm plankton net along the Friday Harbor Laboratories dock. Almost pure *Pseudocalanus* assemblages were obtained by sieving these plankton samples through 0.5 mm sieves and retaining the copepods on a 351 μm mesh sieve. When unavailable at the dock, *Pseudocalanus* were also collected in the surface waters of Friday Harbor using a 65 cm bongo net equipped with 333 μm mesh netting. *Pseudocalanus* collections were made approximately daily and were held in aerated 500 liter aquaria until used. *Calanus* and *Epilabidocera* were hand-pipetted from the > 500 μm fraction retained from the initial sieving of the zooplankton sample for *Pseudocalanus*. These were held in aerated 5 liter beakers in a water table until use the same day. When unavailable from the dock, *Calanus* were collected from deeper water layers in or adjacent to Friday Harbor using the 65 cm bongo net equipped with 0.5 mm mesh netting.

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[1] total length is measured from the tip of the rostrum to end of caudal rami

Functional Components Experiments(FCE). Experiments to document reaction distance and handling time were conducted in aquaria located in a light-tight tend under controlled light levels (Fig. 2a). Lighting was provided by two 8-ft fluorescent fixtures set at 45° angles to the aquarium's water surface; light levels were adjusted between 1 and 100 lux (as measured by a Li-core photometer at the mid-depth point in the center of the aquarium) by varying the number of layers of standard windowscreening placed directly in front of the light fixtures. Two sizes of aquarium, 27.9 cm x 15.6 cm x 7.6 cm (2.7 liters) and 47.6 cm x 57.5 cm x 12.7 cm (34.8 liters) with water 8 to 11 cm deep, were used according to the size of fish and prey being tested. In each experiment a series of predation events were recorded on color video using an Akai Activideo VP-7300U VHS system equipped with a NTSC color camera with a f1.6, 14-84 mm, 6x zoom lens (with macro). Due to the sensitivity to high humidity and temperature, the camera was enclosed in a plexiglass case and was airconditioned by the once-through circulation of air through the case. Additional modifications were made to the camera case to enable remote focus and f-stop adjustment. Vocal documentation of the experiment was simultaneously added to the voice track of the video tape through a microphone installed in the tent.

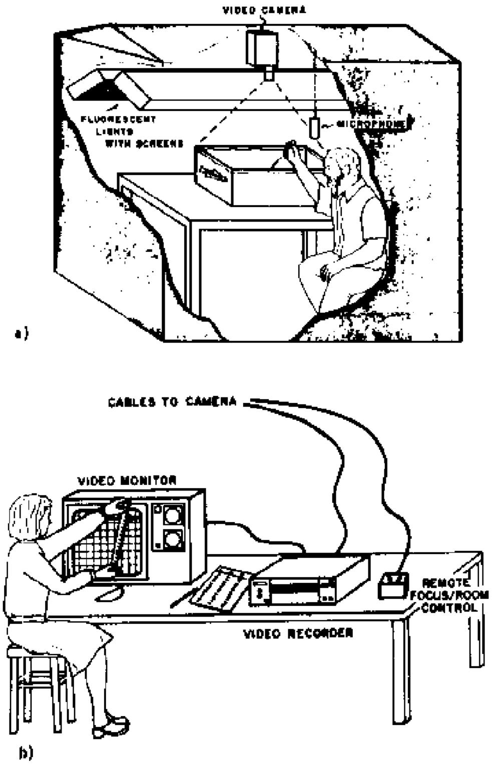


Fig. 2. Experimental apparatus and arrangement used in conduction (a) and transcribing (b) functional components experiments.

Each predation event involved the introduction of a single prey via pipette by the observer into an area of the aquarium out of the fish's field of vision. The observer then proceeded to describe the behavior of the fish and prey through the predation event, including: 1) time of introduction of prey; 2) movement of prey relative to the fish; 3) location of the fish in the water column; 4) time the fish apparently saw the prey; 5) time of initiation of the strike; 6) pitch angle; 7) completion and success of the strike; and, 8) subsequent strike sequences on that prey of the initial strike was unsuccessful. Prey continued to be introduced until 30 predation events had been recorded or until the fish reached satiation, as evidenced by sluggish behavior and a loss of interest in the prey. Each experiment lasted approximately 20 to 30 minutes.

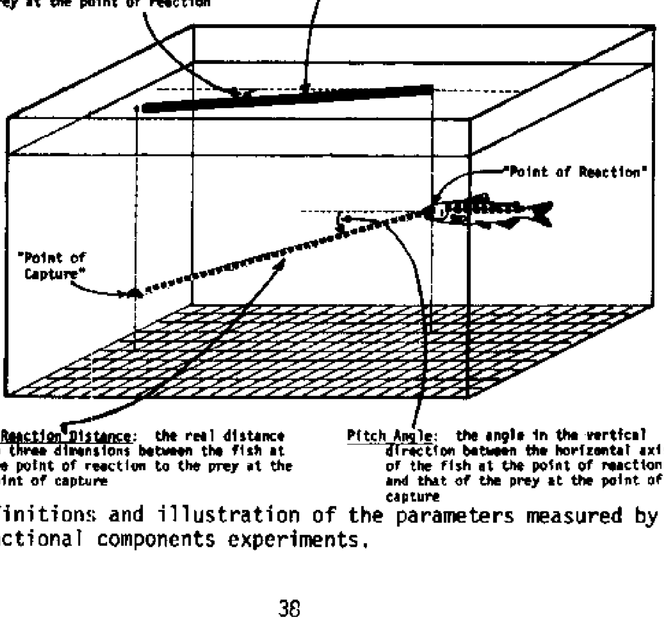
Transcription of the video tapes involved replaying the individual predation events at normal speed to identify and record the discrete points in the cycle of events leading to prey capture as reported vocally by the observer (Fig. 2b). Subsequent multiple playbacks of the event at slow motion permitted us to identify the location and orientation of the fish at the time the prey was seen and the location of prey capture or miss. These positions were drawn on the video monitor screen and measurements of the reaction angle and reaction distance were made using a protractor and a ruler scaled to the actual tank dimensions. Handling time was estimated by counting the number of tape frames between the time of perception and the time of capture of the prey. The actual reaction distance was calculated as,

$$RD = \frac{\text{measured reaction distance}}{\text{cosine pitch angle}} .$$

The cycle of events leading to prey capture and the associated measurements are illustrated and defined in Fig. 3.

Measured Reaction Distance: distance from the eye of the fish at the time of reaction to the prey to the point of capture of the prey

Reaction Angle: looking down on the fish, the angle from the body axis to the prey at the point of reaction



Actual Reaction Distance: the real distance in three dimensions between the fish at the point of reaction to the prey at the point of capture

Pitch Angle: the angle in the vertical direction between the horizontal axis of the fish at the point of reaction and that of the prey at the point of capture

Fig. 3. Definitions and illustration of the parameters measured by the functional components experiments.

Since the smallest prey were usually not visible during replay of the video tape record, the point of capture had to be inferred from the pattern of the fish's movement during the predation event and the vocal narration. After hours of practice we were able to identify distinguishable fish movements associated with the initiation and termination of a predation event. For example, the general behavior patterns were as follows: upon perception of the prey the fish would typically initiate a sharp right angle turn which resulted in a single or series of tail beats in the direction of the prey and would make another sharp right angle turn at the point of capturing or missing the prey.

Capture success was also measured in separate experiments by recording the percentage of predation events initiated that did not result in successful capture. These experiments were run in a 20.3 x 39.4 cm x 17.2 cm (13.7 liter) aquarium under 100 lux light levels. Thirty prey were introduced into the aquarium holding one fish, which had been held for 24 hours without food. The sequence of attempted and successful predation events were recorded on a hand-held casette tape recorder by an observer over the course of a 20-minute trial. The information was subsequently transcribed onto an event chart recorder, providing a record of the distribution of unsuccessful strikes with time as well as an estimate of handling time, i.e. the elapsed time between strikes.

Intermediate Microcosm Experiments(IME). Experiments to test the rate of prey ingestion and prey selectivity were conducted in 102.9 cm dia (409 liter) circular aquaria under 100 lux light levels. Five fish were acclimated in the aquarium and not fed for 24 hours prior to the experiment. Density levels of the two prey were determined at an initial ratio such that the estimated amount consumed by the fish during the course of the experiment did not change more than 5%. The thoroughly-mixed prey assemblage was distributed uniformly in the water column at the initiation of the experiment. Fish were allowed to feed undisturbed for 30 minutes, after which the fish were captured and immediately preserved in 10% seawater-bufferred formalin. The tank was drained through a fine-mesh sieve and the remaining zooplankton were preserved in 50% isopropyl alcohol. The stomach contents of the preserved fish were subsequently examined and the numbers of the two prey recorded; similarly, the zooplanktor remaining after the experiments were sorted and counted and the differrece between that and the initial counts compared to the estimated number consumed.

Densities of the largest prey type were scaled so that the experiments fell under one of the two following situations:

$$\frac{e_2S_2}{H_2} > \frac{\lambda_1N_1e_1S_1}{1+\lambda_1N_1H_1} \quad \text{or} \quad \frac{e_2S_2}{H_2} < \frac{\lambda_1N_1e_1S_1}{1+\lambda_1N_1H_1},$$

where λ_1 is the volume searched (liter sec^{-1}) for the first prey type; N_1, N_2 are the prey density (number liter^{-1}); e_1, e_2 are the body size (μg dry weight animal^{-1}); H_1, H_2 are the mean handling times (seconds) per pursuit; and S_1, S_2 are the probability of capture for the first and second prey types, respectively. In situations where the first inequality above holds, the chum salmon should consume both prey types as encountered (Charnov 1976). In situations where the second inequality above holds, the chum salmon should only consume the largest prey type as encountered to optimize biomass ingested per unit of foraging time. Experiments included comparisons of two epibenthic prey (e.g. *Tigriopus* vs. *Paramoera*), two neritic prey (e.g. *Pseudocalanus* vs. *Calanus*), and epibenthic/neritic prey (e.g. *Tigriopus* vs. *Pseudocalanus*).

Bioenergetic Rationing Experiments(BRE). The effect of prey taxa and daily ration upon somatic growth and survival were examined by maintaining juvenile chum salmon under thirteen feeding regimes: three prey taxa (*Tigriopus*, *Paramoera*, *Pseudocalanus*), four ration levels (excess, 10%, 5%, 1% of body weight day^{-1}), and one starvation over a ten week period. Fish were held in 15 liter aquaria under ambient light and temperature regimes with flow-through, prefiltered water. In order to minimize stress on the fish, excess prey were only removed once a week. The aquaria were also checked daily for mortalities and these fish were immediately removed and replaced with live fish of identical weight.

Individual marking of the small chum was not feasible, thus growth data were based upon the weekly change in mean wet weight of the fish in each aquarium. Relative incremental growth was determined for individual fish, however, by analysis of daily growth ring patterns of the otoliths removed from each fish at the end of the experiment. These otoliths were processed and analyzed using the methods of Brothers et al. (1976), Brothers and McFarland (1979), and Marshall and Parker (1979).

Large Microcosm Experiments(LME). This series of experiments culminated in a large-scale microcosm test of epibenthic carrying capacity wherein the effects of varying fish densities on uniform prey assemblages was examined in a more natural foraging habitat, with sediment, algae and vascular plants, and natural light regimes. Two 4.6 m dia plastic swimming pools were divided in half to form four 6,500 liter semicircular habitats. Seawater from the Friday Harbor Laboratories's system supplied flow to the habitats such that the volume was replaced one to three times daily. Outflow losses of prey organisms were quantified per unit time and assumed equivalent to replacement rates. Sand and eelgrass (*Zostera marina*) were transported from a nearby embayment and distributed uniformly among the four habitats and allowed to stabilize for several weeks. During that period, large numbers of *Tigriopus californicus* were added equally to each habitat and procedures for quantitatively sampling these and other prey taxa were developed. By the end of April *Tigriopus* populations of between 127,140 and 294,590 per habitat had been established; the harpacticoids were not uniformly distributed within the habitats, however, and tended to congregate along the upper portions of the sidewalls and among the diatom mats which were attached to the walls or were floating on the surface. Accordingly, sampling of prey populations was stratified into four microhabitats: 1) upper (top 10 cm) sidewall; 2) lower sidewall; 3) sediments' and, 4) water column. Sampling of the water column was accomplished using a 5 liter Van Dorn water bottle and sampling of the surfaces was accomplished using an electric bilge pump which vacuumed a 63.6 cm^2 surface area. Five replicate samples were collected weekly from the initiation of the experiments on 30 April to its termination on May 29.

Three treatments of varying fish densities were used: 20%, 10%, and 5% of body weight day^{-1} ration levels which, given the estimated prey populations, converted to 5, 10, and 14 fish in each of the habitats, respectively; the fourth habitat with no fish served as the control. The respective fish densities were 0.6, 1.2, and 1.7 fish m^{-2} of bottom area. At the end of the experiment the habitats were drained and the fish recaptured, weighted, and preserved in 50% isopropyl alcohol for subsequent stomach and otolith analyses.

Results and Discussion

While we have not completed the exhaustive analyses of the data collected from the described experiments, we can evaluate our results in terms of our ability to effectively measure the parameters we were focusing upon. Subsequent papers describing the actual results will be forthcoming.

A number of mechanical and biogenic "bugs" characterized these experiments as designed, some of which were never overcome and compromise our results. Hopefully, describing these hindrances will enable future investigators to circumvent them and improve our ability to experimentally document fish feeding behavior.

Mechanical Bugs. The VHS color video tape system we utilized limited our ability to conduct experiments through the ranges of light levels and sizes of fish and prey which we desired to test. Although the reaction distance of planktivorous salmonids have been shown to be truncated by light intensities below 50 lux (Confer et al. 1978) and they may be able to feed at 0.2 lux (Eggers 1978), the minimum illumination level we found feasible was 1 lux, below which depth of field, contrast, and resolution diminished to the point that the fish's movements could not be distinguished. As the size of the aquarium had to increase with the size of fish and prey being tested, and the fishes increased reaction distance, the increasing field of view required created resolution problems. Despite the advantage of the zoom lens, moving the camera further away from the aquarium's surface changed the camera's effective sensitivity to the illumination in the aquarium. Illumination problems might be reduced by selecting a video system with greater light sensitivity such as a black and white video camera. The field of view could also be increased by using a wide angle lens. Further sensitivity to low illumination would require conducting the experiments under infrared (IR) light conditions and use of IR-sensitive video equipment.

One of the most obvious limitations was the visual sensitivity of the human observers under low illumination. Below 10 lux, and especially at 1 lux, our ability to track small prey was seriously compromised. Trying to visually keep track of a 65 μm-long harpacticoid copepodite for 30 minutes at 1 lux required tremendous concentration and curtailed the total number of experiments by one observer per day. One possible solution to this problem would be to utilize light gathering or image-enhancing optics to view the experiments. Another approach would be to couple in another video camera to record the vertical field during the experiment. Video systems are available which can record two signals simultaneously on a split-image format on the tape.

While fluorescent lighting of the type we utilized is inexpensive to operate and less complicated than incandescent lighting, precise control of light levels is much more problematical. Banks of tilt-adjustable incandescent lights, regulated by rheostat, would be preferable if the problem of heat buildup and the proper light spectra could be resolved.

Rapidly moving fish and prey were also difficult to follow under low illumination, as visual planktivores can detect prey at speeds 2-3x faster than can be detected by the human eye (Protasov 1968). This was a problem in playback of the video tapes of experiments involving highly evasive prey (i.e. *Calanus*). Movements of the fish were blurred considerably at the 30 frames sec^{-1} recording rate. Video equipment with a higher recording rate could be preferable if detailed documentation of fish movement is necessary.

The necessity of maintaining fish in both holding tanks and experimental aquaria under strict control of food is difficult when dealing with marine or estuarine fishes and the typically unfiltered, flow-through sea water systems of most marine laboratories. Although we were unable to assemble a satisfactory prefilter and manifold system which would supply enough water flow, the effort to construct and maintain individual filters for each aquarium was sufficient for us to recommend a single prefilter if feasible.

Biogenic Bugs. We observed a number of experimental artifacts imposed upon the fish's foraging and the prey's escape behavior, which were partly avoided by modification of experimental design. The "chamber" pr "bottle" effect of truncating the reaction field of the fish by conducting the experiments in small aquaria can introduce significant bias in estimates based upon the water volume searched. This is especially true for reaction distance measurements made from experiments run in narrow aquaria, as the frontal reaction distance may be quite different than a three-dimensional reaction field (Confer et al. 1978; Luecke and O'Brien 1981). Thus, measurements of reaction angle in sufficiently large aquaria are critical in order to quantify the absolute visual acqity in all directions. Accordingly, fish striking a prey on the walls of the aquarium should be excluded from the data set. Some fish also learned to use the walls and corners of the aquarium to enhance their capture success and such events were ignored in our transcription of the experiments.

While the simple environment of the aquarium is not representative of the natural foraging environment, there are a number of ways to reduce associated biases. Contrast may be standardized by shielding the sides of the aquarium with a neutral, grey-colored material. Moisture must not be allowed to come into contact with the bottom of the aquarium, causing a mirror effect which disturbs the fish.

Selection of representative prey can be a critical factor affecting both the success as well as the relevance of the experiments. While we had no feasible alternative to the use of *Tigriopus*, we have recognized that this species of harpacticoid copepod had minimal morphological or behavioral adaptations against planktivorous predators. Although our measurements of reactive distance may not have been compromised, estimates of capture success, the bioenergetic cost of predation, and the carrying capacity of an epibenthic harpacticoid population based upon *Tigriopus* may not be relatable to the more cryptic, evasive harpacticoids upon which juvenile chum salmon normally feed. Similarly, our initial experiments using large calanoids were conducted with a mixed assemblage of "large calanoids" selected from the zooplankton collections. After observing a number of diverse swimming and avoidance behaviors among this "homogeneous" prey assemblage, and corresponding variation in fish strike behaviors, we realized that the major species included in our assemblage (*Calanus pacificus*, *C. plumchrus*, *Eucalanus bungii*, *Epilabidocera longipedata*) had distinct morphological and behavioral characteristics which the fish were responding to differently. For example, one calanoid would avoid a fish strike by darting laterally 30 cm, while another would evade in a rapid spiralling movement, both of which confused small or naive fish. This condition was minimized by separating these species when possible.

The effect of handling and temperature stress upon the avoidance capabilities of the prey was also seen to be a major source of bias. Prey should be handled with as little stress as possible, especially when collected using zooplankton nets. Use of glass bottle cod ends and short-duration tows are suggested. In the case of the large, sensitive calanoids, hand dipping may be the only feasible way to avoid stress. Similarly, separation of these forms from other zooplankton should be done with a minimum of stress, by hand pipetting instead of sieving if necessary. Although these precautions are time-consuming and limit the number of experiments that can be conducted within a reasonable time of prey collection, the differences between the results of experiments conducted with viable versus stressed prey are too dramatic to ignore.

Establishment of representative prey assemblages in a structurally complex microcosm is a challenging task which requires long-term equilibrating and fine-tuning. We encountered problems with: 1) maintenance of equivalent water flow and temperature regimes among the replicate systems; 2) minimizing loss of prey organisms through outflows; 3) control of epiphytic microalgae blooms; 4) capture of experimental fish on a regular basis; and 5) systematic sampling of heterogeneous distributions of prey. The ideal experimental design and what can ultimately be accomplished given your resources require a number of compromises. We suggest that you seriously consider documenting each of the dependent and independent variables and allocate considerable pre-experiment time perfecting these techniques and allowing the microcosm systems to equilibrate.

Summary

Our multifacited experimental approach to documenting functional aspects of fish foraging behavior exposed a number of constraints which must be incorporated into the experimental design. Despite these potential pitfalls, we discovered that the power of such fine-resolution experimental and manipulative studies to expose causal mechanisms of fish foraging behavior justifies the effort involved. We were particularly stimulated by the variation in prey avoidance behavior and fish feeding behavior which we observed and propose that this is a critical determinant of capture success. While few investigators have attempted to quantify the dynamics of zooplankton escape responses and compensatory behavior of zooplanktivorous fishes (Drenner et al. 1978), such levels of predator-prey interactions must be examined if we are ever to explain why fish eat what they do.

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The Lack of Time Limitation in Fish Foraging

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Introduction

One objective of ecology is to determine the controlling factors in ecosystem structure and function. An important component of this objective is determining the factors that control the amount and composition of the diets of predators. Time has been proposed as a possible limiting factor. Holling (1959a) showed that the time required for a predator to pursue, capture, subdue, consume, and digest a prey sufficiently to resume searching for addition prey (i.e. handling time) could limit the amount of food consumed by a predator at high food densities. Handling time has been used in optimal foraging theory as a controlling variable for diet composition (Charnov, 1973, 1976, Pearson, 1976). This work has been used to analyze food habits and food partitioning in fish (Werner and Hall, 1974; Werner, 1977; Mittlebach, 1981). This paper points out that handling time limitation may be inconsistent with some of the data present by these papers as well as work done by other investigators. Handling times are often so small that fish appear to be able to fill their stomachs in a very small amount of time. Hence handling time limitations may be inconsequential. In the absence of handling time limitation, other possible controlling factors for a predator's diet are examined. The probability of successfully capturing a given prey item and digestion rate are suggested as controlling factors. The apparent agreement of some fish foraging data to the handling time model is discussed, and arguments for the evolution of short and long handling times are presented.

Foraging Model

The diets of fish are determined by the hierarchical decision model (Crow, 1979): when to forage, where to forage, how to forage, and which encountered prey to pursue. The first three decisions allow for a high degree of "selectivity" by the fish, independent of handling time, which is only directly concerned with the fourth decision. To evaluate the importance of handling time a foraging model was constructed (Crow, in prep), which combines diet quality, diet quantity, and bioenergetic demand for food to make the fourth decision subject to a choice of when, where, and how to forage. The diet quality model is based on the handling time criteria presented in Charnov (1973, 1976), the diet quantity model uses the Holling disc equation (Holling, 1959a), and the bioenergetics model is a modification of several bioenergetics models found in the literature used to estimate the daily metabolic demand (e.g. Kitchell et al., 1977).

The diet quality model specifies that a prey item will be included in the diet if the benefit-cost ratio of the prey item exceedes the consumption rate of the predator without that prey in diet. The consumption rate is net consumption per unit foraging time. The benefit function is the weight of the prey item times the capture success times the digestive efficiency. The cost is the handling time. The benefit-cost ratio will be referred to as profitability in the remainder of this paper. Handling time, h, is the amount of time that elapses from the time the predator stops searching in order to start pursuing a prey, until the predator resumes search. Handling time is equal to the average pursuit time plus the expected capture time, where the average capture time is adjusted by the capture success.

The Holling disc equation assumes that the rate of food consumption is limited at low food densities by the rate at which food is encountered, and at high food densities by the time required to handle encountered food items. The fraction of the total foraging time which is spent searching for food, FS, can be expressed as $FS = 1/(1+R)$, where R is the dimensionless ratio of the time spent handling prey to the time spent searching for prey. R can be calculated as the product of handling time per prey and encounter rate (no./time). It can also be expressed as $R = rN$, where N is the prey density and r is the product of handling time and encounter rate. The consumption rate, C (gm/time), is proportional to $N/(1+rN)$. A plot of $N/(1+rN)$ versus R (Figure 1) shows that consumption is relatively unaffected by handling time if $R < 0.25$. If $R < 0.25$, then the consumption rate is so much lower than the profitability of the highest ranked prey that most encountered prey items will be taken and the predator will have a broad diet. Thus, handling time has relatively little effect on either diet quantity or diet quality, if $R < 0.25$. Handling time will also be limiting if the amount of time required to fill the stomach is greater than the available foraging time. Otherwise the saturation consumption rate will be controlled by hunger and stomach capacity (i.e. digestive limitation). Since foraging time equals handling time times $1+1/R$, and R must be greater than 0.25 for handling time to be important, then multiplying the total handling time by a factor of 5 will give the maximum foraging time for handling time to be limiting.

The Holling disc equation (Holling, 1959a), is a handling time limited model and the Ivlev function (Rashevsky, 1959), is a model of digestive control. The Ivlev function was developed for fish populations and fits Ivlev's data better than the disc equation. This suggests that the foraging of fish is digestion limited rather than handling time limited. Three examples will be used to show that handling time is usually unimportant for fish predators (i.e. R is frequently less than 0.25).

Examples of Small R

Werner (1977) and Mittelbach (1981) analyze the diets of bluegill using an optimum foraging model based on handling time. Both authors successfully predict prey size and habitat selection using their model. However, a close examination of some of their results raises some question as to the importance of handling time. Table 1 contains some calculations concerning the amount of time these fish spend handling their prey. These calculations indicate that bluegill are able to fill their stomachs in 1-15 minutes of handling time. This would require a foraging interval of no more than 5-75 minutes for handling time to be important. Because Werner's handling times were measured with 100% capture success, laboratory handling times are over-estimates of field handling times, where capture success is less than 100% (see below). If field handling times are smaller than those measured in the laboratory then R and the foraging interval will be even smaller than the above estimates making handling time even less important. Either fish spend very little time foraging or time is not limiting for fish, especially small fish. This is in agreement with Mittlebach's own findings that the optimum foraging model did not predict the diet of small bluegill very well. Mittlebach attributes the lack of agreement between the predicted and observed diets of small bluegill to the lack of difference in the prey profitability over a broad range of prey sizes. Although this could also be a contributing factor the possibility exists that handling time was not limiting bluegill and they were not attempting to optimize prey profitability.

The above example shows that bluegill sunfish do not appear to be handling time limited. Bluegill are small bodied and should be an ideal case for handling time limitation, since as body size increases the food requirements of fish decrease (i.e. gm food/gm body weight). Under these conditions digestion time increases, and the relative stomach capacity of the fish becomes smaller. Thus, the amount that the fish can eat at one time decreases relative to fish size, while the handling time probably remains constant. As the food requirements decrease, the amount of foraging time required to satiate the predator decreases. Thus, the likelihood that a predator is handling time limited decreases as the food requirements decrease.

I examined this relationship by parameterizing the model for Pacific Ocean perch (<u>Sebastes alutus</u>) foraging on euphausid shrimp. For simplicity the pursuit time is set equal to zero and the capture success is set at one. The capture time (CT) relationship of Werner (1977) is used:

$$CT = 2.0 * 6.0 * x**2.7$$

where x is the prey weight expressed as a percentage of the predator's weight. The factor of 2.0 is included to adjust for the assumed increased difficulty of capturing euphausids as opposed to Daphnia. Using this relationship a 31 gm fish eating 0.2 gm prey would have a handling time of 3.7 seconds. This results in a handling time limited consumption rate of 0.2 gm/3.7 sec = 0.05 gm/sec or 194.6 gm/hr. A rough estimate of the metabolic demand of Pacific Ocean Perch is:

$$C = 0.034 * W**0.72$$

(Crow, in prep), where C is the digestion limit in gm/day, and W is the weight of the fish. A 31 gm fish would demand 0.4 gm/day and can meet this demand in less than 8 seconds of handling prey. This points to the possiblity that handling time may be too small to be a significant factor in determining diet. This conclusion is independent of the precision of the above calculations since they could be off by an order of magnitude and still yield the same conclusion. A more detailed simulation model (Crow, in prep), shows that: (1) fish spend less than 10% of their foraging time handling prey (usually the ratio is less than 1%), hence the amount of food the fish eat is never handling time limited, (2) handling times are so small that an optimally foraging predator eats almost everything it encounters and very few prey are rejected. (In one run of the model, handling times were set at zero with no perceptible effect on the results).

Another example of the unimportance of handling time comes from the optimum swimming speed model proposed by Ware (1978). The handling times proposed by Ware only reduce consumption by 2-3 percent. Likewise the optimum swimming speeds predicted by Ware are only increased by 2-3 percent by eliminating handling times from the equation (table 2). Eliminating handling times has the additional benefit of allowing an analytic solution to the problem.

The results from these calculations suggest that either handling time is not a critical parameter in the diet of fish, or that fish spend very little time foraging (on the order of minutes). If we assume that handling time is not a critical parameter in the diet of fish, then other limiting factors need to be identified. The most likely candidates are encounter rate and capture success.

Encounter Rate

Eggers (1977) showed that encounter rate for a visual predator is primarily a function of light intensity, and the size and inherent contrast of the prey. It is not too surprising that prey have attempted to minimize their exposure to predators by evolving small body size, low inherent contrast, and by spending most of their time in areas of low light intensity (Hobson and Chess, 1976; O'Brien, 1979). Since most foraging takes place under poor lighting conditions encounter rates should be low. Futhermore, Eggers (1977) has shown that at low light intensities and low values of inherent contrast prey size has very little effect on encounter rate. This leaves inherent contrast as the primary difference in the encounter rates of various prey species. However, this should not lead to any differences in the relative encounter rates between predator species. Thus encounter rate affects diet quantity much more than diet quality, and differences between predators should not be controlled by encounter rates. However, if encounter rates are low and have a diel cycle then there may be a very limited time when encounter rates are high enough to permit foraging. Thus foraging time may be quite small, permitting handling time to be limiting.

Capture Success

Capture success appears to be the only part of the predation process where species specific interactions play a significant role. For example both bluegill and largemouth bass can feed on Daphnia and fish. However, bluegill are morphologically adapted to feed on Daphnia, and bass are adapted to eat fish (Werner, 1977). Bluegill have nearly a 100% capture success on the first strike when attacking Daphnia, but have a much more difficult time attacking fish. Conversely, bass are very efficient at capturing fish, but must often take multiple strikes at a

Daphnia. Although capture success has rarely been measured, Griffiths (1980) cites references to capture success rates of 30-40% and Salt (1967) has speculated that capture success in nature may be as low as 10%, and obviously can vary greatly depending on how well a predator is matched to a prey item. This points to capture success as the primary determinate of species differences in diet quantity and quality.

The reason handling time is frequently used in food habit work is due to the success that some investigators have achieved using handling time as a means of predicting diet (e.g. Werner, 1977, and Mittelbach, 1981). But how can a handling time model successfully predict diet if diet is independent of handling time? The key to understanding this paradox is to understand the relationship between handling time and capture success in the laboratory and in the field. Werner measured handling time in the laboratory where capture success was 100% and handling time was allowed to increase to large values (e.g. Werner recorded handling times of over 20 minutes, with pursuit times of over one minute, and up to 6 strikes before capture). It is highly unlikely that handling times would reach these levels in field situations where the prey can escape. It seems likely that laboratory handling times are inversely related to capture success in the field. Werner was able to make successful predictions using handling time because his model was insensitive to whether he was using capture success or the inverse of handling time. Werner ranked prey according to profitability, P, where P = w/h, w is the prey weight, and h is handling time. Alternatively the prey can be ranked according to vulnerability, V, where V = E*CS, E is the encounter rate with a given prey (volume searched/time), and CS is the capture success (no. capture/no. attacked). If CS is inversely proportional to h, and E is directly proportional to w, then V is directly proportional to P. Alternatively, for small prey, h and E are size independent, CS is proportional to w, and V is still directly proportional to P. Pastorok (1981) shows this relationship for Chaoborus larvae and points out that the diet of Chaoborus can be adequately described with either a differential vulnerability model using capture success or a profitability model using handling time. Pastorok also noted that Chaoborus consumption in the field did not appear to be handling time limited, as Chaoborus appeared to take prey as encountered. Hence a prey vunerability model may adequately explain most demonstrations of handling time if capture success is taken into account.

Handling Time

Handling time tends to be unimportant in the above examples because it is so small. The reason why handling time is so small for fish is that their prey are often relatively small. There are several reasons why this should be the case. First, a small prey cannot put up much of a fight and therefore cannot damage the predator. Second, a predator is usually exposed to its predators while it is handling prey. Attacking small prey with small handling times may minimize a predator's exposure to predation. Pearson (1976) discusses a handling time minization strategy of predators in which an optimally foraging predator would attempt to minimize handling time rather than maximize energy intake if its vulnerability to predators increases during the handling of prey. A handling time minimization strategy would not lead to a selection for smaller handling times. However, if vulnerability is also a function of individual handling times (i.e. 3 separate 10 sec handling times may offer less predator exposure than one 30 sec handling time) then small handling times will be selected. Third, small prey are more abundant than large prey (Cushing, 1975), and a predator has a more abundant food resource by choosing small prey. In a similar manner less specialization is necessary to capture small prey and the predator is able to feed on a much broader spectrum of prey species by attacking small prey. These three explanations may be classified as risk minimization. A predator selects small prey to minimize the risk of being injured, being eaten, and of not being able to find food.

Large handling times are found in ambush predators, predators of sessile organisms, and parasites. However, in each of these cases the predator has minimized its risk through other mechanisms. Sit and wait predators (e.g. turbot, pike, trumpetfish, praying mantis), disrupt the prey community when they attack a prey item. Often the largest component of the handling time is the time until the prey resume normal activity around the area where the predator is hiding (i.e. return time). Even though this is part of the handling time, the sit and wait predator is not exposing itself to predation during this time, or during its search time. In fact the sit and wait predator has probably reduced its predation risk through its sit and wait strategy. Futhermore, the handling times of sit and wait predators are relatively independent of prey species and of whether or not the prey was captured. Therefore, sit and wait predators should have constant handling times, and be generalized predators, but should be highly selective with respect to capture success. Capture success is highly dependent on distance from the predator, which is species and size independent.

Predators of sessile prey (e.g. starfish, snails, and pollenators) also tend to have large handling times. However, immobile prey are usually very abundant, and even though the prey are often difficult to eat (i.e. large handling time), they offer minimal danger to the predator. Predators of immobile prey are also relatively immobile and have adapted other mechanisms of predator defense (e.g. unpalatable or protective shells). Here handling times are highly species and size specific and predators of sessile prey are highly discriminatory.

Parasitoids are a different case because they combine foraging with reproduction and attempt to minimize the foraging risk for their offspring. Also because successful foraging (i.e. parasitism) means successful reproduction, greater risks can be taken while foraging. It is important to note that the Holling disc equation was originally developed for parasitoids, extended for predators of sessile organsims (small mammals eating pupae; Holling 1959b), and the optimal foraging development was done with a sit and wait predator (praying mantis; Charnov, 1976).

However, small handling times may also be limiting. Under certain circumstances there is a minimum size of prey below which handling time is constant. With constant handling time, profitability decreases with prey size, and a predator may require a longer forage interval to fill its stomach with very small prey, if the predator handles the prey individually. For example, large bluegill forage on Daphnia with a minimum handling time of 1 second. The profitiability of Daphnia is so low, 0.047-0.073 mg/sec (see Table 1), that they require up to 17 minutes of total handling time to fill their stomachs, which is large enough that handling time could be limiting. Mittlebach points out the large bluegill feed on Daphnia due to the large abundance of the resource, and the lack of predators. Since large bluegill are not concerned with minimizing predator exposure the low profitability is not a problem. However, smaller bluegill would be subject to large mouth bass predation in the pelagic environment and remain in the littoral zone, which permits the high abundance of Daphnia in the deeper water.

The high abundance of Daphnia, and low abundance of large predators in the pelagic zone of the lake make up for the low profitability of the Daphnia and large bluegill become handling time limited.

Summary

Simple calculations of the total handling time indicate that fish may fill their stomachs prior to being limited by handling time as implied by the Holling disc equation. Thus, either foraging is unaffected by handling time, or the foraging interval is extremely short. Capture success is identified as the critical parameter controlling diet, and an inverse relationship between handling time in laboratory experiments and capture success in the field is proposed as being responsible for the success that handling time has met in explaining food habits. The evolution of short handling times is discussed in terms of risk minimization, and some circumstances where handling time may be limiting are identified.

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FIGURE 1

EFFECT OF HANDLING TIME ON CONSUMPTION RATE

Consumption rate is proportional to N/(1 + RN) where N is population density and R is handling time times encounter rate. A is the relationship with no handling time (R = 0), and B is the relationship with R = 1. The horizontal axis is R = RN. Note that if R is less than 0.25, the difference between the two relationships is minimal (i.e. handling time has no effect).

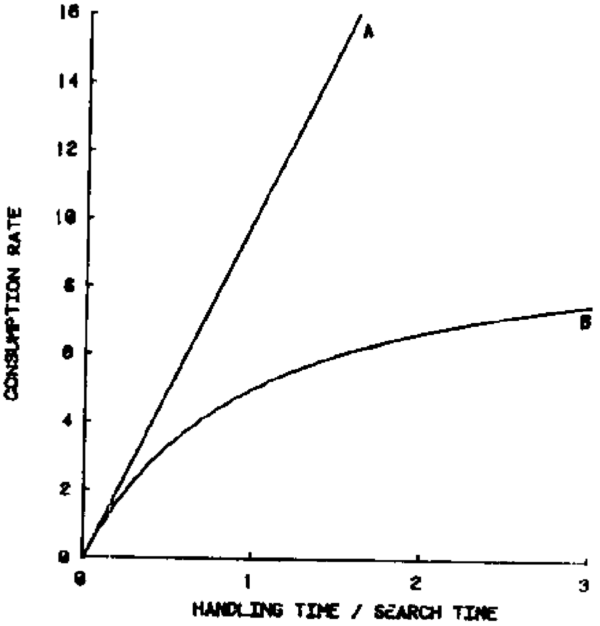

TABLE 1
Sample calculations of total foraging time using data from Mittelbach (1981)

	SIZE OF PREDATOR		
	30mm	75mm	125mm
PLANKTONIC PREY			
size range (mg dry wt)	0.015–0.074	0.041–0.074	0.048–0.074
handling time (sec/prey)	1.06–1.84	1.02	1.02
profitability (mg/sec)	0.014–0.04	0.040–0.073	0.047–0.073
stomach contents (mg)	1	15	35
number of attacks	25–71	68–205	479–1020
total handling time			
(sec)	46–75	148–446	488–1040
(min)	1	2.5–7.5	8–17.3
total foraging time (min)	5	15–40	40–90
INSECT PREY			
size range (mg dry wt)	0.022–0.446	0.054–1.072	0.054–1.072
handling time (sec/prey)	1.2–9.1	1.0–3.4	1.0–1.7
profitability (mg/sec)	0.02–0.049	0.053–0.30	0.053–0.60
stomach contents (mg)	1	5	30
number of attacks	2.2–45	5–92	50–555
total handling time			
(sec)	20–54	16.5–92	50–555
(min)	<1	<1.5	1–10
total foraging time (min)	<5	<10	<60

Table 2
Optimum swimming speeds from Ware 1978 (Table 2)

Weight (gm)	R	Speed (cm/sec)	Speed (h=0)
8	.022	27	27.56
73	.025	36	36.98
267	.027	42	43.98
669	.029	48	49.74
1367	.030	52	54.73
2449	.032	57	59.17

On K. P. Andersen's Interpretation of the Stomach Contents of a Fish

Erik Ursin
Danish Institute for Fisheries and Marine Research

[SYNOPSIS]

Dr. Ursin reviewed for the participants of GUTSHOP '81 his involvement with the implementation of a model developed by K.P. Andersen to interpret the stomach contents of fish in relation to prey abundance. This model was developed to relate prey abundance to utilization and to incorporate this information into species interaction assessment models used in fisheries management in the North Sea. Since many participants are gathering stomach contents data and estimates of prey abundance elsewhere in the world, Dr. Ursin thought it would be useful to summarize how he feeld Andersen's model could be implemented and how useful the resulting interpretation would be to fisheries scientists. Several manuscripts and published references have been produced describing and utilizing this model and they are listed below. Since Dr. Ursin plans to publish his application of North Sea fish food habits data to Andersen's model in another journal, it was decided not to include his entire presentation here in the GUTSHOP '81 proceedings. Should one desire a copy of any of the following references, they can be obtained from the International Council for the Exploration of the Sea, Copenhagen, Denmark, or from Dr. Ursin.

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Predator-Prey Studies of the Shortbelly Rockfish
Offshore Sampling Problems

James R. Chess
National Marine Fisheries Service

Investigations of predator-prey relationships that have considered aspects of prey distribution and availability have, with few exceptions, been confined to well defined sites or areas where precise sampling and/or direct observations can be made. Most such studies have been conducted nearshore, where logistical problems are reduced and where direct observations are often feasible (e.g. Hobson 1968, 1974: Hobson and Chess 1976; Van Blaricom 1977; and Cailliet et al. 1979). Comparable investigations have dealt most often with organisms like flatfishes that live on the sea floor where methods for collecting benthic predators and prey species are relatively precise (e.g. Pearcy and Hancock 1978; Gabriel and Pearcy 1981). When offshore midwater sampling is required, problems arise which are not encountered in most nearshore or offshore benthic studies.

The variations in temporal and spatial distribution patterns of both predators and prey in this large three dimensional environment contribute to inconsistent sampling, especially of the predators. Furthermore, because of the dynamics of the water column and the patchy distribution of the plankton and planktivores, the interpretation of plankton samples that are intended to represent prey availability is often difficult, i.e. do the samples adequately reflect the actual prey items available to the predators.

Shortbelly Rockfish

The shortbelly rockfish, Sebastes jordani, is a large unfished resource in waters off California. During the past several years however, there has been a growing interest in the development of a fishery by fishermen and processors (Lenarz 1981).

A major portion of the shortbelly population occurs between latitude 36°56' and 37°21' (Gunderson and Sample 1980). In this area they appear to aggregate on the continental shelf and slope near submarine canyons or steep dropoffs at depths between 128 and 275 meters.

The shortbelly reaches maturity at about 16.5 cm and attains a maximum size of about 33 cm (Lenarz 1981), an appropriate-sized forage species for larger predators. This species is known to be an important item in the diet of king salmon off San Francisco (Merkel 1957).

Determining the value of shortbellies as a forage species for other large predators and understanding the dynamics of its own predatory activities is important before a large shortbelly fishery is established. It is unusual that the opportunity to study a commercially valuable species has arisen prior to its exploitation.

Objectives of the Study

Originally, the objectives in studying the trophic relationships of the shortbelly were to determine: a. its importance as a forage species, b. diel feeding patterns and prey selectivity, c. seasonal distribution and prey, d. depth/size relationships, and e. the variations in prey selectivity within various size classes.

All but the first, continue to be goals of the study. The collection of guts from the larger predatory fish from trawl samples proved unsatisfactory because of regurgitation of gut contents during trawl retrieval. So the role of shortbellies as a forage species is being considered in another segment of the overall program that samples these predators from sportfishing boats.

Study Areas

Beginning in the spring of 1979, when shiptime was offered by the Northwest Alaska Fisheries Center, attempts were made to locate specific sites where shortbellies aggregated. Our study of diel feeding patterns and prey availability is centered in an area of about 17 square kilometers on the shelf just west of Ascencion submarine canyon (37°00' N, 122°27' W). The bottom depths vary between about 120 and 200 meters. Our collections to determine size/depth distribution patterns and variations in prey selectivity with shortbelly size and depth are taken in an area less well defined near Pioneer Canyon (37°20' N, 23°00' W) where depths vary from about 120 to 275 meters.

Vessels

Twice during the first year of the study we used the NOAA ship *Oregon*. This vessel, however, was a trawler and not equipped to tow plankton nets. So no "prey samples" were obtained. It was well rigged and manned for trawling operations, though, and valuable data were gathered on distribution patterns of shortbellies. Also, during the first year we were able to use the NOAA ship *Miller Freeman* for 3 days. This ship had both trawling capabilities and elaborate acoustical fish monitoring equipment, in addition to standard oceanographic equipment. It enabled us to collect our first sample series of shortbellies and their prey. Since the fall of 1980 we have had the use of the NOAA ship *David Starr Jordan* on an approximate quarterly schedule. This ship, a well-equipped oceanographic vessel, had only limited trawling capabilities during the first three cruises. A recent refitting however, has dramatically increased its trawling capabilities, with improved net reel, door stanchions, hydroacoustic and navigational equipment.

Collecting Samples

We have determined from hydroacoustic tracings, that nearbottom daytime aggregations of shortbellies disperse up into the water column at night. To determine diel feeding patterns, gut samples are needed from both distribution modes, from periods immediately preceding daybreak and dark. Depth stratified plankton samples are also needed from midday and midnight periods to determine the diel distribution patterns of potential prey species.

A three-bridle midwater trawl with 100 ft headrope is used for collecting shortbellies for gut analysis and an opening/closing Tucker net with 1 m^2 effective opening is used for plankton collecting.

Sampling Problems

During this investigation the problems encountered center primarily around our inability to consistently collect adequate samples of shortbellies.

Locating shortbelly aggregations. To locate aggregations of shortbellies, hydroacoustic transects are made, usually in a zigzag or bathymetric pattern within the study area. Daytime shortbelly aggregations usually show a characteristic silhouette on sounder paper, being dense, round-topped and extending several to about 30 m from the bottom. Discrete nighttime aggregations are more difficult to identify. The shortbellies disperse into the water column, sometimes moving up as far as the lower portions of the near surface deepscattering layer, where they mix with other fish species that rise into the water column at night.

The acoustic resolution is variable with the different quality sounders on the various vessels, so the interpretation of target strength and shape and identifying them as shortbellies has often been a problem. A Simrad scientific sounder EK400 with high resolution has recently been installed aboard the *Jordan* and in the future should help us locate and identify fish aggregations. Scanning sonar helps considerably in locating fish aggregations but has been available to us only twice, once aboard the *Miller Freeman* and again aboard a chartered fishing vessel (*Colintino Rose II*).

Setting the trawl. If no acoustic targets are found prior to the sampling period, "blind" trawl sets are usually made at locations near where fish were previously found. As it has turned out, we have been just as successful in obtaining samples during these blind sets as when setting on acoustic targets. Reasons for missing targets have been one or a combination of the following: delays in setting due to deck gear problems, navigational limitations in returning to the target position, or fish movements and drift due to currents or wind.

With the recently installed plotter aboard the *Jordan*, our ability to return to specific targets has been greatly improved. The plotter is coupled with the Loran C navigational system and plots the track of the ship on paper, allowing return to any previously marked position.

The deck gear problems associated with trawl set delays have largely been solved by the recent installation of a split net reel, moving the net reel aft and constructing door stanchions.

Monitoring the trawl. Estimates of the trawl fishing depths were initially made by noting the presence or absence of benthic organisms. Adjustments to the trawl warp length were made in attempting to place the net just off the bottom. The warp length/depth ratios that developed were later modified by use of a time/depth recorder. But not until we were able to use a shipboard net monitoring system, with an acoustic link with the ship, were we able to observe the actual position of the trawl in relation to the bottom, surface and fish targets. This Furuno 200 net sonde has allowed us to more effectively fish the trawl and with a single exception (when about 25,000 lbs of shortbellies were collected during a 12 minute period), to monitor fish entering the trawl and thus limit trawling time in order to avoid unreasonably large samples. It also provides the opportunity to position the trawl, by varying warp length or ship speed to the depth of targets which are detected by the shipboard sounder.

Experience level of personnel. Another important factor contributing to our sample collecting limitations involves the lack of trawling experience of our biologists and technicians. Aboard the Oregon (a NOAA trawler) and the Colintino Rose II (a chartered fishing vessel) we usually had no problem catching shortbellies. Both of these ships were rigged and manned for fishing with experienced captains directing fishing operations. Aboard the Jordan, an oceanographic vessel, the cruise leader has that responsibility, and in our case, the cruise leaders have been relatively inexperienced, and have had difficulty in catching fish. Experience comes slowly when one fishes only 5 or 6 weeks per year. The problems considered in this report might seem naive to an experienced fisherman; however they have frustrated our field efforts significantly.

Conclusions

Most oceanographic vessels are poorly rigged for trawling operations. The specialized gear requirements for these operations are often incompatible with the ship design and refitting may be impractical as well as costly. The electronic equipment used in finding fish and monitoring trawls is costly and affording state-of-the-art instrumentation is out of the question for many scientific programs. However, to consistently collect fishes near bottom or in midwater with a trawl, a vessel that is properly designed and equipped for that purpose is required.

Perhaps equally important as the vessel and rigging is the presence of experienced personnel. In the shortbelly investigation, the presence of a qualified fisherman, hired to direct operations and to train the scientific participants early in the program, would surely have improved our successes and saved a great deal of valuable ship time.

The experiences gathered by all concerned with this shortbelly study as well as the recent modifications and equipment additions to the Jordan however, have improved our fishing successes.

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Session I Discussion
Methodology and Statistical Analysis

Michael E. Crow, Discussion Leader

Questions Following Langton Presentation:

Feller asked how much change would occur in the necessary sample size if acceptable significance levels were changed. Langton responded that this information, while not in his presentation, could easily be worked out and be provided to those individuals who are interested. Breitburg inquired whether the adequate sample sizes resulting from this study were influenced by the decision not to lump major groups of prey, which would give rare prey species as much influence as common ones. Langton responded that the prey importance was measured by its mean weight in the stomach contents and that this should prevent this from becoming a problem. Simenstad asked whether the source of variability was mostly from fish of different size classes or from fish in different tows or from other sources. Langton replied that variability was among individuals, and especially among size classes of fishes. Chapman asked whether the tight requirements for the coefficient of variation were related to the kind of question being asked and Langton concurred that the level of significance required by some questions might differ from those for other questions. Cailliet asked whether the examples given were randomly picked or chosen to make a point. Langton replied that they attempted to choose examples representative of most species studied. M. Crow inquired whether they had included empty stomachs. Langton responded that they did, but Cohen inserted that the number of empty stomachs in this study was very low and that this should not influence the conclusions. M. Crow then suggested that by estimating the percent of empty stomachs they might be able to figure out a way to use smaller sample sizes. But Langton pointed that it would be a difficult type of decision to make on shipboard. They get an estimate of the number of empty stomachs by going through all samples later in the laboratory and this was considered part of the variability.

Questions Following The First Crow Presentation:

Eggers made a comment on the X^2 test, suggesting that the expected values have to be greater than five so that the normal approximations of the multinomial implicit in the X_2 increases the power of the test thus requiring pooling of prey or predator categories to ensure that the expected X^2 value is greater than five. Larson questioned whether or not the number of individual prey seen in the pooled stomachs of a species of fish is the kind of data that goes into a contingency table, since the total number of prey is not exactly attribute data. M. Crow replied that classification of things into certain predator-prey characteristics via a multinomial distribution is appropriate to X^2. Given the wide disparity in the numbers of prey classifications which different predators consume, Cailliet asked whether you have to have equal sample size among predators in order to make the X^2 analysis valid. M. Crow replied that it was not necessary but that a general guideline was that if you are approaching 25 (prey) characteristics, you should include 100 or more stomach samples within each predator.

Feller asked why one would want to pool prey categories at all. M. Crow explained that with extremely high numbers of prey classifications the contingency table has a proportionally large number of cells, and degrees of freedom and is increasingly difficult to interpret. Thus, if you don't pool, you are always going to end up with many prey classifications with few individuals, your expected values are going to be small, and your contingency table analysis is going to be confusing and not statistically palatable.

Questions Following Levy Presentation:

Chapman cautioned that data are often lost in reduction to graphical presentation and it was agreed that an appendix data table should be utilized in such cases. Ebeling and Levy both discussed the relative worth of statistical comparisons, which editors typically require, and graphically explicit differences and it was agreed that, optimally, both should be provided. Larson reminded everyone that these data can also be reduced to rank order data and tested using conventional non-parametric rank tests. Calliet questioned the cost of such graphical illustration and how much Levy incorporated into his proposals to cover these costs, to which Levy replied that in his case the illustration work was performed by a jack-of-all-trades technician and not a costly illustration service.

Questions Following La Bolle Presentation:

Cailliet questioned whether it would ever be possible to construct a laboratory experiment which takes into account two problematical aspects: 1) refuge, the spatial heterogeneity of the laboratory environment; and, 2) the multiple array of prey which fish are usually accustomed to feeding upon. La Bolle responded that, while it depends upon the system and scale with which you are working (i.e. much easier with zooplankton versus complex invertebrate assemblages) it is generally impossible to simulate natural foraging conditions and all we can really accomplish is simple tests of important predator-prey interactions.

Chapman asked whether there is any adaptive significance to the long distance escape movements of prey fish from predators in the field, to which La Bolle replied that while larger prey fish which do swim long distances have a refuge in their size, smaller and gravid fish usually display different tactics, i.e. swim shorter distances and try to hide.

Hunter requested further explanation on exactly why the experiments were performed. La Bolle elaborated further on the history of the studies of predation on juvenile salmonids and his own efforts to elucidate predator-prey interactions involving juvenile salmonids via prey selection experiments.

Questions following Simenstad Presentation:

Citing the normally high turbidity in most estuarine habitats, Cailliet questioned whether the low turbidity conditions in the described experiments represented actual predator-prey functions. Simenstad suggested that trying to document reactive distances under both high turbidities and low light intensities was almost an intractable problem and turbidity was discarded as an independent variable controlled in their aquaria experiments; he suggested that the effects of turbidity could be quantified through controlled microcosm experiments, wherein sampling of prey assemblages and stomach contents could be documented over a spectrum of turbidity levels.

Rowley questioned how one could extend the functional relationships generated around simplistic aquarium experiments, which did not take into consideration the blending in of prey into background color or the reduced escape response capabilities, into a realistic field experiments. Simenstad replied that testing the predictions derived from the simplistic functional components experiments in the more complex intermediate and large microcosm experiments was intended to elucidate the influence of just those factors uncontrolled or manifested in the aquarium experiments. Thus, the maximum reactive distance and capture success data acquired in the aquaria would in all likelihood represent the maximum range of these values, which would then be subject to limiting factors such as turbidity, background contrast, and habitat complexity (i.e. macrophytes) in the more realistic microcosm experiments.

Crowder observed that most of the success in the functional components approach has been achieved through experiments with planktivorous fishes, and that prey avoidance and prey seeking behaviors of prey and predators, respectively, become more diverse and complex in structurally-complex habitats. Simenstad reiterated that, no matter how complex a habitat or prey assemblage or predator behavior, the only way we're really going to begin to understand why we find what we do in fish stomachs is to observationally or experimentally dissect the basic predation process and document the subtle differences in foraging behavior which reflect the *in situ* conditions. Such basic understanding can then be used to structure more complex experiments which could test the influence of the various factors which affect foraging in a structurally-complex habitat.

Herbold asked whether it would be possible to dye or otherwise mark prey with substances which would only be visible to human observers or video equipment, thus enhancing the visibility of small prey or under low light intensities. Simenstad responded that this technique has been utilized, via infrared lighting and infrared-sensitive video equipment, to monitor nocturnal behavior of primates but has not been used in fish experiments. This offers a viable, though perhaps costly, means of circumventing the limitations of human observation under natural light conditions.

Questions Following the Second M. Crow Presentation:

Adams wondered if, contrary to the accepted convention of the Holling disc equation, handling time and searching time do not overlap. M. Crow explained that his asymptotic model assumes that search time is virtually zero. Crowder noted that if search time is also often near zero (i.e. planktivores), taking the ratio of search time to handling time can be a problem. M. Crow replied that search time near zero reinforces his conclusion that handling time is unimportant, as it further reduces the total foraging time necessary to acquire a given meal. Crowder continued to describe how in the laboratory handling time is measured as the time required to get the energy benefit into the system such that as capture success declines (assumed to be 100% by M. Crow) the time it takes to fill the stomach increases dramatically. He further suggested that the reason Werner's laboratory-derived handling times were so high was that the prey couldn't avoid predation, while in the natural environment the fish must allocate time to preparation for capturing the next prey and accounting for escape responses, thus increasing the time required to obtain a unit of energy. Subsequent discussion indicated that different interpretations of handling time will greatly influence the outcome of M. Crow's model.

Questions Following Ursin Presentation:

Grossman asked about the effect on the model of violating the model's second assumption, that change in weight of stomach contents over the change in time is zero. Ursin suggested that lack of stomach contents data from 24-hour sampling may produce severe effects in the model but went on to clarify that the mean stomach contents (weight) over sufficient 24-hours' samples should be a reasonable measure of the average consumption, although considerable variability due to diel foraging periodicity is introduced into the model via this approach.

Chapman asked whether Ursin had actually utilized the model to calculate year class strength in a fish population, to which Ursin replied that they as yet have no data set which is sufficient to make year-to-year comparisons, although they have carried the calculations through the best years' data.

Breitburg suggested that use of the selectivity index as an estimate of the amount of food available would result in underestimation as the preferred items become rarer. Ursin acknowledged that biomass of preferred prey would be a better index.

Simenstad questioned the feasibility of obtaining sufficient data on prey availability during the critical period of fishes' life histories which affect year class strength. Ursin replied that, although that is a critical assumption which may never be met effectively, this method of determining year class strength would not be any worse than the other unsuccessful methods of estimating year class strength. Ursin further suggested that these methods are damaged more by variance than by bias, such that the more ways to estimate year class strength the better.

Knechtel observed that, given the model's function between prey abundance and fish consumption, once you reached fish satiation it would be impossible to measure prey abundance. Ursin replied that the ability to estimate available food and the concentration constant depended upon accumulating data at different feeding levels.

Disturbed by Ursin's statement that feeding levels of young fish are always less than old fish, Hunter asked if that was an output of the model or a result of stomach contents analyses. Ursin replied that data from Georges Bank and Baltic Sea fishes tend to show that result and, in addition, the Von Bertalanffy growth curve or something similar to it often produces exaggerated growth in young fish relative to later ages.

Cailliet suggested that the result observed was a combination of fish which were starving and didn't survive and those which grew rapidly and did survive. Ursin commented that, since we can't know which of the fish eventually survive, the mean of the population must be used, even though there is evidence from North Sea fish growth rate data that some groups (localities) suffer more than others.

General Discussion of Methodology

Given the recent evidence of the carcinogenic effects of formaldehyde, Rinaldo asked whether anyone had used an acceptable alternative other than freezing; no one replied affirmatively.

Cailliet illustrated that there are different needs and occasions for both graphical representation and statistical evaluation. He was, however, bothered by the lack of incorporation of frequency of occurrence data in M. Crow's contingency table, even though it isn't statistically valid, because of the loss of information on the population level. M. Crow replied to both of Cailliet's comments. He first noted that you need two things in comparing fish diets--a bottom-line conclusion (i.e. are they different) and a means of legibly presenting the data--and the statistical approach he proposed in the contingency table and the graphical approach presented by Levy fill these respective needs effectively. M. Crow reiterated that the contingency table is not designed to assess relative importance, only to test differences; but frequency of occurrence can be incorporated by identifying feeding modes and constructing a predator X feeding mode contingency table and use frequency of occurrence as values in that case.

Feller demanded a proper definition of "feeding mode," to which M. Crow explained that that was his term to describe how (strategy, behavior) fish feed based upon the known life history and ecology of the prey organisms extracted from the stomach contents. Feller stated, however, that this was a dangerous approach because of the extreme variability in the location and behavior of prey over time and space. Chapman further suggested that fish feeding randomly over a patchy benthos would illustrate multiple feeding modes despite their uniform feeding behavior due to their encountering of different prey patches. M. Crow argued that these prey should still indicate a similar feeding mode, despite the taxonomic differences in prey as compared to other fish.

Grossman asked if anyone has had success using discriminate function analysis as a multivariate technique to statistically identify differences between feeding habits of species, especially given the different options of transforming data to accommodate the basic assumptions of the technique. M. Crow replied that use of stomach contents data in discriminate function analysis just constituted too gross a violation of the assumptions to be of much use; similarly, he found classification techniques such as clustering and principal components analysis to be of little use in categorizing feeding modes. Feller, however, suggested that discrimainate function analysis can be a useful tool when you're searching for associations and don't know what factors are causing the effects you're observing.

Maule asked M. Crow if a nonparametric test (i.e. Koch) could be utilized to test significance, to which M. Crow replied that the contingency table approach is probably superior from the point of simplicity.

M. Crow stated his impression that the experimental methods described were fraught with complex problems which made them costly, time-consuming and contradictory. Simenstad cited a number of questions relating fish predators and their prey which could only be addressed through identifying the functional relationships between a prey taxon or size, but not without a big jump in cost and effort. Irvine thought it was a matter of further and further refinement in order to get around making inferences. She suggested that, when considering the behavior of both predator and prey, any induced change in prey behavior produced predator responses which as a foundation are not generally applicable.

Chapman commented that the question should concern the problems of laboratory experiments, not whether or not we should utilize experiments at all. As an example of an important factor which cannot be approached in the laboratory, M. Crow cited the effect of schooling or aggregation which is not represented by experiments with individual fishes and non-patchy prey distributions. Chapman said that similar arguments, i.e. not being able to separate relevant factors, could be assessed of field experiments.

Eggers described how the studies described by Simenstad were motivated by the successes and consequences of earlier feeding behavior work, citing Hunter's studies on feeding behavior of larval anchovies.

Herbold's interpretation of Simenstad's experiments was that controlled variables were designed to fit and refine a model (i.e. Holling disc equation), which still did not permit hypothesis testing to produce clearcut answers. Hunter reminded everyone that the various process models were important to the conceptualization of a problem but would seldom themselves be used to determine year class strength or the fate of fish populations.

Session II

Bioenergetics of Fish Feeding

SESSION LEADER

George Boehlert

PARTICIPANTS

Douglas Eggers
Bruce Robison
Tom Bailey
Philip Chochran
James Rice
Mary Yoklavich
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Bioenergetic Significance of Prey Size Preference By Lake Washington Juvenile Sockeye Salmon

Douglas M. Eggers
University of Washington

Introduction

Prey size preference by planktivorous fish has been hypothesized as a strategy to increase feeding efficiency (Werner and Hall 1974; Eggers 1982; Mittlebach 1981). Support for this hypothesis rests on comparison of experimentally determined diet breadth (Werner and Hall 1974; Gibson 1980) or field-determined diet breadth (Mittlebach 1981) to the optimal diet breadth based on a model of prey selection incorporating size selective rates of prey encounter, prey handling time, prey energy content, and prey capture success.

The pattern of prey selection observed for Lake Washington juvenile sockeye salmon (Oncorhynchus nerka; hereafter abbreviated LWJSS) have been reported elsewhere (Doble and Eggers 1978; Eggers 1982). There is a distinct minimum size threshold for prey occurring in the sockeye stomachs. This threshold is greater during the summer and fall months (July - October), when large prey items are present. The threshold is lower during the winter months, when large prey items are either absent from or very rare in the water column. At times of the year there appears to be a preference against evasive forms. The threshold for prey occurrence in the diet is not related to a corresponding threshold in the length of available prey or differential prey encounter due to differential prey visibility (Eggers 1982). These observations are consistent with the predictions of optimal diet breadth models.

The above cited evidence for the optimal diet breadth hypothesis for prey preference observed for LWJSS is largely circumstantial. There has been no demonstration of the actual increase in foraging efficiency for the observed strategy of prey preference. The following is an attempt to determine the variation in the magnitude of biomass ingested for the alternative strategies of prey preferences. A model (Eggers 1977) was used to compare amounts of zooplankton prey consumed under alternative strategies of prey preferences at the various times of the year when the relative abundances of large and small prey items were different.

Methods

The theory of a particualte feeding predator is well developed (Werner 1972; Charnov 1973; Eggers 1977; Obrien 1979). For a prey distribution that is fine grained relative to the predator and consists of multiple prey types, the rate of biomass ingested (E_t) is (cf. Charnov 1973):

$$E_t = \frac{\sum_D \lambda_i N_i S_i E_i}{1 + \sum_D \lambda_i N_i Th_i} \tag{1}$$

where λ_i = volume searched per unit time (l/sec), N_i = density of the ith prey type (#/l), S_i = capture success which is the proportion of pursuits of the ith prey type that are successfully captured, E_i = biomass of the ith prey type (μgC/animal), Th_i = prey handling time (sec), D is the subset of available prey that are pursued upon encounter. The biomass ingested during any feeding perod T is the product of E_t and T.

Depending upon the sizes and availability of prey (i.e., characterized by N_i and E_i) as well as the foraging ability of the predator (i.e., characterized by λ_i, S_i, and Th_i), E_t can be increased by restricting the set of available prey that are pursued upon encounter (D). The particular D for which E_t is the greatest is the optimal diet breadth. The optimal diet breadth may be easily computed (cf. Charnov 1973, 1976) by first ranking the set of prey by the marginal increase in biomass ingested per unit handling time ($\lambda_i E_i S_i/Th_i$); then starting with the highest ranked prey (i.e., $i = 1$), prey are progressively added to the diet breadth D until $\lambda_i E_i S_i/Th_i = E_t$. The optimal diet breadth consists of all higher ranked prey than that for which the above equality holds.

Equation 1 represents the integration of a complex sequence of events into a single rate. It is also the deterministic representation of a stochastic process. It is useful to dissect the cycle of events into the stochastic components and consider each individually. Each predation event can be dissected into a sequence of subevents; search, encounter, pursuit, capture, and consumption (Fig. 1). As the sequence of prey encounters and pursuits continues in time, two quantities of interest accumulate, energy or biomass ingested (B) and time engaged in foraging (T).

The random variables of interest in the predation cycle are defined as follows: Search time is the time from the initiation or resumption of search to the encounter of a prey type. The search time is the inverse of the attack or encounter rate ($\lambda_i N_i$). If prey are randomly distributed in the water column the encounter rate has a poisson distribution with parameter equal to $\sum_D \lambda_i N_i$, and the search time has an exponential distribution with parameter , where:

$$\mu = 1/\sum_D \lambda_i N_i$$

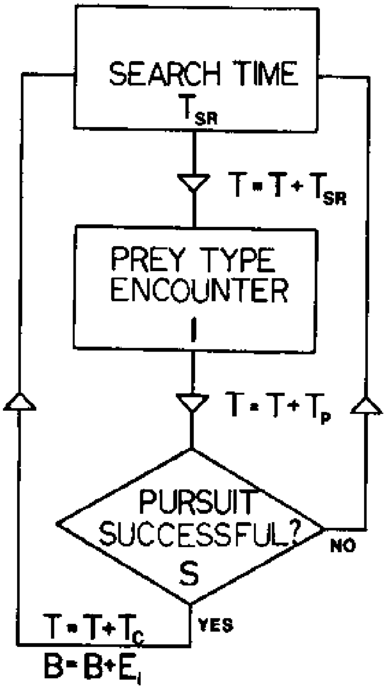

Fig. 1. Schematic representation of the foraging process; see text for definition of parameters.

The particular prey type encountered (I) is the second random variable of interest. It has a multinomial distribution where the probability that a prey contained in D is encountered (P_i) is:

$$P_i = \frac{\lambda_i N_i}{\sum_D \lambda_i N_i}$$

Note that if the prey type i is not contained in D then $P_i = 0$. The above stochastic representation illustrates an implicit assumption that the predator is able to effectively ignore the prey not contained in the diet breadth and that no increase in search time results from the filtering out of prey not contained in D. Once encounter is made, pursuit is initiated. Whether or not the pursuit is successful is the third random variable of interest. The pursuit is either successful or not and is therefore a Bernoulli trial. The parameter is S_i, the probability that the ith prey type is successfully captured given that it is pursued. If the pursuit is successful then the prey is consumed in some finite period of time T_C. Having consumed the prey, the predator resumes searching. If the pursuit is unsuccessful the predator immediately resumes searching.

Note that the pursuit time (T_p) and the consumption time (T_c) were assumed to be constant and not vary with respect to prey type. Most of the time that planktivorous fish take to consume prey is involved in swallowing the prey. Most of the time taken by the predator to pursue the prey is involved in swimming the distance from the point of encounter to the prey. This is the reaction distance and varies among the prey types. Fish accelerate to maximum pursuit velocity during the initial part of the pursuit distance. This reduces the disparity between handling time for smaller, less conspicuous prey compared to larger, more conspicuous prey. Nevertheless, prey handling time can be expected to vary with prey size and the assumption of constant handling time is in theory, inappropriate.

Handling time (T_h) was taken to be $Tp + S_i\ T_c$. The assumption that the predator resumes searching given that the pursuit was unsuccessful is perhaps an oversimplification because it ignores the possibility that the same prey may be pursued again after an unsuccessful strike. If this occurs it would presumably increase the capture success while at the same time increase the pursuit time. The model could be generalized to admit multiple pursuits of the same prey, but S_i/Th_i under the two alternative models could be very similar. Thus, comparable predictions of the optimal diet breadth and rate of biomass ingested would result. The simpler model was assumed in subsequent analysis.

Optimal diet breadth and biomass of prey ingested under alternative diet breadths based on the above model were compared to those observed for LWJSS. Details of the data based considered were given by Eggers (1982). Briefly, four periods of the year were considered, including the November 1974, February 1975, July 1975, and August 1975 sampling trips. LWJSS feed on six species of limnetic zooplankton. In order of increasing size, these include the small cladocerna *Bosmina longirostris*, the small cyclapoid copepod *Cyclops biscuspidatus*, the small calanoid copepod *Diaptomus ashlandi*, the intermediate sized cladoceran *Diaphanosoma lechtenbergianum*, the large calanoid copepod *Epischura nevadensis*, and a class of large cladocerans comprised of several species of *Daphnia*. In the analysis of prey selection by LWJSS, the size distribution of individuals within species was also considered. Prey were grouped by 0.025 mm size classes. Since each prey species consisted of discrete size classes, there was a relatively large number of prey types or categories considered.

The values of paramters, λ_i, S_i, and Th_i were estimated as follows. The volume searched per unit time ($_i$) was assumed to be some fraction of the reactive field volume searched per second. The reactive field was assumed to be spherical with radius equal to 100 times the total body length. The radius of the reactive field was equivalent to the reactive distance and near the maximum observed for a wide variety of fish species (Obrien 1979). The proportion of the reactive field searched per unit time was taken to be that which yielded a predicted optimal diet breadth that was closest to the observed diet breadth for the February sampling trip. The prey community exploited by LWJSS during February was the simplest since the large prey types were either absent or very rare in the water column. The estimated fraction of reactive field searched per unit time was therefore not confounded with other variables, principally prey, evasive ability as there is relatively little difference in evasive ability of the two small copepods present during February. The value resulting from this exercise was

30% of the reactive field searched per second. S_i was taken to be 1.0, 0.7, 0.7, 0.6, 0.5, and 1.0 for the prey species Bosmina, Cyclops, Diaptomus, Diaphanosoma, Epischura, and Daphnia, respectively. The capture success was assumed not to depend on prey size within species. These values reflect that copepods and Diaphanosoma have the greatest evasive ability, that the cladocerans Bosmina and Daphnia are not evasive and are almost always captured at each pursuit, and that the larger evasive prey types are somewhat more evasive than the smaller evasive prey types. The assumed pattern of evasive ability among prey types is consistent with the results of Drenner et al. (1979) and Vinyard (1981), as well as preliminary results of experiments where evasive neretic zooplankton were fed to juvenile chum salmon (Oncorhynchus keta) (Simenstad et al., this volume).

Values of 1.0 second were assumed for pursuit time (T_p) and 0.5 seconds were assumed for consumption time (T_c). These were assumed to be constant among all prey types and were very similar to those observed for bluegill sunfish (Lepomis machrochirus) feeding on zooplankton (Werner 1974) and juvenile salmon feeding on zooplankton (Simenstand et al., this volume). Handling time (Th_i) was equal to $T_p + S_i\ T_c$.

Model predictions were also based on ambient conditions of prey density (N_i) and biomass per animal (E_i). Methods by which N_i and individual prey body lengths were estimated were reported in Eggers (1982). Biomass (µg C/animal) were estimated from unpublished relations (simple linear regression lines) between carbon per animal (µg) and total body length (mm) for Lake Washington zooplankton.

Results

The four sampling periods considered differed greatly in the availability of prey. During the two summertime sampling trips the large prey types, Daphnia and Epischura, were relatively abundant. During the wintertime sampling trip only the two small copepods, Cyclops and Diaptomus, were available. During the November sampling trip large prey types were available but in densities much lower than during the July and August sampling trips. The diets observed for LWJSS reflect this availability of prey. However LWJSS are much more selective than would be expected assuming passive mechanisms that increase the rate of encounter of larger prey types (Eggers 1982).

Optimal diet breadths were computed for each sampling trip based on ambient conditions and the above assumed parameter values (Table 1). The diet composition assuming that sockeye are pursuing only prey types contained in the optimal diet breadth is very similar to those observed for LWJSS (Table 1). However, the predicted within-species diet breadth (i.e., the minimum sized individual of that species pursued upon encounter) was usually much greater than that observed (Table 1). This may indicate some noise in the sockeye's ability to discriminate the optimal diet; whenever the diet breadth bisected the size distribution of an individual prey species the smaller size classes of that species were underrepresented in the sockeye diet (cf. Eggers 1982).

The implicit hypothesis in optimal foraging theory is that restricting pursuit to certain "valuable" prey types greatly increases feeding efficiency, which is commensurate with fitness (Schoener 1971). To test this, the biomass of prey ingested in a one hour feeding period was

Table 1. Comparison of observed diet to that which is predicted to maximize biomass intake per unit foraging time.

Time	Diet composition	Bosmina	Cyclops	Diaptomus	Diaphanosoma	Epischura	Daphnia
Nov. 1974	Observed % by no.	1.0	17.7	3.0	25.7	50.1	3.4
	minimum size	---	0.59	0.74	0.79	1.36	0.96
	Predicted % by no.	0.0	0.0	19.5	9.5	45.0	26.1
	minimum size	---	---	1.06	1.19	1.56	0.99
Feb. 1975	Observed % by no.	T	13.3	79.8	0.7	6.3	T
	minimum size	---	0.51	0.66	0.89	1.43	---
	Predicted % by no.	0.3	16.9	77.9	0.3	4.6	0.0
	minimum size	---	0.84	0.81	1.48	1.47	---
July 1975	Observed % by no.	0.0	1.1	6.8	0.4	1.8	90.0
	minimum size	---	---	0.71	---	1.31	1.24
	Predicted % by no.	0.0	0.0	0.0	0.0	8.0	92.0
	minimum size	---	---	---	---	2.14	1.51
Aug. 1975	Observed % by no.	0.0	0.1	0.1	0.0	1.1	98.7
	minimum size	---	---	---	---	1.48	0.94
	Predicted % by no.	0.0	0.0	0.0	0.0	4.1	95.9
	minimum size	---	---	---	---	2.36	1.74

computed for the two contrasting strategies of pursuit, pursuing all prey as encountered, and pursuing only the optimal diet breadth as encountered (Table 2). The stochastic version of the particulate feeding model was used to generate the predictions in Table 2. The biomass of prey consumed in one hour are the average of ten realizations, using random number generator, of the stochastic process. There is a large increase in the biomass consumed due to restricting pursuit to the optimal diet breadth. This was particularly true for the periods of the year when large prey types were available.

Table 2. Increase in biomass of prey consumed due to prey size preference.

Trip	Biomass of prey consumed in 1 hour (mg. carbon)		Increase in biomass consumed
	Pursuing all prey as encountered	Pursuing optimal diet breadth	
Nov. 1974	5.36	9.10	70%
Feb. 1975	3.45	4.46	29%
July 1975	9.21	23.30	153%
Aug. 1975	16.5	27.50	67%

The reason for the greater divergence of biomass ingested under the two alternative strategies of prey pursuit during the summer months is illustrated in Fig. 2. The two months, February and August, indicated the greatest contrast in biomass consumed per unit prey handling time. Prey were also more abundant in August (Eggers 1982). When all prey are pursued as encountered there is a greater dillution of biomass intake rate (E_t) due to time spent pursuing small prey types. In February, the density of those larger prey types was so low that the search time was high enough so that it was more profitable to spend that time pursuing smaller more abundant prey types. In February, since there were relatively fewer prey types not contained in the optimal diet breadth, there was a smaller dillution of biomass ingestion rate due to pursuit of the suboptimal prey types.

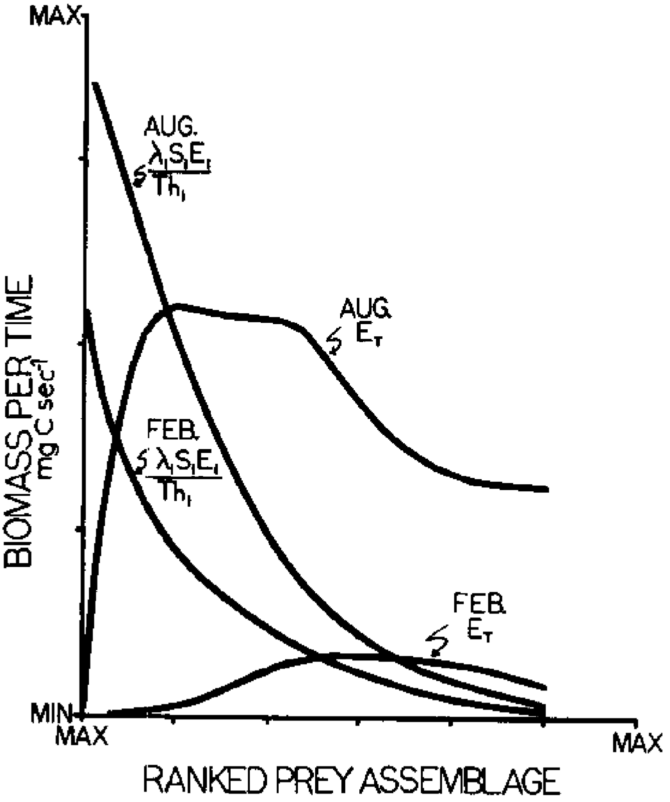

Fig. 2. Marginal increase in biomass ingested per united handling time and per unit time for ranked prey assemblage.

Discussion

The approach above, where a model was used to demonstrate that strategies of prey selection increase foraging efficiency, suffers from inherent circularity. This is because the value of a key parameter, the fraction of the reactive field searched out per unit time was unknown and was estimated by forcing the model to predict observed patterns of prey selection. The fact that model prediction using the parameter estimated from the February data was consistent with observed patterns of prey selection in other months lends credibility to the above exercise, however.

Doble and Eggers (1978) gave estimates of zooplankton (dry weight/day) by LWJSS. Assuming that roughly one half of the dry weight is carbon, Doble and Eggers (1978) observed that daily meal ranged from 8.9-20.8, 15.6-35.6, 0.3-6.3, and 1.8-8.2 during August, October December, and February, respectively. The data were stratified by fish body length contributing to the variability in the values of daily meal observed.

LWJSS show substantial seasonal differences in diel feeding chronology (Doble and Eggers 1978; Eggers 1978). During the summer months feeding is restricted to a 1-2 hour period during the evening crepuscular hours. During the winter the population appears to be stratified into feeding and non-feeding segments (Woodey 1972; Doble and Eggers 1978), with the feeding component appearing to feed continuously during the diurnal hours.

The predicted amount of zooplankton consumed in one hour (Table 2) is consistent only with the summertime observed daily meal. The model would significantly overestimte the daily meal during the fall and winter months.

The inconsistency between the predicted daily meal and that observed could be decreased by using a smaller reactive field volume or a smaller fraction of the reactive field searched out per unit time. Sockeye occur in low light intenstiy particularly during the fall and winter (Eggers 1978), justifying to some extent these parameter values. However, observed patterns of prey selection would be inefficient at the reduced searching ability of LWJSS and the optimal diet breadth would be lower than those observed.

The model used above also utilized an inappropriate assumption, that prey handling time does not depend on prey size. Larger, more conspicuous prey are pursued at greater distances than smaller, less conspicuous prey. Due to this, the pursuit time component of prey handling time tends to be greater for large prey. This reduces the expected biomass ingested per unit prey handling time. Therefore optimal diet breadth estimates based on the model where handling times are constant tend to be smaller than those estimated with the more correct model. Reactive field volume increases with the cube of prey length and handling time is, at most, proportional to prey length. Because of this, the assumption of constant handling time will not change the relative ranking of prey types and, therefore, any of the qualitative predictions regarding the species components of optimal diet breadth.

The above model was patterned after the functional components analysis first applied by Holling (1965) to praying mantids. The model gives instantaneous rates of prey ingestion. It is perhaps impossible to achieve meaningful predictions of quantities such as growth and daily meal for a pelagic or limnetic planktivorous fish with this type of model. To do so, the model must integrate over a day or longer time frame. The functional components model is also very sensitive to ambient conditions that influence the rate of prey encounter, including prey density, prey visibility and light intensity. There is a one or more order of magnitude variation in these quantities in the ambient environment routinely exploited by LWJSS.

LWJSS show very complicated seasonal and diel patterns of feeding behavior (Eggers 1978), including depth of occurrence, schooling, diel feeding chronology, as well as prey selection. There is a substantial instantaneous variation among individuals of the population. At times the population occurs in a wide depth interval, with shallower occurring individuals in schools and the deeper occurring individuals not in school. The eplimnetic and metalimnetic regions of the water column where zooplankton are abundant are exploited only by the shallowest occurring individuals of the population. It is conceivable that a continuous interchange of individuals among depth strata occurs in Lake Washington, with individuals venturing into regions of high prey availability to feed briefly then returning to deeper strata. This would be impossible to detect with the sampling methods employed in our studies. The high rates of prey ingested predicted by the model would then be more consistent with the scenario of brief feeding bouts.

To effectively increase feeding efficiency there is also an implied time constraint on feeding for strategies of prey preference. If the only constraint on feeding was the amount of time when light intensity was great enough for feeding to occur, gut capacity would limit the amount of prey consumed even for the most conservative parameter values that reflect the searching ability of LWJSS. There would be no difference in the magnitudes of prey consumed under alternative strategies of prey preference if foraging time were not constrained. Crow (this volume) makes a similar point. One would expect to observe strategies of prey preference only in situations where foraging time was constrained. The obvious constraint is piscivorous predation (cf. Eggers 1978).

The above discussion may appear as rampant speculation. The major issue that cannot be resolved is the quantitative nature of the searching ability of Lake Washington juvenile sockeye salmon. This quantity may be estimated in experiments that measure the temporal aspects of the sequence of events in the particulate feeding process (Fig. 1) for various prey densities and light intensities. However, to do this requires some technological innovation. To do this one should consider even recorders routinely used in animal behavior studies. The event recorder gives a real time record of the rapidly evolving sequence of events. The record can then be interfaced with a computer so that the voluminous amounts of data can be reduced and analyzed.

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Nutrient Energy Flux in Midwater Fishes

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Introduction

Oceanic midwater fishes are notoriously difficult to keep alive in captivity (Robison, 1973). The sole exception, a zoarcid--Melanostigma pammelas--has been maintained under laboratory conditions for two years in our lab, but it is atypical of midwater fishes in many respects. Because of the maintenance problem it has not been possible to experimentally determine the energy intake, assimilation, and utilization patterns of midwater fishes. Such determinations, however, are very important because midwater fishes are the dominant members of the third major trophic level in the largest ecosystems on our planet.

In the past, estimates of nutrient energy flux have been based chiefly on stomach content assays; and have usually been expressed as a daily ration in terms of the percent of body wet weight ingested per day (Hopkins and Baird, 1977).

There are some very real problems with this approach, especially that of stomach content contamination through "net feeding" (Lancraft and Robison, 1980). We have determined, by placing "bogus" prey items (e.g. copepod-sized styrofoam balls and euphausiids dyed with vital stains) in trawl net cod ends, that an average of 50% of the fish in a 1 hr trawl haul will have ingested material in the cod end. Of that 50%, roughly 25% of the material in their stomachs was ingested there (Robison and Lancraft, in prep.).

By conducting these experiments on thousands of fish we have determined contamination indices for the common midwater fish species off southern California, and have used these indices to correct the overestimates of ingestion based on stomach contents alone. Comparisons between species show striking differences in the levels of contamination

Our goal in the present study is to quantify nutrient flux through the third level of oceanic ecosystems. This is a very challenging problem and we have really only just begun. Presented here are our preliminary findings and while crude, they do reveal some interesting patterns that have already aided our understanding of the ecological structure patterns in pelagic communities.

Our approach has been to calculate nutrient energy assimilated by measuring the amount of food ingested through stomach content analyses corrected for net feeding, and subtracting the nutrient energy egested in feces. Again, it must be stressed that these are preliminary results and are relatively crude. Nevertheless, the method is simple, direct and it provides consistent results that make sense. The values presented here are not precise in an absolute sense, however as relative values they are reliable.

We have been aided in this approach because there is a good body of published data on the chemical composition of most of the prey types we encounter (e.g., Childress and Nygaard, 1974). We have reassessed many of these assays and have developed new microanalytical techniques for the small sample sizes that are necessary for working analyses of fish feces.

Methods

Fishes were collected by midwater trawls in the Santa Barbara and San Nicholas Basins off southern California. Specimens were frozen at sea on dry ice, and transported to a -20°C freezer in our laboratory. The samples were stored frozen until the chemical analyses were performed. There is no significant difference between the chemical composition of feces collected from fresh fish at sea, and feces obtained from fish that have been quickly frozen.

Chemical analyses were performed on thawed material obtained in one of two ways: extrusion by gentle pressure along the ventral surface of the intact fish; or extrusion by gentle pressure along the rear portion (distal to the ileo-rectal valve) of the excised fish intestine. The validity of this approach has been demonstrated in comparisons of naturally or laboratory produced feces with the rectal portion of intestinal contents (Montgomery and Gerking, 1980; Bailey and Robertson, ms.; Robison and Bailey, 1981). Fecal samples from three to ten fish were pooled prior to analysis.

Wet weight - dry weight

The pooled fecal samples were placed in pre-weighed aluminum weighing boats. The boats were reweighed with the sample and then dried in a 60°C oven to constant weight (2-4 days) and again re-weighed. The difference in weights before and after drying was taken to represent the water content. Wet weights of samples on which chemical analyses were run, were calculated from their dry weights using the mean value for water content.

Chemical analysis

Pooled samples were thawed, transferred to a glass tissue grinder and homogenized in 2 ml of distilled water. The volume of the homogenate was made up to 10 ml with distilled water and then dispensed immediately into vessels for the different chemical analyses.

Aliquot dry weight and ash-free dry weight. Three 0.5 ml aliquots of each homogenate were dispensed into pre-weighed, pre-ashed aluminum weighing boats and then dried in a 60°C oven to constant weight (2-3 days). The dried sample was weighed, then placed in a 485°C muffle furnace overnight then reweighed. The difference between the weight before and after combustion in the muffle furnace represents the ash weight of the sample. The difference between the dry weight and the ash weight equals the ash-free dry weight. The mean of each triplicate was taken as the value of each sample.

Protein. Two 0.5 ml aliquots of each homogenate were analyzed for protein using a modification of the Lowry method (Merchant et al., 1964) with bovine serum albumin as the standard. The mean value from each pair was taken as the protein concentration of each sample.

Carbohydrate. Two 0.5 ml aliquots of homogenate were analyzed for carbohydrate using the method of Dubois et al. (1956) with glucose as the standard. The mean value from each pair was taken as the carbohydrate concentration of each sample.

Lipid. Lipid was extracted from two 0.5 ml aliquots of each homogenate using the method of Bligh and Dyer (1959). The extracts were dried under either nitrogen or argon in a 30°C water bath and then analyzed for lipid using the charring method of Marsh and Weinstein (1966) with stearic acid as the standard. The mean value from each pair was taken as the lipid concentration of each sample.

Chitin. Two 0.5 ml aliquots of each homogenate were analyzed for chitin using the method adapted from that of Parsons and Strickland (1968) by Childress and Nygaard (1974). Glucosamine-HCl was used as the standard. The mean value from each pair was taken as the chitin concentration of each sample.

Carbon, hydrogen, and nitrogen. Two 0.1 ml aliquots of each homogenate were pipetted into pre-weighed, pre-ashed aluminum CHN boats and then dried to constant weight in a 60°C oven for 24 hours. Dried samples were stored in a dessicator until the analyses were performed. The dried samples were weighed and then analyzed for carbon, hydrogen, and nitrogen with a Hewlett-Packard model 185B CHN analyzer or a Perkin-Elmer model 240B elemental analyzer. Acetanalide and EDTA were used as standards. The mean values from each pair were taken as the carbon, hydrogen, and nitrogen concentrations of each sample.

Caloric content. Values for caloric content were calculated using the following factors: protein, 4.1 Kcal/gram; carbohydrate, 2.5 Kcal/gram; lipid, 8.0 Kcal/gram. Chitin was assumed to have the same caloric value as carbohydrate. These conversion factors were used rather than the absolute caloric values (e.g., 5.7 Kcal/gram for protein; 4.1 Kcal/gram for carbohydrate; 8.7 Kcal/gram for lipid) since they more accurately and realistically reflect the energy value of fish feces to potential consumers (Brett and Groves, 1979).

Results and Discussion

Table 1 shows the chemical composition of the fecal matter from several southern California midwater fish species. Table 2 shows how these values compare with the measured values for other types of particulate organic detritus. These data have proven very revealing in several respects.

We have learned that midwater fish feces contribute significantly to the vertical flux of nutrients in the oceanic water column. They sink at an average rate of 1 km per day, and they represent a "missing link" in vertical nutrient flux budgets (Robison and Bailey, 1981). Most calculations of this flux reveal an anomaly in that there is more organic matter in the benthos than can be accounted for by the known mechanisms for getting it there. This situation has led many authors to propose a hypothetical class of large, nutrient-rich, fast sinking particles in order to balance the vertical flux budgets (Menzel, 1974; McCave, 1975; Gordon, 1977; Bishop et al., 1977, 1978; Knauer et al., 1979). It is now clear that midwater fish feces represent just such a class of particles and that they account for the bulk of the "missing" nutrient transport. We estimate that midwater fish feces contribute about 10% of the annual organic nutrient transport to the bottom of the Santa Barbara basin off southern California, and comparable amounts in similar regions (Robison and Bailey, in prep.).

Also, by conducting proximate analyses of midwater fish stomach and intestine contents we have been able to demonstrate that the widespread myctophid Ceratoscopelus warmingii is capable of herbivory. We found portions of diatom mats (i.e., Rhizosolenia) in the stomachs of these fishes and were able to show that they had indeed been digesting this plant material by finding significant levels of silicate, chlorophyll, and phaeophytin pigments in their intestinal contents. This is a significant finding because it shows a capacity for herbivory in a group of fishes that was previously regarded as being exclusively carnivorous (Robison, ms.).

With regard to nutrient energy assimilation, we will use another myctophid, Stenobrachius leucopsarus, as an example. Our corrected feeding data show that on the average, each S. leucopsarus consumes the equivalent of 7 Euphausia pacifica each day. The caloric equivalent of this average meal is about 14 calories (Childress and Nygaard, 1974).

The fecal output of S. leucopsarus is about 3 mg (dry weight) per day. The fecal matter averages about 3 calories per mg dry weight. Thus each day, each S. leucopsarus egests about 9 calories of fecal matter.

With an intake of 14 cal/day and an output of 9 cal/day, the calculated assimilation level is 5 cal/day; or an assimilation efficiency of a little over 35%.

When we apply this approach to different species we find assimilation patterns consistent with other known ecological patterns. For example, we recognize five general guilds for midwater fishes: 1) vertically migrating zooplanktivores (e.g., myctophids); 2) non-migrating zooplanktivores (e.g., sternoptychids); 3) stalking predators (e.g., stomiatids); 4) ambush predators (e.g., ceratioids); and 5) pursuit predators (e.g., evermannellids).

Within these groups we find that relative assimilation efficiency varies with food scarcity; and that the greater the food availability the lower the assimilation efficiency. Within the guild of vertical migrators, S. leucopsarus has an assimilation efficiency of about 35% Triphoturus mexicanus, an ecological counterpart, has an assimilation efficiency of about 32%. Among non-migratory zooplanktivores, the hatchetfish Argyropelecus affinis has an efficiency of about 40% while a deeper living species, Sternoptyx diaphana has an efficiency of about 42%. The stalking predator Stomias atriventer, a regular feeder, shows an efficiency of about 30%. Our data on the two following guilds is sketchy and the best we can say at present is that ambush predators, which are intermittent feeders, have relatively high efficiencies; while pursuit predators, which feed regularly, have relatively low efficiencies.

Similar patterns are also apparent among fishes which eat different types of prey. Ichthyococcus and Leuroglossus are fishes which consume prey with low nutrient densities--gelatinous zooplankton which are 95 to 99% water. Typically these fishes have elongated intestines. The ratio of intestine length to body length is a reliable index for comparing this characteristic. For Ichthyococcus which eats gelatinous zooplankton almost exclusively, this ratio is 1.5. For Leuroglossus which eats a mixed diet of gelatinous and crustacean zooplankters, the ratio is 0.5. For S. leucopsarus which consumes chiefly crustaceans, the ratio is 0.28. Assimilation efficiencies appear to run counter to the decline in ratio value. For S. leucopsarus again the value is about 35% while for Leuroglossus it is above 40%. We have too few data on Ichthyococcus as yet to make a convincing case as these fishes are relatively rare. For all fishes examined however, the trend is for higher assimilation efficiencies with greater gut lengths.

When we compare ecologically equivalent species from oligotrophic waters in the central gyre of the North Pacific with those from high productivity waters in the coastal zone, we find higher assimilation efficiencies where the food supply is lower.

The same patterns are evident when we compare fishes with different depth ranges; the deeper the habitat of the species (and thus the lower the food supply), the greater the assimilation efficiency.

In summary, we find higher assimilation efficiencies when the food supply is scarcer or of poorer quality.

Some additional, intriguing findings have shown us that there are extremely high lipid levels in the livers of hatchetfishes and very low lipid levels in their feces. We interpret this as a response to lower regularity of feeding, because lipids appear to be the most efficient means of storing nutrient energy.

Also, we find very low chitin levels in the feces of Ichthyococcus and Leuroglossus, a pattern that correlates with their diets of gelatinous zooplankton.

Finally, we see evidence of lower assimilation efficiencies during seasons of highest productivity for a single species, S. leucopsarus, in a single area.

What we have done is measure nutrient intake and output. In conjunction with studies on respiration, reproduction, and growth, it should not be too long before we can construct valid energy budgets for the major midwater fish species. Then with reliable data on their quantitative abundance, we can model energy flux for the third trophic level of oceanic ecosystems.

Table 1a: Water content, dry weight (% wet weight), proximate composition (% dry weight), C:N ratio (weight and molar ratios), and caloric content of rectal contents of three species of midwater fishes. Numbers in parenthesis are standard errors of the mean. The two S. leucopsarus samples here and in Table 1b represent seasons of high (V79-A) and low V79-B) productivity.

Species	Water (% wet wt.)	Dry weight (% wet wt.)	Ash-free dry weight (% dry wt.)	Protein (% dry wt.)	Carbohydrate (% dry wt.)	Lipid (% dry wt.)	Chitin (% dry wt.)	Carbon (% dry wt.)	Nitrogen (% dry wt.)	C:N (weight)	C:N (molar)	Calories (cal/mg dry wt.)
Stenobrachius leucopsarus (V79-A)	75.1 (1.6)	24.9	81.2 (0.6)	42.7 (2.0)	5.4 (0.3)	14.9 (2.1)	14.4 (2.5)	27.0 (1.0)	4,7 (1.1)	5,7 (0.3)	6.7	3,44
Stenobrachius leucopsarus (V79-B)	75.4 (2.9)	24.6	82.8 (0.3)	25.8 (2.1)	6,5 (0.4)	14.8 (5.0)	24.3 (6.2)	28.5 (1.6)	4,6 (1.9)	6,2 (1,6)	7.2	3.01
Argyropelecus affinis	81.7 (1.1)	18.3	76.1 (0.6)	28.4 (1.4)	7,9 (1.7)	2,0 (2.5)	28.7 (7.3)	25.5 (2.2)	7.1 (2.0)	3.6 (0.4)	4.2	2.24
Leuroglossus stilbius	86.9 (0.6)	13.1	78.1 (0.3)	26.8 (3.3)	4.4 (0.6)	23.5 (6.8)	13.2 (5.9)	37.7 (3.1)	6.7 (1.8)	5.6 (0.3)	6.5	3.42

Table 1b: Quantity of chemical component and calories released per defecation.

Species	µg wet weight	µg dry weight	µg Ash	µg Protein	µg Carbohydrate	µg Lipid	µg Chitin	µg Carbon	µg Nitrogen	Calories
Stenobrachius leucopsarus (V79-A)	1482	369	69.4	157.6	20.0	54.9	53.1	99.6	17.3	1.27
Stenobrachius leucopsarus (V79-B)	3211	791	136.2	204.1	51.6	116.7	192.2	225.4	36.4	2.38
Argyropelecus affinis	4088	749	179.0	212.4	59.3	15.0	214.9	191.0	53.2	1.68
Leuroglossus stilbius	9037	1183	259.1	317.6	51.5	278.2	156.2	446.0	79.3	4.05

Table 2. Comparative data on the nutrient composition of midwater fish feces with published values for other organic detritus (as % of dry weight).

SOURCE		Protein	Lipid	CHO	Ash	$\bar{x}$ C:N
Our data - midwater fish fecal matter		25-43	2-24	13-29	17-24	4.9
Alldredge (1979) -	zooplankton aggregates	13-17	3-4	5	72-74	9.4
	other aggregates	11-19	3-9	9	62-73	10.7
	total particulates	17-21	3-3	1	55-63	7
Johannes and Satomi (1966) - shrimp fecal pellets		28	2.5	13	26	
Particulate detritus						
Knauer et al. (1979)	50-75 m depth					8.8-11
	250-575 m "					9.9-15
	750-1050 m "					13-29
Bishop et al. (1977)	32 m depth					7.3-7.9
	50 m "					7-8.3
	113 m "					7-10
	188 m "					9.3-9.8
	294 m "					9.4-12.4
	388 m "					5.8-9.9

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A Comparison of Bioenergetics and Direct Field Estimates of Cumulative Seasonal Food Consumption by Largemouth Bass (*Micropterus salmoides*)

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Introduction

Estimates of food consumption by fishes in nature may be based directly on stomach contents collected in the field, coupled with information on gastric evacuation rates, or food consumption may be measured indirectly using energy budgets derived from laboratory studies. The latter approach is being used with increasing frequency as laboratory data accumulate, and the bioenergetics models being constructed have broader applications than the estimation of food consumption rates (Norstrom et al., 1976; Kitchell et al., 1977; Kitchell and Breck, 1980). Elliott (1979a) recommended that when energy intake is estimated indirectly from the sum of the other components of an energy budget, a direct estimate should also be made so that the adequacy of the indirect method can be checked. There are few cases, however, where bioenergetics models have been compared to independently collected data on food consumption and growth. Rice and Cochran (MS) have recently made such a comparison using a bioenergetics model and independent field data for largemouth bass, Micropterus salmoides. The purpose of this paper is to extend this comparison to a consideration of cumulative food consumption by largemouth bass over the 1978 growing season.

The largemouth bass bioenergetics model (Rice et al., in press) is similar to those presented by Kitchell et al. (1977) and Breck and Kitchell (1979). Briefly, the balanced bass energy budget is summarized in the following equation:

$$dB/Bdt = C - (R_{S+A} + R_{SDA} + F + U)$$

Where: B = body weight
dB/Bdt = specific growth rate
C = specific consumption rate

R_{S+A} = specific rate of standard metabolism plus metabolism due to activity
R_{SDA} = apparent specific dynamic action
F = specific egestion rate
U = specific excretion rate

Specific consumption rate, C, is calculated using a function structurally identical to that of Kitchell et al. (1977) with parameter values determined for largemouth bass. Maximum specific consumption at any fixed temperature decreases as weight increases; at any fixed weight it increases from near zero at 0°C to a maximum at 27.5°C, then falls to zero at 37.0°C. A proportionality constant, P, ranging from 0.0 to 1.0, is multiplied by the maximum consumption rate to specify consumption rates below maximum. At any given temperature and body weight, therefore, P is a reflection of prey availability. In typical applications of this sort of model, consumption rate is estimated by specifying the thermal regime over an interval, specifying the initial body weight, and varying P until the predicted final body weight matches the observed endpoint. Although the model can also be used to predict growth given information on food consumption, it is usually used to estimate food consumption from growth since the latter is much easier and less costly to measure in the field.

The specific rate of standard metabolism plus metabolism due to activity, R_{S+A}, decreases as weight increases and increases with temperature and swimming speed. Specific rates of egestion, F, excretion, U, and apparent specific dynamic action, R_{SDA}, are all constant proportions of consumption rate. For an in-depth explanation of these relationships, refer to Rice et al. (in press).

The field data used in this paper were collected by Cocran and Adelman, 1982, who estimated daily ration (% body weight) and mean body weight of age III largemouth bass on 10 dates in 1978 in Lake Rebecca, Minnesota. the method of Elliott and Persson (1978) was used to estimate daily ration (see Cochran, 1979; Eggers, 1979; and Elliott, 1979b for further discussion of this method). Water temperatures ere collected with recording thermometers at a depth of about 1 m, the approximate depth at which bass were captured (Cochran, 1980); the thermometers were inoperative during some intervals.

Rice and Cochran (MS) used the Lake Rebecca water temperature data and estimates of daily ration as input to the largemouth bass bioenergetics model and compared predicted to observed growth. Predicted weights were within 2 S.E. of the observed mean weights on 7 of 9 sampling dates. (The first sampling date was excluded from analysis because mean weight on that date was known to be overestimated (Cochran and Adelman, in press).) The close fit of model predictions to the observed data was not greatly affected by variation in assumed mean swimming speed or simulated bias in input temperature. The use of daily ration estimates based on mean stomach contents rather than medians, however, produced an unsatisfactory overestimate of growth, in keeping with Cochran and Adelman's (in press) conclusion that the use of median stomach contents provided a more realistic estimate of the food consumption of individual bass.

Methods

The following procedures were used to generate estimates of cumulative food consumption by largemouth bass from the second to the last sampling dates (June 5-October 5) of Cochran and Adelman, 1982.

1. Extrapolation of the direct field estimates - the mean body weight and daily ration estimates of Cochran and Adelman, 1982 were linearly interpolated between sampling dates. The product of body weight and daily ration was obtained for each day and totaled over the sampling season. This procedure did not involve the bioenergetics model.

2. Adjustment of P-values using the bioenergetics model - Values of P, the proportionality constant used to adjust consumption rate, were varied until predicted body weights matched observed endpoints over a) the entire sampling season, b) each of the 8 sampling intervals, and c) 3 intervals corresponding to apparent changes in prey availability (Rice and Cochran, MS). Corresponding estimates of consumption were calculated and totaled over the sampling season. This procedure is similar to previous applications (e.g., Kitchell and Breck, 1980).

3. Use of the bioenergetics model to predict daily ration from weight - The field estimates of body weight from Cochran and Adelman, 1982 were linearly interpolated between sampling dates, as in Procedure 1, but used instead as input to the bioenergetics model to generate an estimate of daily ration for each date. This was multiplied by body weight and the resulting estimates of food consumption were totaled over the sampling season.

In procedures involving the bioenergetics model, mean swimming speed was set at 5 cm/sec (Rice and Breck, MS), a conversion coefficient of 1 gram/4.184 kjoules (Rice et al., in press) was assumed for both bass and their prey, and missing values from the Lake Rebecca temperature data of Cochran (1980) were estimated by linear interpolation.

Results and Discussion

One obstacle to the comparison of direct field estimates of food consumption and those generated using energy budgets is that they are calculated with respect to different time scales. Direct field methods are generally applied over 24 hours, yielding "point" estimates on a seasonal scale, whereas budgeting approaches can only yield mean rates of food consumption integrated over periods of time sufficient to detect significant changes in weight. For this reason it was necessary to interpolate the daily ration estimates of Cochran and Adelman, 1982, over the intervals between sampling dates. When this was done using linear interpolation, the direct estimate of consumption (Procedure 1) yielded a cumulative consumption estimate of 503 g (Fig. 1). Because prey availability may be subject to discontinuous changes, it may be an oversimplification to assume that daily ration changes in such a simple continuous fashion. Use of a step function, however, with daily ration held constant for one-half the intervals preceding and following each sample date, resulted in a cumulative consumption estimate of 500 g and an almost identical seasonal trajectory.

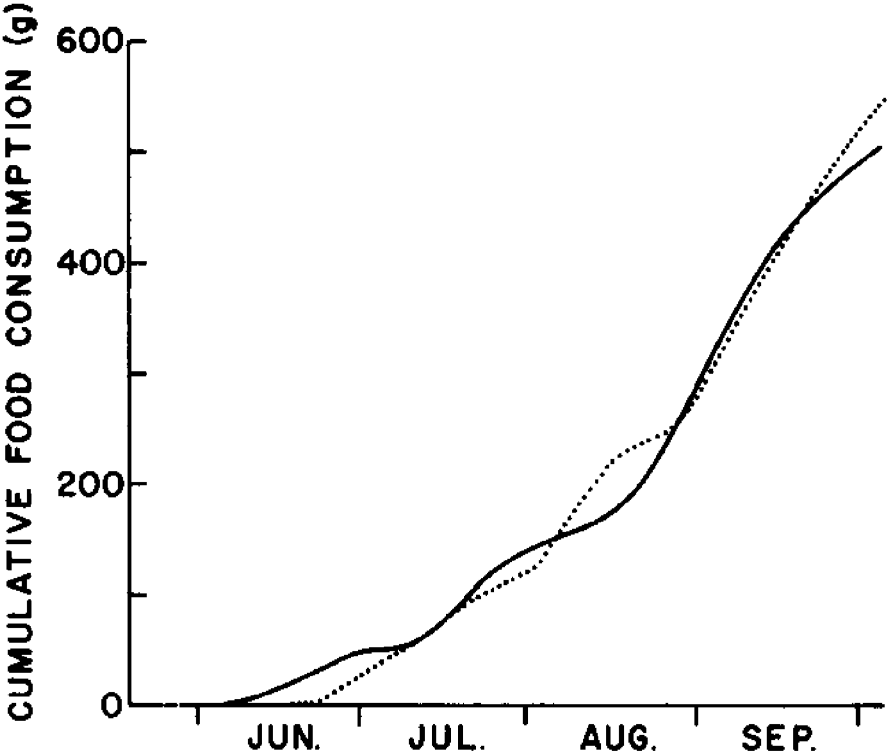

Figure 1. Cumulative food consumption of age III largemouth bass in Lake Rebecca. Solid line: Extrapolation from field estimates of Cochran and Adelman, 1982 (Procedure 1). Dotted line: Bioenergetics model predictions (Procedure 3). For both estimates, body weight was linerly interpolated over intervals between sampling dates.

Cumulative consumption estimates generated with the bioenergetics model (Figs. 1 and 2) were comparable to the direct field estimate except when a constant P-value was fit to the endpoints of growth over the entire sampling season. Kitchell and Breck (1980), using a bioenergetics model for sea lamprey (Petromyzon marinus), fit a constant P-value to the endpoints of growth over an entire season and produced a close fit to observed intraseasonal growth. In contrast, Rice and Cochran (MS), using the Lake Rebecca bass data could not produce an adequate fit of predicted to observed body weight by fitting a constant P, indicating that intraseasonal changes in prey availability had an effect on consumption rates. Use of that constant P-value (0.55) resulted in a cumulative consumption estimate of 592 g (Fig. 2). Fitting a separate P-value to each of the 8 sampling intervals yielded an estimate more comparable to the direct field estimate.

Although closer fits to field data may be obtained using the bioenergetics approach as P-values are fit to smaller time intervals, conceptually simpler explanations without much loss of fit may sometimes be obtained by pooling some intervals. Rice and Cochran (MS) found that the P-values fit to the separate intervals fell into three relatively discrete groups and pooled the intervals accordingly (P = 0 for May 17-

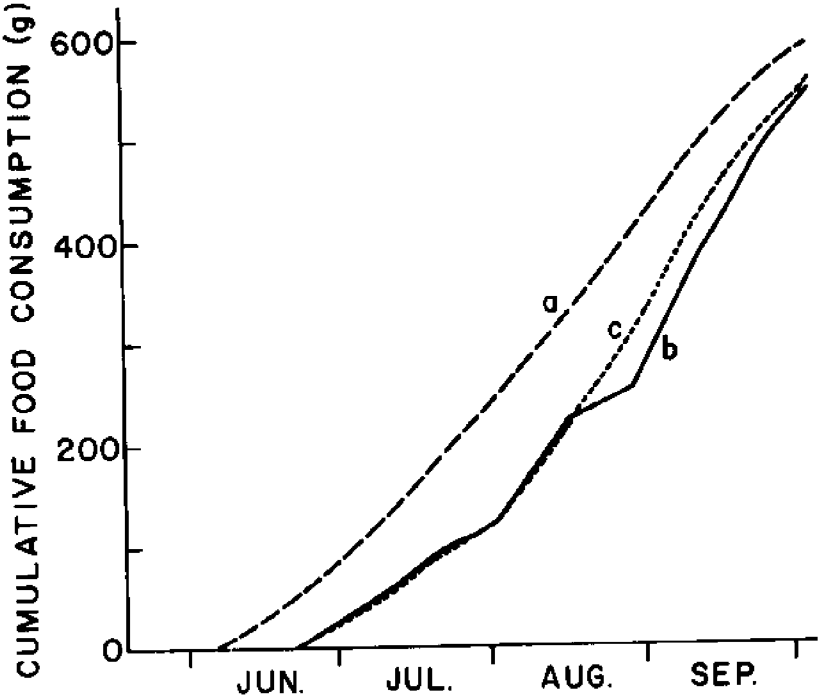

Figure 2. Cumulative food consumption estimated with the bioenergetics model by fitting a constant P-value to observed endpoints of growth (Procedure 2) over a) the entire sampling season, b) each of the eight sampling intervals, c) three intervals corresponding to apparent changes in prey availability.

June 22, P = 0.43 for June 22-August 2, and P = 0.77 for August 2-October 5). The first of these intervals corresponds to the part of the season preceding the availability of young-of-year (YOY) bluegills and bass, while the last interval was a time of high YOY fish abundance, increased mean size of prey, and falling water temperatures. A plot of cumulative consumption using these three intervals and P-values is not greatly different from that using a separate P-value for each sampling interval (Fig. 2).

The impact of a predator on its prey base may be measured in numerical terms as well as in terms of biomass consumed. Numbers and biomass are not linearly related through the season if growth of individual prey occurs. Slight differences in the assumed seasonal distribution of food consumption may not greatly affect estimates of cumulative biomass consumed but may have more marked effects on numerical estimates. Estimated number of prey consumed, therefore, provides a further criterion for comparison between procedures for estimating cumulative food consumption. Using information on the composition by weight of Lake Rebecca bass stomach contents (Cochran and Adelman, 1982, coupled with information on seasonal changes in prey size (Cochran unpublished data), it was possible to estimate the cumulative consumption of YOY largemouth bass and bluegills (Lepomis macrochirus) in terms of numbers and biomass (plotted in Figs. 3 and 4 for Procedures 1 and 2). Model estimates of both biomass and numbers agreed fairly well with field estimates. As expected, however, proportional differences between procedures for numerical estimates were generally greater than or about equal to differences in biomass, and differences in numerical estimates were relatively greater for YOY largemouth bass, the faster-growing prey type. The impact of bass predation on YOY bluegills relative to YOY bass was much greater when measured numerically than when measured in terms of biomass.

Conclusion

Since both the direct and bioenergetics estimates of food consumption are subject to error, the general agreement between the two cannot strictly be considered a validation of the bioenergetics model. The observed consistency between the two independent methods, however,

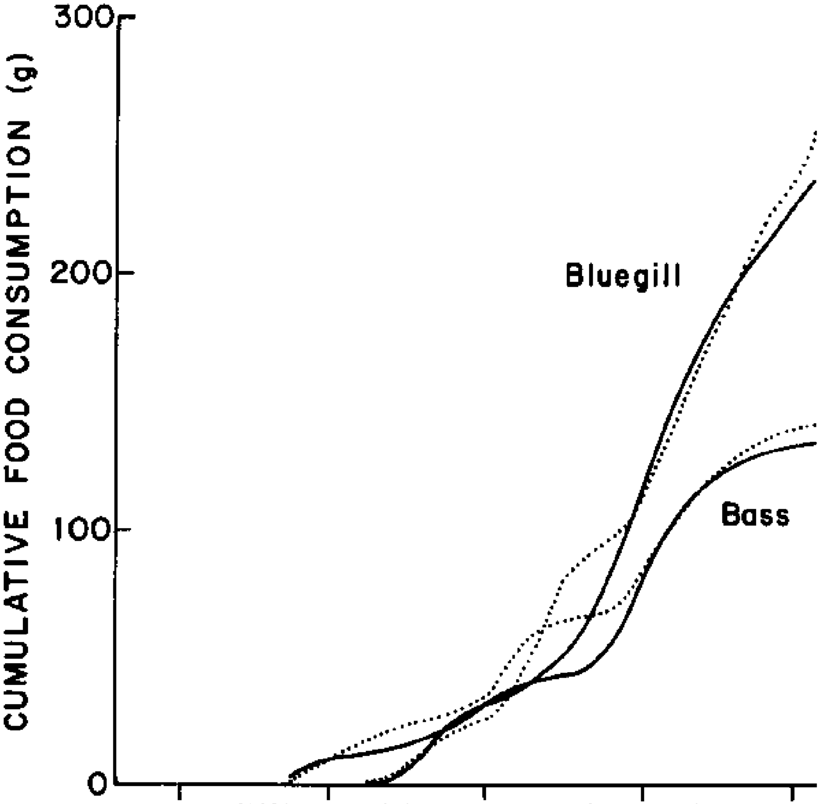

Figure 3. Cumulative biomass of young-of-year largemouth bass and bluegills consumed by age III largemouth bass in Lake Rebecca. Solid line: Extrapolated field estimates (Procedure 1). Dotted line: Bioenergetics model predictions (Procedure 3).

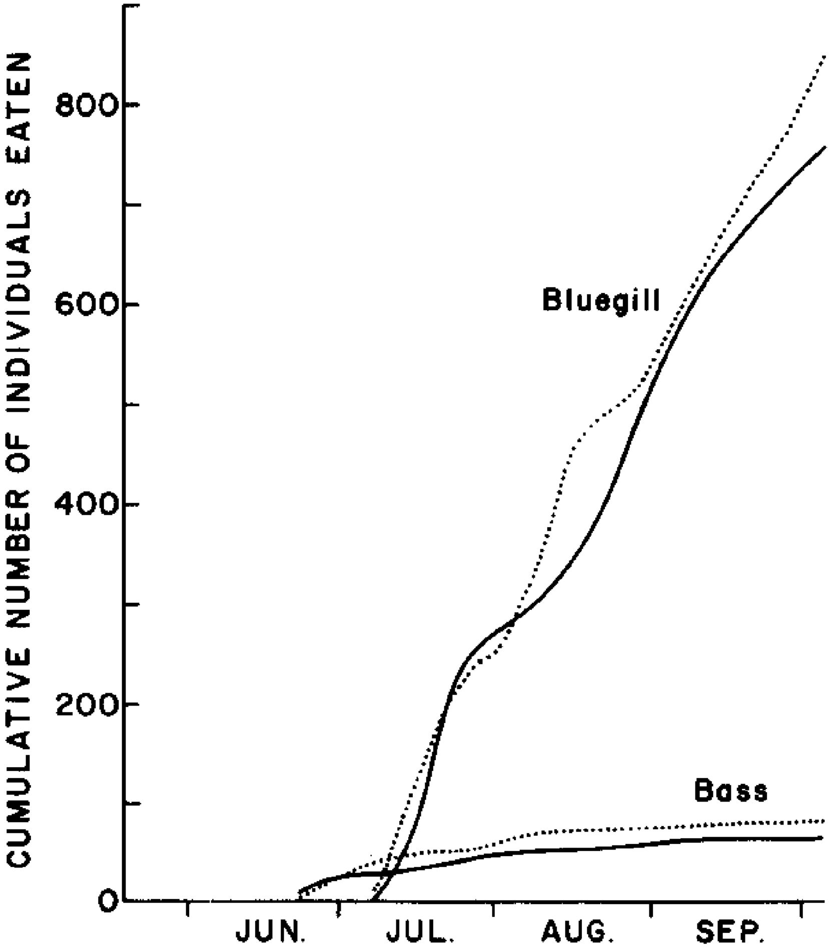

Figure 4. Cumulative numbers of young-of-year largemouth bass and bluegills consumed by age III largemouth bass in Lake Rebecca. Solid line: Extrapolated field estimates (Procedure 1). Dotted line: Bioenergetics model predictions (Procedure 3).

generates confidence in their extension to other applications. While direct field methods remain valuable for determining fine-scale (e.g., diel or day-to-day) variations in food consumption, long-term information can be much more easily obtained using the bioenergetics approach. In the case of largemouth bass at Lake Rebecca, for example, it is now evident that information on cumulative food consumption comparable to that obtained by conducting a series of 24-hour sampling runs could have been obtained with much less manpower and expense by using the bioenergetics model and collecting only a series of estimates of mean body weight.

In the present study it was possible to use a bioenergetics model for largemouth bass to identify a seasonal bottleneck in its food resources. By using the same model and additional field data, it would be possible to evaluate a significant component of the mortality of another species, the bluegill (Figs. 3 and 4; see also Stewart et al., 1981). The bioenergetics approach, therefore, can be used to investigate a variety of ecological phenomena, and, unlike some other modeling approaches, it can be readily integrated with field data to study real situations.

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Growth, Food Consumption, and Conversion Efficiency Of Juvenile English Sole (*Parophrys vetulus*)

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Introduction

Pacific coastal embayments and estuaries support seasonal populations of migratory fishes during their early development. Juvenile English sole (Parophrys vetulus) are the most abundant flatfish occurring in some of these shallow, protected areas during early spring and summer months (Misitano, 1970; Pearcy and Myers, 1974; Ambrose, 1976; Bayer, 1981). Newly metamorphosed juveniles (18-20 mm, standard length), after being spawned offshore, concentrate in bays and estuaries north of Point Conception. As they approach age class I, juveniles recruit to their adult habitat and become one of the dominant species of fish in an offshore benthic assemblage. This change in habitat is accompanied by thermal and trophic changes, both of which can influence growth and survival of the fish.

In Elkhorn Slough, California, English sole exhibit dramatic seasonality in distribution (Ambrose, 1976). Postlarval juveniles enter the slough in late February, steadily increase in numbers through April, and are the most abundant fish caught in the mid- and upper regions of the slough from May through July. This pattern of distribution is reversed by August, with the majority of fish congregating at more seaward locations. In the offshore environment of Monterey Bay, English sole are most abundant in summer and fall months, corresponding to the movement of young age class I fish from nearby Elkhorn Slough (unpublished data). Similar migrations of this species have been noted by Ketchen (1956) in British Columbia, Misitano (1970) in Humboldt Bay, California, and Olson and Pratt (1973) in Yaquina Bay, Oregon. English sole in Elkhorn Slough can experience temperatures as high as 18°C, while bottom temperatures in adjacent offshore areas average about 12°C (Broenkow, 1977). Determining fish growth rates and energy requirements over the environmental range of temperatures where the population is naturally abundant is essential in assessing the role the estuary plays in the survival and recruitment of juvenile fish to the offshore environment.

Although many investigators have qualitatively described the feeding habits of both juvenile and adult English sole, little quantitative information on their energy requirements has been reported. In general, this species is characterized as an opportunistic, benthic predator whose diet is composed primarily of infaunal polychaetes, amphipods, and whole bivalves (Ambrose, 1976; Kravitz et al., 1976; Hulberg and Oliver, 1978; Toole, 1980). Daily growth of juveniles has been estimated from modal analysis of length frequency distributions (Kendall, 1966) and from size at age data using fortnightly growth rings on otoliths (Rosenberg, 1980). Williams and Caldwell (1978) estimated daily growth and ration for 0-group English sole fed an artificial diet in the laboratory. The present study determined growth, daily ration, and conversion efficiencies for two age classes of English sole under laboratory conditions which reflect the temperature regime and type of prey available in their natural environment.

Materials and Methods

Elkhorn Slough is a shallow coastal embayment centrally located in Monterey Bay, California. Both salinity and temperature are highly variable. From late February to early October, the months when juvenile English sole inhabit the slough, salinities range from 30 to 36°/₀₀ and water temperatures range from 13 to 18°C. In upper areas of the slough, temperatures reach as high as 27°C in summer months (Broenkow, 1977). The offshore sandflat area of Monterey Bay, with a water depth of about 25 meters, has a more stable bottom salinity and temperature regime, ranging from 33 to 34°/₀₀ and 12 to 14°C, respectively.

English sole were collected in Elkhorn Slough and Monterey Bay using small otter trawls. 0-group fish (less than one year of age) had initial wet weights ranging from 4.8 to 21.9 g and standard lengths from 72 to 114 mm. The most abundant age class of English sole collected offshore, that of age class II, had initial wet weights from 58.3 to 101.8 g and standard lengths from 156 to 188 mm. Ages were determined from otoliths following experimentation.

Three experiments were designed to measure individual daily growth, ration, and gross conversion efficiencies. 0-group fish were acclimated to 13.0°C and 17.5°C, the limiting temperatures of the range encountered in the slough. Age class II fish were held at 13.0°C, an average offshore bottom temperature. Temperatures were controlled to ± 1.0°C. The experiments proceeded consecutively, beginning with the age class II fish on 23 May, 0-group fish at 13°C on 23 Sept, and 0-group fish at 17.5°C on 4 Nov.

The marine polychaete, *Nereis virens*, was used as food in all experiments. Although this species does not occur naturally in the diet of English sole, it contains about the same caloric value as other polychaetes and is commercially available. An *ad libitum* ration, (maximum, unrestricted feeding), estimated to be 10% of the fish's wet body weight, was provided daily and was adjusted each week to reflect fish growth. With few exceptions, the fish rarely consumed their entire allotment of food. The uneaten portion was removed eight hours later, blotted dry, and reweighed. The amount of food consumed per day was calculated and recorded to the nearest mg for each fish. Initial and final wet weights of fish were taken after fish were starved for 24 h. Feeding began several hours later and continued daily for 42 days with age class II fish and 28 days with 0-group fish. Wet weight of fish was monitored weekly, although this information was not used in calculating daily growth since weights varied with the amount of food remaining in the stomach.

To eliminate variability due to water and lipid content of the fish and prey, wet and dry weight ratios and ash and caloric values were determined for the ration, for a representative sample of fish prior to experimentation, and for all fish following the experiments. Samples were dried at 80°C to a constant weight and placed in a desiccator for 24 h. prior to weighing. Further processing included homogenizing and pelletizing the samples and combusting in a Parr 1411 semimicro oxygen bomb calorimeter. Independent estimates of percent ash were made using a muffle furnace at 500°C for four hours.

Instantaneous relative growth rate (% body weight per day) was calculated on an individual basis over the entire experimental period using the formula: $G = \ln [W_f/W_i]$

where W_f/W_i is the ratio of final weight to initial weight. Since the amount of food consumed by each fish varied from day to day, daily ration was calculated on an individual basis over the entire experimental period. Individual gross conversion efficiencies (K_1) were determined by dividing total growth by total ration and multiplying by 100.

Results and Discussion

Growth was positively related to daily ration at both temperatures and age classes. Mean daily ration was significantly higher at 13°C ($t=3.33$, $P=.01$) than at 17.5°C for 0-group fish (Table 1). Ingestion rates averaged 6.55% body weight/day at 13°C, ranging from 4.53 to 8.93%, while at 17.5°C they averaged 4.96%/day and ranged from 2.91 to 7.80%. In general, maximum ration increases as a function of increasing temperature but declines as the fish's upper thermal tolerance level is approached, reflecting a loss of appetite at relatively high temperatures (Brett, 1979). No difference in daily ration was determined between age classes at 13°C.

Table 1. Daily ration, growth rate, and food conversion efficiency of age groups 0 and II English sole, *Parophrys vetulus*, on unrestricted diets at two temperatures.

Treatment (Temperature/ Age Class	Daily Ration (% dry body wt)		Relative Growth Rate (% body wt per day)		K_1 Conversion Efficiency (% by dry wt)		K_1 Conversion Efficiency (% by cal)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
13°C/0-group (n=14)	6.55	0.31	1.87	0.17	26.76	1.32	34.48	1.18
13°C/age class II (n= 8)	6.78	0.27	0.84	0.10	12.14	1.05	17.82	0.99
17.5°C/0-group (n=14)	4.96	0.36	1.17	0.14	22.40	2.06	32.90	2.10

Lower daily rations observed for 0-group fish at 17.5°C are reflected in the significantly lower growth rates at this temperature (Table 1 and Figure 1). Relative growth at 17.5°C ranged from 0.33 to 1.90% body weight/day, with a mean of 1.17%; this compares with 0.93 to 3.10% and a mean of 1.87% at 13°C. Relative growth rates of the age class II fish at 13°C ($\bar{X}$ = 0.94%) were considerably lower than those of 0-group fish at the same temperature, although mean daily rations were similar (Figure 2). Maximum ration and growth were not well defined by the present data since the ration-growth relationships (Figures 1,2) were clearly linear with no asymptote being reached.

Mean growth rate of 0-group fish at 13°C compares favorably with growth rates estimated from field data. Using modal analysis, an average relative daily growth rate of 1.60% was calculated for 0-group fish collected by Ambrose (1976) in Elkhorn Slough from March through October. A similar analysis of data from Smith and Nitsos (1969) provides a growth rate of 1.99%. Although estimates of daily ration in the field are not available, the agreement between laboratory and field growth indicates that the presumed "maximum ration" of 0-group fish at 13°C adequately expresses field ration.

Individual gross conversion efficiencies, derived from daily ration and growth, generally increased with increasing ration for 0-group fish at 13°C (b=3.2, r=.78). An overfeeding effect, i.e. higher rations resulting in decreased efficiency (reviewed by Brett, 1979), was not apparent in these data. At 13°C, gross efficiencies ranged from 20.2 to 34.4% for 0-group fish and averaged 26.8% (based on dry weight). Estimates based on caloric content were higher, due to the greater caloric content of the fish compared with prey. Although ingestion and growth were lower at 17.5°C, efficiencies were not significantly different than those at 13°C (22.4 vs. 26.8%, respectively). All 0-group fish were caught near the mouth of the slough during the months when they were preparing to migrate offshore. Imposing an out-of season thermal condition (that is, 17.5°C in October) on this species could result in a decrease in appetite and subsequently lower rations and growth rates. Also, the fish at 17.5°C were presumably older than those at 13°C, as this final experiment was initiated on 4 Nov. Increasing size with the approach of migration has been shown to result in decreased growth in juvenile *Sebastes diploproa* (Boehlert, 1981).

Conversion efficiencies for 0-group fish at both temperatures compare favorably with those reported for other species of juvenile flatfishes held under optimal experimental conditions. Chesney and Estevez (1976) reported a mean of 21.2% (dry wt basis) for age I winter flounder at 10°C, with no significant difference in efficiency noted at 20°C. Edwards et al. (1969) estimated an efficiency of 36% (caloric basis) and a 2% relative daily growth rate for 0-group plaice. Williams and Caldwell (1978) however, reported a much lower maximum conversion efficiency of 10.5%, established at an optimum temperature of 9.5°C and an 8% ration for 0-group English sole. Both this low efficiency and low growth rate (0.95% per day at 9.5°C) were attributed to the nutritional inadequacy of the diet, Oregon Moist Pellets.

While it was apparent that both age classes at 13°C were ingesting the same relative amount of energy, average relative growth of age class II was less than half that of the 0-group fish, resulting in a significantly lower conversion efficiency. In general, as fish age their energy

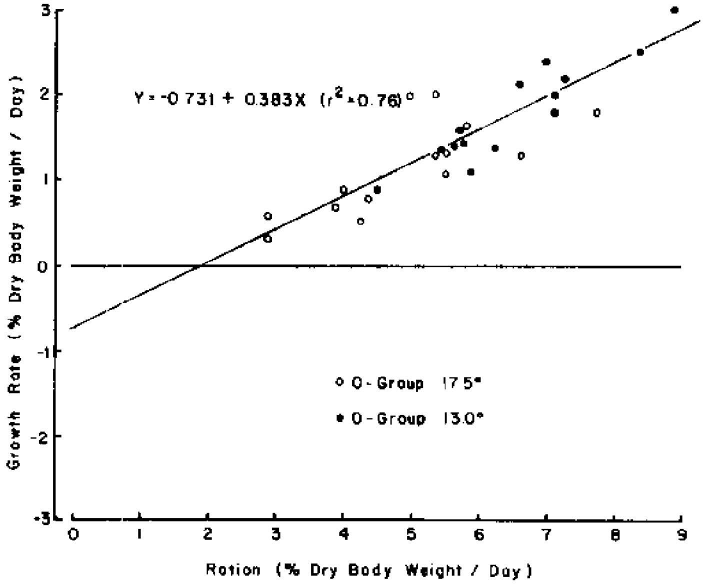

Figure 1. Growth and ration for *Parophrys vetulus* at two temperatures. Points are individual fish.

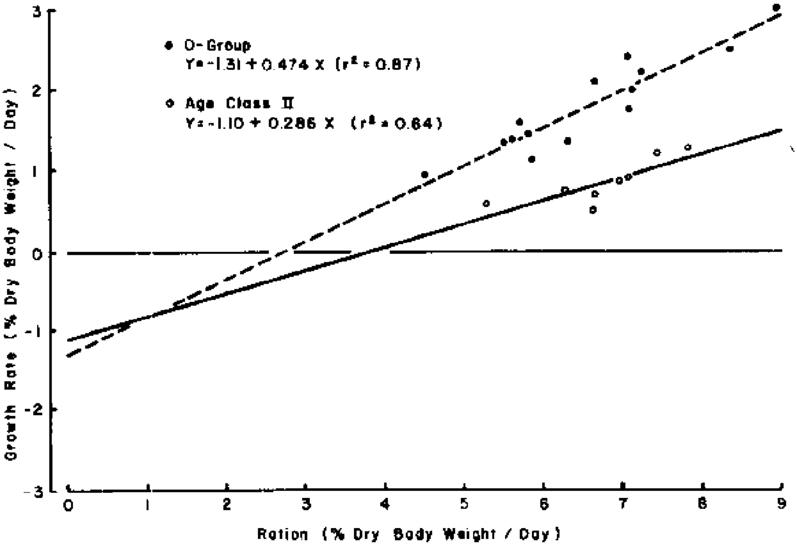

Figure 2. Growth and ration for 0-group and age II *Parophrys vetulus* at 13°C. Points are individual fish.

requirements, as well as metabolism and growth, decrease. However, maturity of English sole occurs at 2-3 years for males and 3-4 years for females (Ketchen, 1956). The age class II fish in the present study are likely to be in a prespawning condition, which in other species denotes an accumulation of high energy lipids in body tissue in anticipation of large energy outputs in gonadal development and spawning (Shul'man, 1974). This could account for the relatively high ingestion rates and lower conversion efficiencies of the older fish. It is expected therefore, that the body tissue of the older fish would contain higher amounts of lipids compared with 0-group fish. Although proximate analysis of the fishes' tissues was not performed, caloric content of the fish was determined both before and after experimentation. Caloric content of fish in all experiments increased (Table 2) but age class II fish increased proportionally to a greater degree than did 0-group fish, possibly indicating the additional storage of high energy lipids in preparation for spawning.

Table 2. Mean (± S.D.) % water, ash, and caloric values of the polychaete, Nereis virens, and English sole, Parophrys vetulus.

Tissue	Initial Composition Water (%)	Initial Composition Ash (%DW)	Initial Composition Energy (Cal/g AFDW)	Final Composition Water (%)	Final Composition Ash (%DW)	Final Composition Energy (Cal/g AFDW)
Nereis virens	77.60 (1.22)	7.82 (0.45)	5233.56 (104.81)			
0-group fish 13°C	77.36 (1.46)	14.48 (0.35)	5608.23 (66.93)	77.86 (1.46)	12.12 (1.68)	6088.88 (112.28)
0-group fish 17.5°C	77.36 (1.46)	14.48 (0.35)	5608.23 (66.93)	77.06 (2.25)	12.86 (1.73)	6186.52 (247.44)
Age II fish 13°C	79.61 (1.56)	19.11 (1.32)	5562.25 (152.74)	78.40 (2.71)	15.30 (1.85)	6218.38 (126.78)

The results of the present study are helpful in understanding the feeding and growth ecology of juvenile English sole inhabiting the nearshore Pacific coastal environment. Fish tend to move toward an optimal temperature where growth and efficiency are maximized and mortality rates are low. A relationship between growth optima and final thermal preferences was established by Jobling (1981). The shallow embayments frequented by juvenile fish tend to be very turbid, possibly lowering the incidence of predation. These areas also have a relatively high productivity, compared with offshore areas; a more dense infaunal prey assemblage could potentially yield higher growth rates in the estuaries. However, Rosenberg (1980) found no significant difference between growth rates of 0-group English sole collected in Yaquina Bay estuary and those from a nearshore open-coast environment; he suggests that survival, and not growth is enhanced in the estuary. From the present data, English sole appear to be much more efficient at utilizing their resources in Elkhorn Slough in terms of growth than do the older fishes offshore. Additionally, these areas could offer optimal thermal conditions for growth; as these conditions change seasonally and as thermal preferences change with growth the fish migrate offshore. Without experimental data on growth at temperatures lower than 13°C, it is not possible to establish this species' thermal optima.

Inferences can be drawn from the experimental evidence regarding the effect of temperature on distribution and abundance of juvenile English sole within the nursery area and also latitudinally along the Pacific coast. Although adults are distributed offshore from Baja California to Unimak Island in western Alaska (Hart, 1973), there are few records of juveniles using southern California bays as nursery grounds. Fierstine et al. (1973) report low numbers of juveniles in Morro Bay, California in early spring and summer. Temperatures commonly exceed 18°C in these shallow southern bays. As is shown in the present study, growth of 0-group fish declines near temperatures approaching 17.5°C, making the potential for survival and growth at southern locations poor. Elkhorn Slough is the most southern bay reported to be utilized by English sole to a large extent.

Limitations on distribution due to thermal tolerance is also supported by English sole's use of intertidal areas on the nursery grounds. In northern bays and estuaries, such as Yaquina Bay, Oregon (Bayer, 1981), Humboldt Bay, California (Toole, 1981), and Puget Sound, Washington (Kendall, 1966), postlarval sole are commonly found on intertidal mudflats. They do not occur in large numbers, however, in the tidal creeks of Elkhorn Slough, where temperatures could prohibit their occurrence throughout the year (Barry, 1982). Ambrose (1976) has demonstrated that juveniles are evenly distributed in large numbers throughout the main channel of the slough from February through April. Large concentrations are found at the most inland locations from May to July, with fish migrating seaward from August through October. When comparison is made between this distribution and a temperature profile during the same months, it is apparent that, as temperatures approach 17 to 20°C in late summer and early fall, a conincidental migration of juveniles out of the slough occurs. Both distribution and length of stay of English sole in Elkhorn Slough could be limited by their thermal tolerance and that, provided sufficient ration, these fish occur most commonly in areas that the present study indicates would produce higher growth.

Acknowledgements

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Energetics of the Sablefish, *Anoplopoma Fimbria*, Under Laboratory Conditions

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Introduction

Laboratory energetics studies can provide important physiological information not generally obtainable from field studies. The range of growth, metabolic and excretion rates measured under controlled laboratory conditions offers insights into the physiological capabilities of a marine fish; one may then better understand the physiological and ecological functions of the fish in its own environment. Energetics studies of *A. fimbria* were initiated to learn more about energy allocation of a relatively deep-living fish. *A. fimbria* has an extremely broad geographic distribution along the continental slope, occurring from Baja California, Mexico to the Bering Sea ans westward to Japan. Its bathymetric distribution also is broad, extending from surface waters in the northernmost range to 1550 meters off southern California (Hart, 1973; Phleger et al., 1970). *A. fimbria* are exploited commercially throughout their range, and are sold on Canadian, Japapese and domestic markets. Because they have no swimbladder, *A. fimbria* can be brought to the surface in good physiological condition and maintained in chilled aquaria for extended periods of time.

Field data have been collected on food relationships and general population ecology of *A. fimbria* off southern California (Conway, 1967; Phleger et al., 1970), and off Oregon and Washington (Holmberg and Jones, 1954; Pruter, 1954). Large numbers of *A. fimbria* were reared in large floating pens off British Columbia; this work is summarized by Kennedy (1974). However, growth, metabolic and excretion rates of individual fish have not been determined.

The goal of the present study was to examine the physiological capabilities of *A. fimbria* collected off southern California and maintained in chilled aquaria on varying ration levels. A laboratory study of the energy allocation of starved vs. fed fish can offer insight into the effects of lower food supplies that may be associated with greater depths. The results will be presented in four sections: (1) diurnal patterns of standard metabolic rates in starved vs. fed A. fimbria, (2) measurements of ammonia excretion in fed and starved A. fimbria, (3) respiration rates of A. fimbria with varying body size, and at low oxygen tensions, and (4) growth rates on varying ration size.

Materials and Methods

A. fimbria were collected by setline in La Jolla Submarine Canyon off San Diego, California at a depth of 486 meters. Prior to the experiments, fish were held in the laboratory for three weeks in 2100-liter tanks containing chilled running-seawater. The running chilled seawater system exhibited seasonal fluctuations from 6.0°C in the winter to 11.0°C in the summer. All tanks were in a darkened enclosure and were kept covered to minimize disturbances and to eliminate light. A. fimbria were confined individually by nylon mesh barriers to minimize activity and identify individuals. All fish were fed chopped mackerel and squid prior to the experiments. Three treatment groups were used: (1) high-ration fish fed 15% of their wet body weight per week, (2) low-ration fish fed 7% of their wet body weight per week, and (3) starved fish. Uneaten food was removed after two hours, dried and weighed for calculation of ingestion rates. Fish were weighed every two weeks in air, a process which required about four minutes of handling time. This report represents preliminary findings of a large-scale laboratory experiment involving 18 fish (6 per treatment group) lasting 36 weeks. High ration level was determined by daily feedings of mackerel and squid to estimate maximum ingestion levels in the laboratory.

Respiration measurements were made in 64.5-liter chambers equipped with a circulating pump and a Yellow Springs Instruments Oxygen Electrode. Chambers had a built-in filtration system, and a port for extracting water samples for ammonia determinations. Oxygen electrodes were calibrated daily with O_2-saturated and N_2-purged seawater. Fish were allowed to acclimate to chambers for 24 hours before beginning experiments, and individual fish were kept in a chamber for seven days, with six days of experiments following one day of acclimation. The chambers were either flow-through or closed systems; the appropriate chamber blanks were run to determine microbial metabolism. Respiration rates were expressed in milligrams oxygen per kilogram wet weight per hour. Ammonia determinations from water samples extracted periodically from chambers were done by spectrophotometric assay (Strickland and Parsons, 1973). Ammonia excretion rates are expressed in milligrams nitrogen per kilogram wet weight per hour.

Results

Diurnal patterns of oxygen consumption in starved and fed A. fimbria.

Oxygen consumption was measured in an open respirometry system for two A. fimbria, one starved for three weeks, and one fed 15% of its wet weight per week for three weeks prior to the experiment. Each fish was acclimated to the respirometry chamber for 24 hours prior to the experiment. The fed fish was fed on the following day, designated day 1. Oxygen consumption by both fish was monitored on days 1, 2, 4, and 6.

There was a pronounced diel pattern in respiration rate of the fed fish, with oxygen consumption being the highest between 2400 and 0100 (Figure 1A). This pattern remained the same throughout the week, but absolute rates of oxygen consumption decreased on the fourth and sixth days of feeding (Figure 1A). In contrast, the starved fish showed no diel variation in respiration rate, and its respiration rate was much lower, about one-third as high as the maximum rates of the fed fish (Figure 1B). On the fourth and sixth days after feeding, daytime respiration rates of the fed fish were comparable to those of the starved fish.

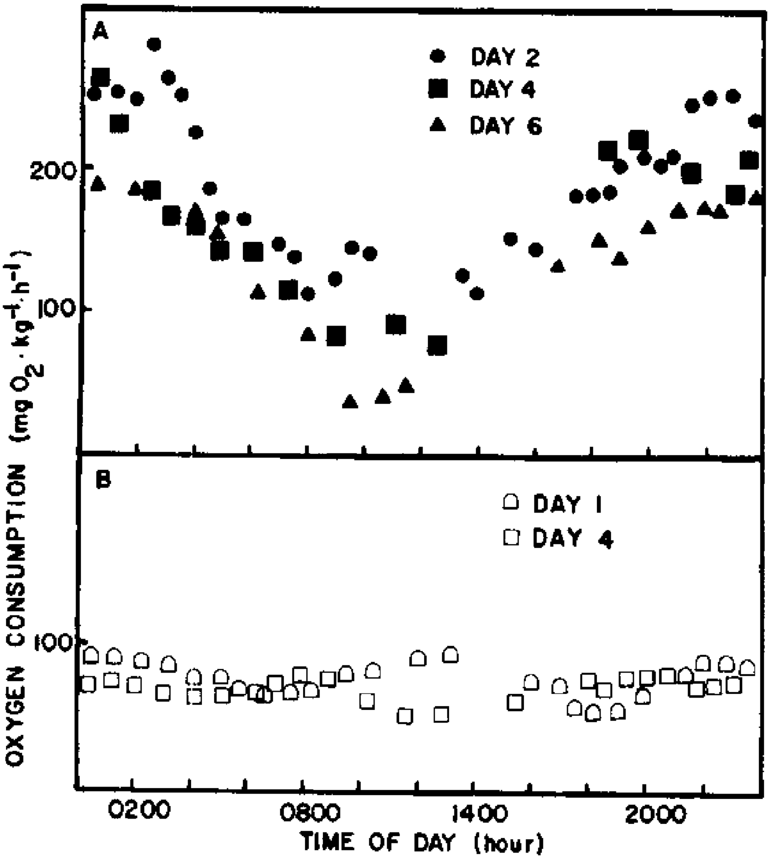

Figure 1: A. Diurnal standard metabolic rates for A. fimbria on days 2, 4 and 6 after being fed 15% ration on day 1. Fish weighed 1.4 kg and had been in laboratory for 6 weeks. B. Diurnal standard metabolic rates for starved A. fimbria. Fish weighed 1.01 kg and had been in laboratory 6 weeks, and starved for 3 weeks.

Other fish examined followed this same trend, with fed fish having a 30% to 50% difference between day and night respiration rates; however, peak oxygen consumption rates occurred at times between 1900 and 0300. Starved fish showed very little change in oxygen consumption rates throughout the day, or throughout the week after the second week of starvation. The second week of food deprivation resulted in more erratic respiration rates on both diurnal and weekly scales.

Measurements of ammonia excretion in fed and starved A. fimbria.

Ammonia excretion rates of five A. fimbria were monitored over a six-day period (Figure 2). Three of the fish were starved, and the two remaining fish received 7% and 15% of their body weight, respectively. These fish were fed on the morning of day 1. Water samples were collected initially four to six hours after feeding, and every eight to ten hours afterwards. Water temperature was constant at 10°C.

In fed fish, nitrogen excretion rates remained elevated for up to three days after feeding. Peak excretion rates of 20 mg $N \cdot kg^{-1} \cdot h^{-1}$ occurred 12-18 hours after feeding (Figure 2). By the end of the week, excretion rates of fed fish were the same as those for starved fish. Patterns of nitrogen excretion suggest that A. fimbria does not return to the post-absorptive state for up to four days after feeding. This period of elevated ammonia excretion rates corresponds to the period of elevated oxygen consumption rates following feeding.

Respiration rates of A. fimbria with varying body size and at low oxygen tensions.

Oxygen consumption measured in an open respirometry system at 8.0°C showed a decrease in the weight specific respiration rate with increase in body mass (Figure 3). Measurements represent an average oxygen consumption rate over 3-12 hours for fish in a post-absorptive state between 0600 and 1800. All fish were acclimated to the chamber for 24 hours. The solid line is represented by the equation $y = -43x + 192.4$ where y is weight specific metabolic rate and x is log (body mass). The regression co-efficient (r) is -0.73. The size range included mature (generally fish greater than 1800 grams) and immature individuals.

The allometric equation $E_m = aM^b$ where E_m is rate of oxygen consumption, a is a proportionality constant and M is body mass, yields a value for b, the exponent, of 0.81±0.03 (1 S.D.). When the allometric equation is plotted on double logarithmic paper, it yields a straight line with a slope of b. This b value can be compared to data for different fish species. Values for freshwater fish and salmonids range from 0.70 to 0.85 (Brett and Flass, 1973).

Oxygen consumption in closed respiration chamber at 10.0°C for starved and fed A. fimbria showed a decrease in weight specific respiration rate with decreasing oxygen tension (Figure 4). Starved fish, with already depressed respiration rates, showed little change in oxygen consumption rates over a wide range of oxygen tensions. Fed fish showed a sharp decrease in respiration rates with a lowering of oxygen tension to rates comparable with starved fish. In these closed chamber experiments, ammonia was chemically scrubbed from the circulating water, thus the build-up of toxic waste products did not compound the effects seen in the closed system. Fish did not appear stressed at the conclusion of the closed experiments.

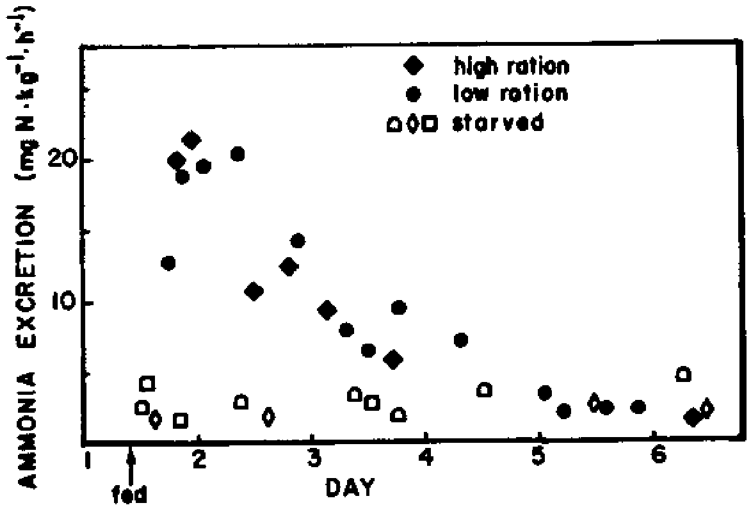

Figure 2: Ammonia excretion in milligrams nitrogen per kilogram wet weight per hour over the course of a week for starved and fed A. fimbria. Fed fish were fed the morning of day 1. Fish ranged in in weight from 1.0 to 1.9 kg.

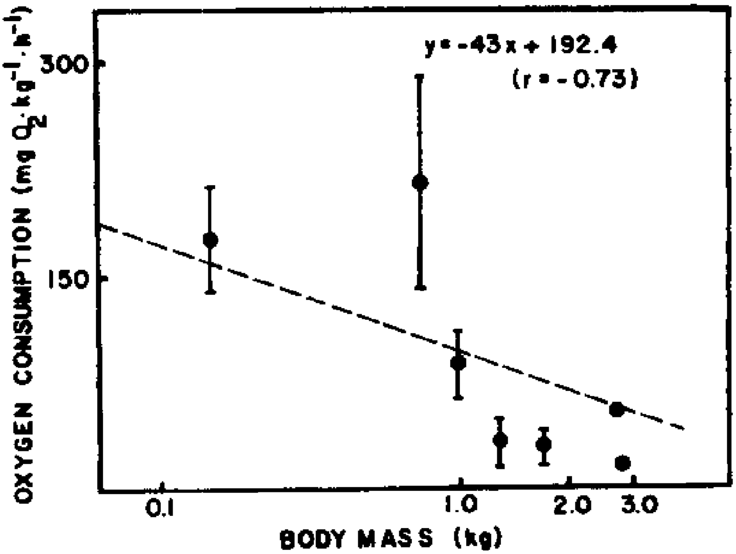

Figure 3: Oxygen consumption in milligrams oxygen per kilogram wet weight per hour vs. log wet body weight in kilograms for A. fimbria. Temperature is 3.0°C; measurements made between 0600 and 1800.

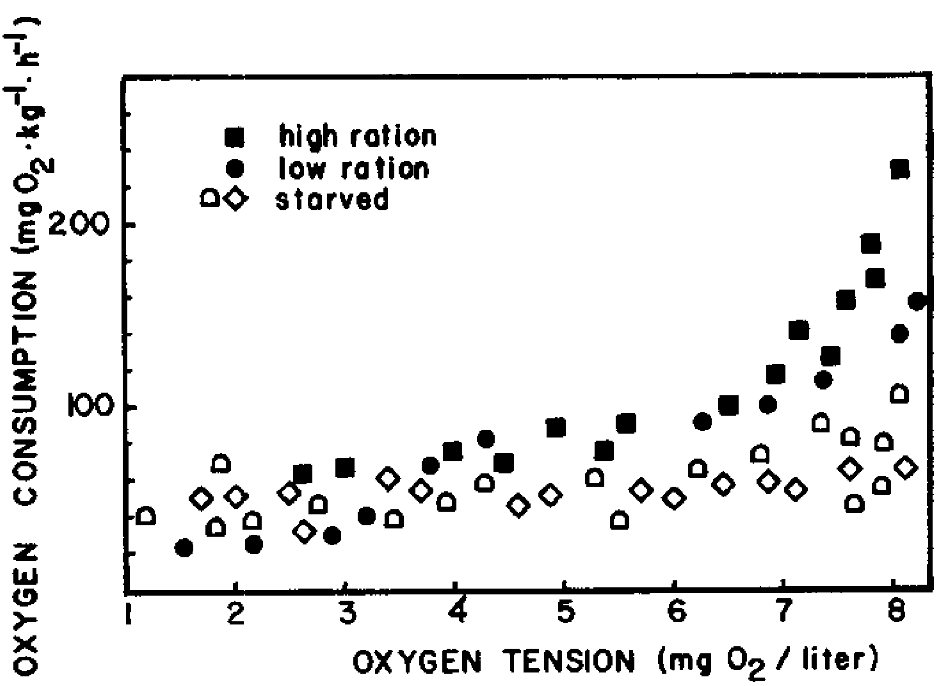

Figure 4: Oxygen consumption vs. external oxygen tension for fed and starved A. fimbria.

Growth rates of A. fimbria on varying ration size.

Growth rates (% wet weight increase per week) were measured in relation to ration size (% wet weight per week) for laboratory-held A. fimbria in a five-month growth experiment (Figure 5). Growth rates and ration levels represent an average value over that five-month period; each point (Figure 5) represents one fish. The equation fit to the data by least squares linear regression was $y = 0.19x - 0.46$, where y = growth and x = ration ($r = 0.91$). From this linear relationship between growth and ration level, the maintenance ration can be interpolated to be 2.5% of the wet body weight per week. Fish used in the experiment had initial weights ranging from 1320 to 1740 grams wet weight. Temperature during the experimental period was between 8.0°c and 10.0°C.

Discussion

The diel pattern in oxygen consumption of laboratory-held A. fimbria suggests an endogenous rhythm most likely associated with feeding. Only fish that had been fed regularly exhibited this pattern; fish that were starved two or more weeks did not. Diel fluctuations in oxygen consumption have been noted for sockeye salmon (Oncorhynchus nerka) fingerlings under laboratory conditions (Brett and Zala, 1975). In fed salmon, the metabolic rate reached a maximum at 0800 before the fish were fed at 0830. However, starved fish showed a diminishing diel fluctuation in metabolic rate with starvation. Starved A. fimbria may be conserving energy by employing a different energetics strategy of waiting for available food.

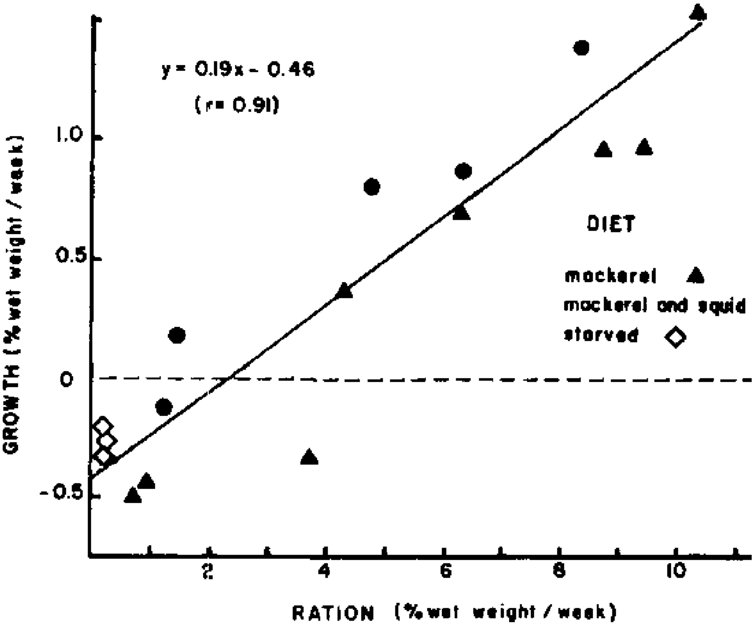

Figure 5: Growth (% wet weight increase per week) vs. ration (% wet weight per week) for laboratory-held A. fimbria on varying ration sizes.

Preliminary ultrasonic tracking data from one A. fimbria tagged and released in La Jolla Submarine Canyon suggest that fish in the field may be most active at night, moving to shallower depths. Although only one fish was tagged, both the laboratory diurnal patterns in respiration and these field data would support the hypothesis that A. fimbria is feeding at night, and perhaps migrating to shallower depths to do so. Since the seawater system used in the laboratory is running, there exists the possibility that laboratory fish are receiving a chemical day/night cue from the water source. The experimental chambers were kept in a dark, enclosed area, and thus, there was no reason to expect higher respiration rates at night (i.e., due to pumps turning on, people entering the area, etc.). The lower respiration rates for starved fish are not surprising; however, one wonders what the effect of prolonged starvation (e.g., over a season) would be on strategies of feeding and energy allocation. Figure 1A shows a lowering in the absolute rate of oxygen consumption four to six days after feeding, but the range of respiration rates over 24 hours remains the same.

Nitrogen excretion rates for fed fish showed a prolonged elevation after feeding. Ammonia production did not return to pre-feeding levels for three days. Starved fish and fed fish in the post-absorptive state have rates of ammonia production that were not significantly different. Brett and Zala (1975) found that, in fingerling sockeye salmon fed a ration of 3% of their body weight per day, nitrogen excretion rates rose sharply after feeding, reaching a peak in four hours, and declining to post-absorptive levels in 10 hours. A. fimbria in the laboratory given one large meal once a week ingested 10%-15% of its body weight at one feeding. Not unexpectedly with a meal that size, nitrogen excretion remained elevated for three days post feeding. Preliminary feeding experiments indicated that *A. fimbria* showed higher ingestion rates on a monthly basis with large weekly meals rather than small daily meals.

Respiration rates measured in the laboratory showed a great deal of variation of routine metabolism. Although all measurements were made during the day (0600-1800), diel patterns of activity may vary with size and with individual fish. Comparisons between immature fish of different sizes may not be appropriate if there are ontogenetic changes in weight specific metabolism (Hoar, 1975). It will be valuable to follow individual fish over several months of growth. The duration and magnitude of the elevated oxygen consumption after feeding (post-prandial oxygen consumption) varies with temperature, size and composition of the meal (Jobling, 1930); *A. fimbria* is more receptive to a single large meal, requiring 3-4 days after feeding for oxygen consumption to return to post-absorptive state. However, both the diel and post-prandial changes in oxygen consumption can be eliminated when the fish is subjected to low oxygen tension. It should also be noted that fed fish have a much shorter survival time at oxygen tensions lower than 1 mg O_2 per liter than starved fish (6-10 hours compared to 3-4 days).

A. fimbria are capable of surviving a wide range of external oxygen tensions. Environmental oxygen tensions encountered by *A. fimbria* off southern California range from 0.76 to 0.34 mg O_2 per liter at depths greater than 450 meters (Emory, 1960). Thus, *A. fimbria* in the field spend at least part of their time in waters which are colder and less oxygenated than water used in this aquarium study. A limited number of respiration measurements made at 6.0°C and the measurements made under low oxygen tension suggest that *A. fimbria* would have a much lower standard metabolic rate *in situ* than in the aquarium.

Laboratory studies of *A. fimbria* with limited mobility and varying ration size suggest that the fish is capable of a wide range of growth rates and significant energy storage for long periods of starvation. Growth rates obtained in this study agreed with growth rates obtained by Kennedy (1974) with pen-reared sablefish; a 1.0-kg fish fed 2% of its body weight per day gained 0.2% of its wet weight per day. This is an extremely low growth efficiency compared to cultured fish such as trout and carp of similar size which may gain 1.1% and 1.3% of wet body weight per day on the same 2% ration (Huisman, 1976).

A. fimbria can physiologically adjust to a wide range of ingestion levels, and this ability may allow them to survive long periods of starvation in the field, or exploit varying levels of food availability.

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Ontogenetic Changes in Growth and Their Relationship with Temperature and Habitat Change

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Growth rate of fishes may act as a sensitive indicator of environmental conditions. The dependence of growth upon physical and biological factors, however, may vary with life-history stage. Young stages generally tolerate and prefer higher temperatures than adults, both in the laboratory (Ferguson, 1958; McCauley and Huggins, 1979) and in the field (Norris, 1963; Brandt, 1980); thermal optima for growth may similarly be higher (Jobling, 1981). Movement to colder habitats as fish grow may be either gradual or rapid. When a natural temperature gradient exists (either spatial or temporal) as with depth or season, small movements may result in a gradual change in thermal environment as noted for *Girella nigricans* by Norris (1963) or for *Alosa pseudoharengus* by Brandt (1980). Where larger differences exist between larval and adult habitats, however, rapid changes in thermal environment may occur, as in *Sebastes diploproa* (Boehlert, 1977, 1978). An energetic approach to analysis of growth can explain these ontogenetic trends in thermal relationships.

Two species of the scorpaenid genus *Sebastes* were considered for comparison of the changes in growth patterns occurring with gradual and rapid ontogenetic changes in thermal environments. The black rockfish, *Sebastes melanops*, gives birth in mid-winter; pelagic larval and juvenile stages (10-40 mm standard length) are captured in winter and spring, and 40-50 mm benthic juveniles first appear in tidepools, estuaries, and other inshore waters in June, apparently recruiting throughout summer months (Laroche and Richardson, 1980; Bayer, 1981). During the first six months of life, young stages of this species are subjected to a variety of thermal regimes. Winter and spring temperatures offshore are about 14-15°C, whereas summer temperatures in nearshore areas may be as low as 8°C during summer upwelling but as high as 18°C in estuarine areas(Huyer, 1977; Gonor and Thum, 1970). Since adults live in relatively shallow nearshore waters, young may recruit gradually from the estuarine and nearshore areas they inhabit.

The splitnose rockfish, *Sebastes diploproa*, is characterized by a more precipitous change in thermal environment. Larvae and prejuveniles are epipelagic for approximately one year prior to migrating to the benthic habitat of juveniles and adults at 200-500 m. The low, seasonally constant temperatures in the benthic habitat (6-8°C) contrast with the seasonally variable surface temperatures (13-22°C). The migration, however, occurs during late May through September, when surface temperatures are high (Boehlert, 1977, 1978). This results in a rapid change in thermal environment. In this paper I discuss the differences in ontogenetic growth response to temperature in these two species and describe the energetic basis for these changes in *S. melanops*.

Materials and Methods

S. diploproa were collected as offshore pelagic prejuveniles from under drifting kelp; the range of initial length was 30-55 mm standard length (SL). *S. melanops* juveniles were collected from estuarine areas using small fish traps and otter trawls; the range of initial length for this species was 35 to 92 mm SL. Since *S. diploproa* migrates to the benthic habitat during a distinct season, both photoperiod and temperature were manipulated in the growth experiments. Animals were brought to the laboratory and maintained under ambient temperature and photoperiod. After division to the experimental groups, temperature and photoperiod were changed at 0.5°C and 15 min per day, respectively, until reaching the two photoperiods and three temperatures of acclimation (12 Light: 12 Dark, 16L:8D; 10°, 15°, 20°C). The 16 h photoperiod is characteristic of the migratory season, 12 h of non-migratory season. Standard length was measured at the beginning and end of the experiments (average 53 d) and growth was expressed as a length increment (mm/day). During the experiments fish were fed to satiation once daily on a mixture of trout chow, ground squid, and frozen brine shrimp. An average of 26 fish was used for each experiment.

Experiments with *S. melanops* were conducted under a constant 8 h photoperiod and at temperatures of 7°, 12°, and 18°C; in these experiments, ration (starvation and 25%, 50%, and 100% of maximum ration at each temperature) was introduced as a variable. Preliminary experiments determined the approximate level of full ration at each temperature. The amounts fed in partial ration experiments, which were always fully consumed, were based upon this value and the weight of fish in each tank. In full ration experiments, fish were given excess food and allowed to feed for one hour; excess food was removed, dried, and weighed each day to estimate the amount fed. Acclimation conditions and times followed those for *S. diploproa*. An average of 18 fish were used in each fed treatment and 10 in starvation treatments. At the start, midpoint, and end of the 57 d experiments fish were starved 48 h to allow evacuation of stomach contents, anesthetized, and both length and weight were measured. Ration levels were modified after the second weighing to reflect gains or losses of weight in each tank. Growth was expressed as instantaneous relative growth (% body weight per day; Ricker, 1975).

Growth data were analyzed using stepwise multiple regression models. For *S. diploproa*, the two models were fit by photoperiod treatment in the form:

$$G = a + b_1L_i + b_2T + b_3T^2 + b_4L_iT$$

where G = growth rate (mm SL per day), L = initial length (mm), T = acclimation temperature (°C), a = constant, and b's = regression coefficients. For S. melanops, the equation included ration and was in the form:

$$G = \hat{a} + b_1R + b_2T + b_3(\log W)$$

where G = instantaneous relative growth rate (% body weight per day), R = ration (% body weight per day), T = temperature (°C), W = initial weight, and b's = regression coefficients. A second model was constructed for S. melanops which considered only those experiments at full ration to better understand the effects of temperature upon optimum growth; although weight replaced length as an independent variable, the patterns of growth are comparable. Inclusion levels for independent variables in all models was P = 0.10.

Results

For Sebastes diploproa, mean laboratory growth rates were dependent upon temperature and photoperiod and averaged 0.105, 0.164, and 0.093 mm/day at 12L:12D and 0.150, 0.211, and 0.096 mm/day at 16L:8D at 10°, 15°, and 20°C respectively. Comparison of these values, however, is confounded by the effects of initial length. Simple correlation coefficients show that at 16L:8D, length is positively correlated with growth at 10°C (r=0.78) but negatively correlated at 15° and 20°C (r=-.99 for both); at 12L:12D, length and growth are negatively correlated at 10° and 15°C (r=-.97 and -.94, respectively) and no significant correlation is apparent at 20°C (P=.01). The multiple regression models help to clarify the relationship of growth with temperature and initial length; the fit of the models is as follows:

$$\text{12L:12D} \quad G = .1378 - .0112L + .0459T - .0021T^2 + .0004LT \quad N=98 \quad (1)$$

$$\text{16L:8D} \quad G = -.8090 + .0080L + .1264T - .0033T^2 - .0007LT \quad N=60 \quad (2)$$

All regression coefficients are highly significant; the multiple correlation coefficients (R) are .919 and .933, suggesting that these variables explain 84.5 and 87.0% of the variation in growth for 12L:12D and 16L:8D, respectively. Effects of temperature were similar at both photoperiods; growth increased to an optimum temperature and then declined, as indicated by the negative value of the coefficient for temperature squared (Figure 1A, B). The temperature of optimum growth increased slightly with length at 12L:12D but clearly decreased at 16L:8D. Growth showed a clear relationship with initial length at 12L:12D, with decreasing growth with length at all temperatures (Figure 1B). Zero values of growth are predicted by the model and were observed in some experiments at larger initial lengths. Under 16L:8D, growth was generally greater as compared to 12L:12D, but the relationship with initial length was more complex. At approximately 10.5°C, the model predicts a nodal point where fish of all initial lengths show the same growth rate; growth increases with length below this temperature and decreases with length above it (Figure 1A). At these higher temperatures in 16L:8D and at all temperatures in 12L:12D, the relationship of growth rate with length suggests a temperature-dependent growth asymptote.

General results of the growth and ration experiments for S. melanops are shown in Table 1. Growth in length in maximum ration experiments was similar to that for S. diploproa, but the growth pattern differed with respect to temperature. Relative growth was a linear function of ration at all temperatures (Figure 2). At equivalent rations, growth was actually faster at lower temperatures, but when one considers relative growth as a function of the percentage of maximum ration consumed, the

Table 1: Growth of *Sebastes melanops* in the temperature-ration experiments.

Temp (°C)	Daily Ration (% body wt./day)	N	Growth (mm/day)	Relative Growth (% body wt./day)
7	2.41	20	.092	.376
	1.01	18	.036	-.016
	0.51	17	.032	-.027
	0	10	-.006	-.298
12	5.00	19	.260	.993
	2.73	18	.135	.449
	1.48	18	.066	.097
	0	10	-.011	-.453
18	6.58	20	.314	1.495
	3.83	18	.167	.698
	2.10	18	.069	.154
	0	10	-.023	-.689

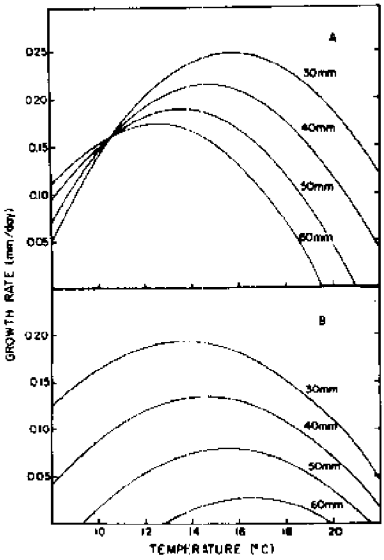


Figure 1. Growth of *Sebastes diploproa* (mm/day) as a function of temperature and initial fish length. Values are predicted from equation (1). A. 16L:8D experiments. B. 12L:12D experiments.

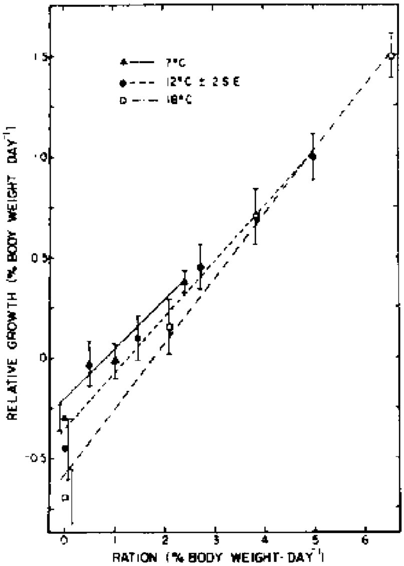


Figure 2. Instantaneous relative growth of juvenile *Sebastes melanops* as a function of ration and temperature. Bars indicate ± 2 S.E. The three fitted lines are significantly different in slope and elevation (Analysis of covariance, P<.05).

respective growth is significantly less at low temperatures (except in the starvation treatment, where weight loss, as expected, increases with increasing temperatures). Graphical estimates of maintenance ration (where growth is zero) are 0.92, 1.29, and 1.81% body weight per day, representing 38.4, 25.7, and 27.4% of maximum ration at 7°, 12°, and 18°C, respectively. Gross conversion efficiencies at maximum rations were 16.05%, 20.38%, and 20.36% at 7°, 12°, and 18°C. With decreasing ration, conversion efficiencies decreased at 7°. At 12° and 18°C, however, conversion efficiencies were approximately equal at 100% and 50% maximum ration and decreased at 25% ration. For the two higher temperatures, optimal conversion may therefore be at intermediate rather than full rations.

The multiple regression models for experiments with *S. melanops* are as follows:

$$G = -1.1118 + .2227\ T - .0037\ T^2 - .0042\ TW + .0446\ W \qquad N=59 \qquad (3)$$

$$G = -.3221 + .2915\ R - .0180\ T + .2375\ \log(W) \qquad N=196 \qquad (4)$$

The growth model based upon full ration experiments is presented in equation (3). All included variables were significant and explained 85.7% of the variation in growth. Effects of weight in this model are shown in Figure 3 and are similar to the length effects on *S. diploproa*. Again, a nodal point occurs at 10.6°C; above this temperature, relative growth is greater for smaller fish and below it is less. Growth continues to increase with increasing temperature but growth optima, apparent for 20 g fish at approximately 18.7°C (Figure 3), were not approached in the experimental temperatures for smaller fish. As compared to *S. diploproa*, which shows distinct growth optimal near 15°C (Figure 1), the temperatures of optimum growth for *S. melanops* juveniles are much higher.

The growth model of all ration-temperature experiments is presented in equation (4). All regression coefficients were highly significant and the multiple correlation coefficient (R) suggested that the variables in this model explain 86.7% of the variance in growth. Temperature has a negative effect as shown by the regression coefficient. This would also be expected from a plot of the raw data, since over the range of ration consumed at low temperature, growth was greater at 7° as compared to 12° and 18°C (Figure 2). The limitation on ration at low temperatures, however, results in greater relative growth at higher temperatures when ration is not limiting (Figure 3). In this model, relative growth increases with increasing weight as compared to the maximum ration model; this may be due to the fact that smaller

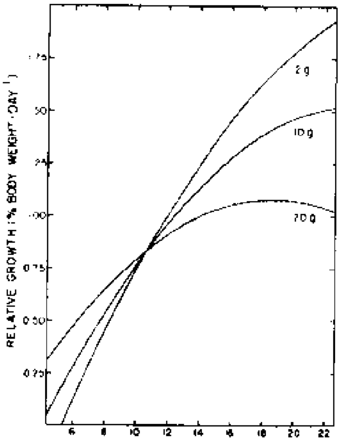
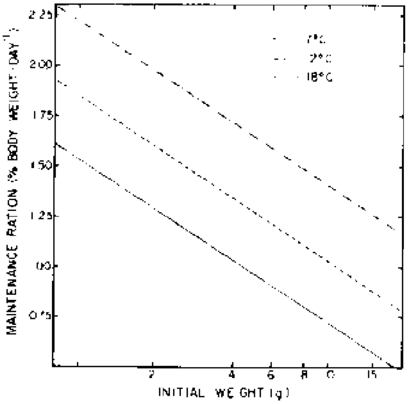


Figure 3. Relative growth of juvenile *Sebastes melanops* as functions of temperature and initial weight. Values are predicted from equation (2).

fish show less favorable growth under limiting ration.

Setting relative growth equal to zero in the model described in equation (4), one can estimate maintenance ration as functions of temperature and weight. The resulting values suggest that maintenance ration increases with increasing temperature but also increases with decreasing size (Figure 4). The values estimated from Figure 2 agree with values in Figure 4 if one uses the mean weights for the experiments.

Figure 4. Maintenance ration for juvenile Sebastes melanops as functions of initial weight and temperature. Values are predicted from equation (3).



Discussion

The patterns of growth as affected by temperature clearly differ for Sebastes diploproa and S. melanops. S. diploproa migrates rapidly from relatively warm surface waters (near 20°C) to the cold benthic habitat of juveniles and adults (6-8°C). Growth rate under photoperiod conditions characteristic of the non-migratory season are low for larger fish at all temperatures (Figure 1B), whereas under photoperiod conditions characteristic of the migratory season, growth rate improves for larger fish but only at lower temperatures (Figure 1A). Thus the ontogenetic change in thermal growth response is suited to the change in habitat; larvae and early juveniles inhabit surface waters while temperatures are high; as temperatures increase the following year, larger fish migrate to the colder benthic habitat.

Sebastes melanops shows a more gradual pattern of recruitment; the pelagic stage is shorter, and movement from inshore juvenile habitats to the relatively shallow adult habitat may take place over several months. While this species shows a similar pattern on ontogenetic change in growth to that in S. diploproa, it is over a significantly different temperature range. Optimal growth was predicted by the model at temperatures higher than 18°C (Figure 3), whereas thermal optima for growth in S. diploproa are nearer 15°C. Even in the young stages, which inhabit similar thermal regimes, the effect of temperature upon growth therefore reflects the thermal regime of the adult habitat.

The ontogenetic changes in thermal optima for growth are clearly related to the energetics of feeding, as shown by the ration and growth experiments with S. melanops. Based upon temperature effects alone, it is obvious that ration consumed on a daily basis is dependent upon temperature (Table 1, Figure 2). Evacuation experiments suggest that temperature affects energy turnover; Boehlert and Yoklavich (MS) showed that after 24 h, 54%, 42%, and 29% of a full meal remain unevacuated at 7°, 12°, and 18°C, respectively. Thus as temperature decreases, the amount of food which can be consumed is limited by digestion rate, thereby also limiting growth rate. This is apparent in Figure 2, where the long-term daily consumption increases from 2.41% to 6.58% body weight per day as temperature increases from 7° to 18°C.

The interaction of temperature and size is more complex. Several studies have found that relative food consumption decreases with increasing size (Gerald, 1976, Wurtsbaugh and Davis, 1977). In the present study, however, fish were fed only once each day and there was no evidence that smaller fish could consume a single meal which was larger as a percentage of body weight. Since maximum relative rations were equivalent within experiments, the observed size-related changes in growth with increasing temperature (Figure 3) may be a function of size-specific differences in maintenance ration (Figure 4). The decrease in maintenance ration with increasing size is associated with size-specific respiration rates. Respiration rates can generally be described by the power function $T=aW^b$, where T= total metabolism, W= weight, and a and b are fitted parameters (Paloheimo and Dickie, 1966). In fishes, values of b are generally between 0.65 and 0.85 (Glass, 1969). The slope of the lines relating maintenance ration to size (Figure 4) are -0.81 suggesting the importance of metabolic rate to maintenance costs. The effects are more clearly understood by considering percentage of total ration consumed by maintenance costs; the "scope for growth" is the energy available for growth after maintenance ration and other energetic costs are considered (Warren and Davis, 1967). As maintenance ration increases as a percentage of total food intake, scope for growth must decrease. At 7°C, nearly 64% of the total ration for a 1 g fish goes to maintenance ration as compared to only 23% for a 16 g fish (Table 2). The difference in maintenance cost between lower and higher temperatures is significant for smaller fish but decreases as size increases (Table 2). Thus the "scope for growth" decreases as temperature decreases and the impact is much greater for small fish. This relationship explains the decrease in optimum temperature for growth and particularly the poorer growth of smaller fish at low temperatures observed for both species (Figure 1A; Figure 3).

Table 2: Effects of temperature and fish size on maintenance ration (as a percentage of maximum ration) in juvenile Sebastes melanops.

Weight (g)	7°	12°	18°
1	63.9	37.0	33.7
8	33.2	22.2	22.5
16	23.2	17.2	18.9

Habitat segregation of different ontogenetic stages is common among fishes; in many cases this may involve ontogenetic changes in thermal preference (Ferguson, 1958; McCauley and Huggins, 1979; Brandt, 1980). Several selective benefits have been ascribed to this phenomenon, including increased abundance of appropriate sized food, avoidance of potential competition with or cannibalism by adult stages, decreased predation pressure, and the general nursery habitat concept, which encompasses all of the above benefits (McHugh, 1967; Weinstein 1979; Brandt, 1980). As demonstrated in the experiments with S. melanops, increased environmental temperature allows increased food consumption, growth rates, and growth efficiency for smaller fish. Thus for certain species a clear energetic benefit exists for inhabiting warmer environments during early stages. Availability of appropriate thermal habitat for larval and juvenile growth may therefore effectively limit the areas and seasons of successful reproduction.

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Contributions to the Bioenergetics of a Tropical Fish

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Introduction

This paper summarizes some of our recent publications (Pandian and Vivekanandan, 1976; Vivekanandan, 1976; Vivekanandan and Pandian, 1977) as well as the results obtained from more recent research on *Channa striatus*. *C. striatus* is a tropical freshwater fish of economic importance, attaining a maximum body weight of 2 Kg in about 2 years. It is an obligate air-breather and visits the surface every few minutes. Experiments designed to prevent air-breathing in different ontogenetic stages revealed that development of the air-breathing organ (see also Das, 1927) and the regular surfacing behaviour (Vivekanandan, 1977) are completed as the fish grows from a fry (7 mg live weight) to fingerling (750 mg). Individuals weighing less than 100 mg can depend on gill-breathing alone for quiet sometime; larger individuals (>0.750 g) can depend on air-breathing or gill-breathing alone for more than 20 hrs. Hence the 0.75 g fingerling represents 'the critical life stage', at which breathing from water and air are both obligatory. It is at this stage, the fingerlings are transported for stocking in ponds. Most of our experiments were performed on this critical fingerling stage. Water depth, ration, temperature, feeding frequency and rearing density are some factors considered as important to enhance survival of this critical stage. Standard procedures were followed to estimate food consumption (C), faeces egested (F) and growth (=conversion P) of the fish during the experimental period (see Pandian and Vivekanandan, 1976); the data presented here are based on the performance of 3 to 6 individuals reared for a period of 21 to 30 days; for want of space, standard deviations are not given but can be known from original publications.

Results and Discussion

Effect of aquarium depth

The air-breathing habit of C. striatus and the consequent need to surface at more or less regular intervals impose a considerable drain of energy, which otherwise could have been utilized for fish production. By rearing the fingerlings (4.5 cm body length) in transparent cylindrical aquaria (diameter 6 cm) containing different depths of water, they were forced to swim varying distances per unit time in order to exchange atmospheric air. For instance, the fish surfaced once in 46 ± 6.0 sec in a 40 cm water depth, requiring a total period of 10 ± 1.7 sec to cover a distance of about 80 cm. Except for the regular interval of about 36 sec resting at the bottom, the fish was observed to exhibit a sustained swimming activity; besides, the experimental design permitted long term feeding and growth estimates.

In shallow aquaria containing 2.5 cm water at 32°C, the fish surfaced 1860 times per day travelling 81 m at a metabolic cost of 114 cal/g live body weight. By comparison, in 40 cm of water the fish expended 164 cal/g/day on metabolism and swam 1.7 Km in the course of 2612 visits to the surface (Table 1). In the shallowest aquarium (2.5 cm H_2O depth), the fish consumed food equivalent to 180 cal/g/day and converted it at a net efficiency (K_2) of 27%, whereas the fish in the deepest aquarium (40 cm H_2O depth) consumed as much as 225 cal/g/day but converted it with a lower efficiency of 16%. Therefore culturing the fingerlings in shallow nurseries greatly enhances growth (see Pandian and Vivekananadan, 1976; Pandian et al., 1976). Supporting evidences for the energy cost of surfacing have been reported for the air-breathing catfishes Heteropneustes fossilis (Arunachalam et al., 1976) and Corydoras aeneus (Kramer and McClure, 1981). In addition, surfacing activity in the air-breathing fishes not only costs energy but also time. C. striatus spends 15% of the time on surfacing and associated activities (Pandian and Sampath, 1981). Kramer and McClure (1981) reported that C. aeneus spends 5% of its time on activities associated with air-breathing.

It is relevant here to point out the evolutionary implication of time and energy costs of surfacing in aquatic animals. The density of water is about 840 times that of air, while viscosity is about 50 times as great, and oxygen is approximately 30 times more concentrated per unit volume in air than in saturated water (Schmidt-Nielsen, 1979). Hence the energy cost of aerial respiration ought to be much less than that of aquatic respiration: For instance, estimates of the metabolic cost of ventilation in fishes (10-43% of resting metabolic rate) are far greater than those of man (0.6-3.2%) (Jones and Schwarzfeld, 1974). However, air-breathing fishes are less common than aquatic respiring species in most habitats, including tropical freshwaters which frequently become hypoxic, thereby greatly increasing the apparent advantage to air-breathing. Though beneficial for survival in oxygen-deficient waters, the need for surfacing and associated swimming activities impose a considerable drain of energy on the obligate air-breathing fish. Kramer and McClure (1981) explained that time and energy costs of surfacing have limited the scope for evolution of air-breathing among fishes.

Table 1. Effects of water depth and temperature on surfacing frequency and energetics of *Channa striatus* fingerling fed *ad libitum* for a period of 28 days (from Vivekanandan and Pandian, 1977; modified).

Water depth (cm)/ Temperature (°C)	Surfacing frequency (times/day)	Swimming distance (m/day)	Consumption (cal/g/day)	Absorption (cal/g/day)	Metabolism (cal/g/day)	Conversion (cal/g/day)	Conversion efficiency (K_2) (%)
Effect of water depth at 32°C							
2.5	1860	81	180	173	114	47	27
5.0	1857	161	190	181	129	38	21
15.5	2074	563	212	206	157	32	16
31.0	2272	1220	225	216	166	31	14
40.0	2612	1721	225	216	164	34	16
Effect of temperature at 40 cm water depth							
17	283	218	45	41	39	0.5	1
22	1054	527	111	107	84	13	12
27	1879	1315	223	210	165	27	13
32	2616	1721	225	216	164	35	16
37	1203	643	203	193	149	27	14

Effect of temperature

As shallow waters in the tropics undergo considerable diurnal and seasonal temperature cycles (Jhingran, 1975), fingerlings of *C. striatus* reared in shallow nurseries, as recommended above, may be subjected to large variations in temperature. Studies on surfacing frequency and food utilization in fingerlings reared in cylindrical aquaria of 40 cm depth were thus conducted at 17, 22, 27, 32 and 37°C. At 32°C, the fish visited the surface most frequently and swam the longest distance; it also consumed the greatest ration (225 cal/g/day) and converted with the maximum efficiency (K_2 = 16%) at this temperature (Table 1). Hence, rearing *C. striatus* fingerlings in shallow waters at the habitat temperatures between 27 and 32°C would appear optimal (see Vivekanandan and Pandian, 1977). Supporting evidence is also obtained from a similar study undertaken on the air-breathing larvivorous fish, *Polyacanthus cupanus*, which thrives in paddy fields and adjacent shallow irrigation canals.

Effect of ration

When growth rate is plotted against ration, one can obtain: (i) maintenance ration in which the growth is zero, (ii) optimum ration, with which the fish exhibits the highest efficiency, and (iii) maximum ration, the highest ration consumed under given experimental conditions. To optimize feed cost, one requires basic information on the metabolic demands of maintenance, growth, swimming, and other activities. While there are several publications covering the effect of feeding rate on growth of fish (e.g. Brett et al., 1969), effects of ration on the swimming activity of a fish was perhaps first reported by Vivekanandan (1976). Surfacing and swimming activities of *C. striatus* in 15 cm of H_2O at 27°C increased from 550 ± 26 times and 58 ± 37.7 m per day for a starving fingerling to 1635 ± 137 times and 439 ± 38 m per day for fish fed maximum ration (43.3 mg dry weight, or 220 cal/g/day). Likewise, swimming speed also increased from 2.4 ± 0.70 cm/sec to 5.2 ± 0.11 cm/sec in these individuals. The maintenance energy cost and the optimum ration were equivalent to 45 cal/g/day (10.5 mg/g/day) and 125 cal/g/day (25.5 mg/g/day) (Figure 1). Therefore, a reduction in the ration to about 2/3 of the *ad libitum* economizes the feed cost.

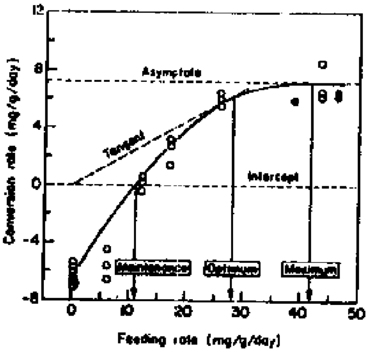

Figure 1. Geometric derivation of various parameters of conversion rate with accompanying feeding rate in *Channa striatus* (0.9 g); for comparison, data obtained by Pandian and Vivekanandan (1976) for *C. striatus* (.75 g) held in 15.5 cm of water are also given (closed circles) (from Vivekanandan, 1976; modified)

Interaction between rearing density and feeding frequency

In intensive fish culture, frequent feeding and high stocking density are often utilized to maximize production. Feeding frequency is positively related to food consumption and thereby to growth (e.g. Ponniah, 1978), whereas stocking density is inversely related to growth. For *C. striatus*, it was considered essential to identify the optimum feeding frequency and rearing density as well as to understand the interaction between these two factors.

Five fish densities (1, 2, 4, 8 and 16 individuals/aquarium; 7 l capacity) were chosen and each was subjected to 5 different feeding regimes (twice a day, once a day, once in 2 days, once in 3 days, and once in 4 days). Feeding once a day was shown to be the optimum regime for *C. striatus* fingerling (Table 2). At the density of 2 individuals/aquarium, rates of feeding and conversion amounted to 51 and 4 cal/g/day, when fed once in 3 days; these values increase to 248 and 96 cal/g/day in once a day feeding series; further increase in feeding frequency resulted in decreased food intake and conversion. The highest gross conversion efficiency (K_1) was exhibited by the series feeding once a day; the efficiencies ranged from 39 to 33% in different density groups; the corresponding values are 37 to 30%, 20 to 17%, and 8 to 3% for the series fed twice in a day, once in 2 days and once in 3 days, respectively. On the whole, feeding *ad libitum* once a day ensures not only maximum food intake but also optimal efficiency.

Table 2. Feeding and conversion rates (cal/g/day) of *Channa striatus* as functions of rearing density and feeding frequency (from K. Sampath and T.J. Pandian, unpublished).

Density (No/aquarium)	Feeding frequency (time/days) 2/1	1/1	1/2	1/3	1/4
			Feeding rate		
1	207 ± 41.3	261 ± 42.4	96 ± 12.2	58 ± 4.5	40 ± 1.5
2	220 ± 46.1	248 ± 0.5	99 ± 3.7	51 ± 3.3	36 ± 2.3
4	233 ± 9.2	186 ± 5.5	93 ± 3.6	51 ± 3.2	35 ± 2.1
8	197 ± 22.1	172 ± 12.7	84 ± 2.4	50 ± 2.1	34 ± 2.1
16	173 ± 23.4	151 ± 6.3	74 ± 2.5	45 ± 1.5	30 ± 2.2
			Conversion rate		
1	76.3 ± 16.1	102.5 ± 14.4	17.5 ± 2.0	4.4 ± 1.0	-4.2 ± 1.1
2	74.2 ± 17.4	95.5 ± 1.0	19.6 ± 2.3	3.9 ± 0.7	-4.5 ± 1.4
4	93.5 ± 12.1	62.1 ± 8.8	17.3 ± 1.3	3.2 ± 1.1	-4.7 ± 0.9
8	68.1 ± 16.3	65.7 ± 5.5	15.0 ± 2.0	2.8 ± 0.1	-6.9 ± 0.4
16	52.7 ± 12.1	54.0 ± 3.4	12.7 ± 2.4	1.3 ± 0.01	-7.3 ± 1.1

Generally, an increase in density results in decreased food intake and conversion. When subjected to once a day feeding, individuals converted the food at 103, 96, 62, 66 and 54 cal/g/day at rearing densities of 1, 2, 4, 8 and 16 individuals/aquarium, respectively. Though there is a gradual decline in the conversion rate, the decrease becomes stastically significant only when the density rises beyond 4 individuals/aquarium. Therefore, 4 individuals may be taken as optimum density; in other words, to obtain the highest production, 1.8 l of water should be provided per gram of stocking biomass of C. striatus.

Finally, subjecting the data to two-way analysis of variance showed that feeding frequency has a highly significant effect on rate and efficiency of food conversion, whereas the density effects are not statistically significant (Table 3). This implies that negative effects of density could be compensated by increasing the feeding frequency and the quantitative aspects of such compensation are being currently studied.

Table 3. Summary of analysis of variance for the data on conversion rate as functions of feeding frequency and rearing density of C. striatus (from K. Sampath and T.J. Pandian, unpublished).

Source of variation	SS	Df	MS
Total	33104.06	24	
Between feeding frequencies	30320.9	4	7580.2
Between densities	936.7	4	234.2
Interaction	1846.5	16	115.4

F(1) 4, 16 = 65.69 $<$ P 0.0005
F(1) 4, 16 = 2.029 $>$ P 0.05

Interaction between steroid and dosage

Commercial fish farming necessitates the search for new culture techniques to enhance productivity level by decreasing feed cost and shortening production period. It has been observed that when reared in high densities, C. striatus fingerlings become cannibalistic. The juveniles (50 g) are less vulnerable and easily escape predation. Application of anabolic steroid to enhance the rate and efficiency of food utilization in animal husbandry has resulted in substantial savings in the production cost and time. Therefore, administration of a steroid to C. striatus fingerling was considered as a possibility to minimize cannibalism, and possibly predation by others in a polyculture system. With regard to fish, most studies have been restricted to the effect of hormone on weight gain (e.g. Higgs et al., 1977). Few workers have attempted to relate the growth response of hormone-treated fish to feeding and conversion efficiency, and those studies available have reported conflicting results. For example, diet supplementation of Diethylstilbestrol, a synthetic mimic of estrogen, retards growth of Ictalurus punctatus (Bulkley, 1972) and Salmo gaidneri (Cheema and Matty, 1978), while enhancing that of Pleuronectes platessa (Cowey et al., 1973). Moreover, Mugil auratus receiving as much as 1000 mg Testosterone/Kg/day fails to display a positive growth response (Bonnet, 1970), while Oncorhynchus kisutch registers a significant increase in growth even at a low dose of 10 mg Testosterone/Kg/day (McBride and Fagerlund, 1976). A critical review of pertinent literature revealed that none of the present workers have attempted to experiment with an array of steroids at a wide range of doses and to fix the optimum for the suitable hormone.

The required doses of the tested steroids, listed in Table 4, were prepared using sesame oil as carrier solution. Volume of the hormone solution injected into *C. striatus* was maintained constant at 60 µl for all the tested doses (*including* the controls) and was administered using a 100 µl sterilized syringe (Scientific Glass Engg., Australia) on the first day of the feeding experiment. The test individuals were allowed to feed *ad libitum* on live fish *Lepidocephalichthys thermalis*. Controls fed at *the rate of* 77 cal/g/day and converted the food with 23% (K_2) efficiency. From our experiments on hormone-treated *C. striatus*, the following facts become apparent: (i) 17α Methyltestosterone and Docabolin act as appetite-stimulants and increase the food intake of treated fish to about 1.5 times the control at almost all tested doses from 5 to 30 mg/Kg fish. They also enhance food conversion efficiency of the treated fish about 2 times the control, when administered at dosages between 10 and 30 mg/Kg. Thus, the accelerated growth in the treated *C. striatus* is due to appetite-stimulating and anabolic properties of *these hormones*, i.e. the application 17α Methyltestosterone or Docabolin may reduce the production time alone. (ii) At the tested dose range, Testosterone, Diethylstilbestrol, and Estroid do not significantly increase food intake, but enhance the efficienty alone by about 1.5 to 2 times the control, when given at dose of 20 mg/Kg. The growth acceleration in the treated fish is due to the anabolic property of the hormone. In other words, the application of any one of these hormones reduces the production cost and time. (iii) The response to a dose as well as a particular steroid is a species specific feature among fishes. Further work is in progress to identify the route (diet supplementation or injection) and the frequency of administration that ensure the maximum growth of *C. striatus* fingerlings at minimum feed cost.

Table 4. Feeding rate (cal/g/day) and conversion efficiency (%) of *Channa striatus* as a function of the tested hormones. All values represent the mean (±SD) performance of 3-6 individuals (from A.R.C. Nirmala and T.J. Pandian, unpublished).

	Feeding rate				Conversion efficiency			
Dose (mg/Kg fish)	5	10	20	30	5	10	20	30
I Androgenic hormones								
1. **Testosterone** **(German Remedies, India)**	96 ±2.4	82 ±2.1	77 ±2.0	77 ±2.7	30 ±2.1	30 ±2.2	39 ±1.0	8 ±1.3
2. **17α Methyltestoterone** **(Sigma, USA)**	80 ±2.1	110 ±1.6	92 ±1.7	113 ±1.4	30 ±2.0	38 ±2.0	39 ±2.9	25 ±1.6
II Estrogenic hormones								
3. **Docabolin** **(Organon, India)**	110 ±2.6	112 ±2.3	118 ±2.5	123 ±2.8	24 ±0.7	28 ±1.7	44 ±2.5	49 ±2.7
4. **Diethylstilbestrol** **(Sigma, USA)**	73 ±2.4	66 ±2.4	80 ±2.8	77 ±2.2	33 ±2.7	47 ±0.6	38 ±2.4	30 ±1.8
5. **Estroid** **(German Remedies, India)**	83 ±2.2	69 ±1.2	77 ±2.5	82 ±1.9	23 ±1.4	40 ±2.5	45 ±1.3	46 ±2.8

Summary

The fingerling stage of the air-breathing fish Channa striatus represents a 'critical phase', during which both gill and air-breathing are obligatory. Using a new experimental design to collect data on surfacing frequency and food utilization, it was found that rearing this critical stage in shallow nurseries at 27-32°C and 2/3 of the *ad libitum* ration provided maximum growth at minimal feed cost. In high density culture, feeding once a day and providing 1.8 l of water per gram of stocking fish ensured maximum food intake and growth. Studies on interaction between feeding frequency and rearing density showed feeding frequency to be more important; the negative effects of high density can be compensated by increasing frequency of feeding. Administration of 10 to 30 mg 17α Methyltestosterone or Docabolin/Kg fish increased food intake by 1.5 times and conversion efficiency by about 2 times the control. Fingerlings treated with 20 mg Testosterone, Estroid or Diethylstilbestrol/Kg fish show 1.5-2.0 times higher conversion efficiency, but took an equal amount of food, as the control. The first group of steroid thus displays appetite-stimulating and anabolic properties, while the second exhibits anabolic property alone.

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Session II Discussion
Bioenergetics of Fish Feeding

Questions Following Eggers Presentation:

Citing evidence from Lake Pend Oreille that juvenile kokanee did not illustrate maximum size-selective predation until they were larger than 40 mm, La Bolle asked Eggers if he had encountered anything similar. Eggers recounted that during the only period of time that juvenile sockeye are smaller than 40 mm, during the winter period of low prey availability, there was no significant difference between diets of the 0+ and 1+ year fish; they were not able, however, to capture the younger age class fish until after they had grown for sometime and may have missed such an effect.

Questions Following Robison Presentation:

Cailliet commented that it was difficult for him to differentiate between 35% and 40% assimilation without knowing, 1) how do you know that the feces production rate is correct? 2) how much variability is there among individuals? and 3) is assimilation rate affected by the method of measurement? Expressing that this was a very preliminary cut at the problem, Robison explained how they used the one species they have been able to hold in the laboratory (Melanostigma pammelas) to test experimentally whether or not they are defecating in the trawl (no indication they are) and to compare fecal matter in the intestines to that of fish captured in the trawl, with no indication of any difference between them. In terms of volume of fecal output, they have performed detailed diel sampling to follow a meal through the fish's digestive system and document its loss in biomass prior to elimination.

Ebeling asked if other organisms such as invertebrates utilize and recycle the sinking fish feces, to which Robision cited additional studies which indicated that the rapid sinking rate and low detectability of fecal matter would probably prevent midwater invertebrates from picking it up. Robison went on to suggest, however, that the luminous bacteria in the guts of the fishes are probably incorporated into the feces and as a result the fecal matter probably glows when it is released and may offer a valuable cue to midwater detritivores.

Questions Following Cochran Presentation:

Chapman asked if Cochran could differentiate between changes in frequency distributions due to changes in distribution versus those due to population dynamics. Cochran explained that they were working within a relatively confined system wherein the distribution of the population was not significantly variable.

Larson asked if the bioenergetic model took into account the growth of gonads, to which Cochran replied that since the largemouth bass population they worked with were nonreproductive, they could legitimately ignore that energetic loss.

Ebeling questioned the biological source of the variability of P (proportionality constant) in daily ration. Cochran suggested that early in the season it was due to the variable availability of suitably-sized prey, while later in the season it was due to either natural sampling variability or the temporal and spatial patchiness of preferred prey.

Boehlert asked Cochran how confident he would feel if he was to start working on laboratory bioenergetics data for another species without field-based calibration of the daily ration estimates, to which Cochran suggested that it would be advisable, depending upon the state of the bioenergetic literature on the species. But he would now feel confident in going to other lakes and simply documenting temperature and largemouth bass growth rates.

Rice commented further that this is one of the few instances where there are data available for an independent comparison of prey consumption derived from a bioenergetic model and it illustrates that the model can be used to narrow down the range, eliminate, or set priorities of testable hypotheses regarding food consumption.

Since the fish did not seem to be very sensitive to temperature, Chapman questioned why the long-term changes in daily ration were easier to predict than short-term changes. Cochran replied that the inability of the model to predict short-term changes was a function of the differences in scale in the measures they were trying to compare, rather than the model itself.

Interested in the fluctuation in daily ration, Karpov asked about the sampling methodology relative to sample size. Cochran described the sampling frequency and sample sizes they utilized, as well as the variability in daily ration estimates which could be attributed to variable temperature, prey availability, and sample composition. Karpov commented further on the inadvisability of transferring bioenergetic data to other species, considering the drastic differences in digestion rates among species.

Questions Following Yaklavich Presentation:

Herbold asked about the salinity of Elkhorn Slough, which Yoklavich described as varying between 28% and 36%; her experiments were conducted in ocean water.

Observing that there are not as many estuaries in Southern California as in Northern California, Chapman asked if the statistics on English sole occurrence might not affect the results. Yoklavich replied that it was more a matter of reduced abundance south of Pt. Conception, which might be partially due to temperature tolerance factors.

Noting that the results illustrated optimum growth at 13°C, Rowley asked why the juvenile English sole would recruit to Monterey Bay and achieve maximum growth at that specific temperature. Yoklavich replied that is as yet unexplained, although Boehlert will be addressing that question in further studies.

Boehlert noted the variability Yoklavich observed experimentally in maximum ration and asked if she would assume, given the similar growth rates observed in the field, that maximum relative rations were equally variable in the field. In the light of the lack of any field verification, Yoklavich agreed that rations probably are highly variable in the field.

La Bolle asked how English sole activity patterns differed between the laboratory and the natural environment. Yoklavich did not document activity rates but replied that the English sole's relatively sedentary behavior facilitated such laboratory studies as compared to more active fish. But it was acknowledged that different activity patterns under similar consumption rates could affect different growth rates.

Questions Following Sullivan Presentation:

Relative to the one sablefish tracked in the La Jolla submarine canyon, Cailliet asked if the environmental oxygen tensions at those depths were low enough to induce the movement. Sullivan described how the fish moved at night from 500 m to 200 m where the oxygen tension was double that at the deeper depth. Cailliet also asked if the energetic reserve the starved sablefish drew upon over eight months originated from the liver and gonads, to which Sullivan replied that it appeared to come from the muscle and bones.

Robison asked whether the activity patterns were correlated with diel oxygen changes, feeding, heartbeat, or motility. Sullivan replied that only oxygen tension was correlated. Robison asked if there was any indication that they were feeding at night; both Sullivan and Cailliet cited some evidence that this was the case.

Herbold asked Sullivan if varying feeding times or frequencies affected oxygen consumption, to which Sullivan replied that the peak oxygen consumption consistently occurred at night, even with starved fish although it did occur more erratically.

Observing that nitrogen excretion was back to starvation level after six days while the oxygen consumption rate was still halfway between maximum and starvation, Ursin asked if there was a good explanation for this phenomenon. Sullivan explained that starved and fed fish had equal oxygen consumption rates during the day but that the oxygen consumption rate in fed fish went up at night, thus changing the O:N ratio.

Boehlert asked about the lighting conditions under which the experiments were conducted, to which Sullivan replied that they were all conducted under depressed or night light levels.

Feller asked how the respiration measurements were made. Sullivan described how the fish were held for six days in 65 liter chambers from which oxygen tension was measured by daily-calibrated YSI electrodes; both flow-through and closed systems were used.

Concerning questions about the reproductive patterns of sablefish in Southern California, Sullivan had indications of peak reproduction (gonad development) in August and September, which is considerably earlier than in northern latitudes. Others (Cailliet) suggested that the southern California population may not be representative of the other (northern) populations, particularly relative to age-specific birth rates and growth.

Questions Following Boehlert's Presentation:

Chapman asked if fish adapt to temperatures or are they forced by temperatures to do what they do. Boehlert suggested that often we are observing fish utilize temperature as an ecological resource, i.e. some species such as Sebastes melanops may need higher temperature to effectively grow. In situations where reverse thermal regimes exist, i.e. with Atlantic mehaden, the energetic adaptations may affect different growth responses.

Crowder asked Boehlert if he had looked at either preference or growth as a function of the ration provided, citing evidence that as the ration available is reduced the temperature preference declines and retracts the optimal temperature for growth. Boehlert illustrated that, compared to larger fish, small fish appeared to be at a bioenergetic disadvantage at reduced ration levels but that was the only effect examined.

Norton asked if there were any data generated on the temperatures of peak digestive efficiency for different size classes of fish. Boehlert replied that such data are not available.

Chess asked if there was any obvious change in distribution of juveniles during spring upwelling, to which Boehlert replied that juveniles can be found in tidepools and estuaries under cold water upwelling conditions but that temperatures are usually quite variable in those habitats or the fish occurrence is similarly variable.

Asked by Singer if there were any data on changes with diet with age, Boehlert suggested that there are probably no significant diet changes which could impact growth.

Lea asked how far offshore Boehlert has found pre-migrating juvenile Sebastes diplopnoa, to which Boehlert replied that they have found them as far as they have sampled; other evidence (Hunter, Mitchell, Hubbs) has suggested that they may extend 50 km offshore, particularly in association with drift kelp.

No questions were recorded after the Pandian paper was read by Bob Feller.

General Discussion of Energetics

Boehlert introduced the general discussion by describing the new ground broken by the papers presented in this session, especially considering the diversity of fish taxa and habitats covered.

La Bolle asked Robison if he had any mechanisms in mind that accounted for the inverse relationship between assimilation efficiency and prey quality, to which Robison replied that there were distinct differences in digestive tract morphology which affected stomach and intestine surface area and indications, through based upon insufficient data, of longer retention time. Enzymatic differences and their relationship to assimilation efficiency of midwater fishes feeding on different prey taxa is presently being pursued by Robison's colleagues.

Van Blaricom asked Robison if there was any relationship between degree of herbivory and length of gut, to which Robison responded affirmatively, citing the dramatic differences between two species of Ceratoscopelus, one of which has an intestine at least half again longer than the other. Van Blaricom also asked if there was any indication of reingestion of the bioluminescent feces in the fish stomach contents. Robison replied that although he has not seen any indication of it, there are strong arguments for this hypothesis from the standpoint of selection of the bacteria against sinking out of the water column.

Given the digestion efficiencies of 10-20% for freshwater fishes, Rice asked why Robison's measures of marine midwater efficiencies were so high. Robison suggested that his values were high but still within the range documented for marine species. M. Crow wondered why Robison's assimilation efficiency values were almost half that documented for other fishes, to which Robison replied that his values (30-40%) fit data generated for other species of midwater fishes and may represent major differences in the bioenergetics of fishes in different habitats.

Concerning the energy flux and fecal matter results, Cailliet asked Robison how confident he was about his sinking rate estimate and why mucus-net or filter feeders wouldn't be able to catch that material. Robison felt confident, considering the number of independent measurements they made from different fish species, that the sinking rate values were real and due primarily to the high density of the fecal material.

Eggers asked why the fecal material would not be collected by sediment traps. Robison explained that the relatively small area sampled by a sediment trap, compared to the sparse and patchy distribution of midwater fishes, appeared to explain why sediment traps would not work.

Feller cautioned that just finding the chlorophyll degradation products in the myctophid fish stomach contents does not necessarily indicate that the fish is herbivorous, since the herbivorous copepods consumed by a fish will contain these digestive by products. Robison replied that he is convinced by the dramatic differences (order of magnitude) between the concentrations of these byproducts in the stomach of the one myctophid species and closely related species in the same assemblage. Feller asked how they might consume the algae and Robison described the diatoms (Rhizoselenia) occur in dense mats at densities of 4-5 mats m^{-3} in open water, increasing in density with depth (data of Alice Aldredge and Mary Silver; UCSB and UCSC, respectively); they appear to be suspended within the watermass. Feller also noted that the bioluminesence in the stomach contents and feces of the midwater planktivorous fishes may originate from bioluminescent prey (copepods). Robison acknowledged that prey may well provide the source of the bioluminescence but that independent bioluminescent bacteria are also available within the water column and could be consumed indirectly.

Chapman asked what percentage of the myctophid species had the diatoms in the stomach contents, to which Robison replied that approximately one third had diatoms in the stomachs. There was no evidence in support of net-feeding or other indirect feeding upon the diatoms based upon the lack of co-occurrence of diatoms in the net collections containing the myctophids with diatoms in their stomach contents.

Boehlert asked if anyone who had done field-oriented sampling on stomachs had any idea how to document the natural variability in rations. Chess observed that in some schooling rockfish it is possible to identify almost exactly the time when they start feeding and observe the variation around this and prey composition. Rowley added to the question by asking if anyone had ideas on how to get at individual variability in stomach contents, since a tacit assumption of nearly all diet studies is that the composition of a fish's stomach contents is representative of the population. Karpov recommended that samples had to be taken over 24 hours just to sort out temporal feeding variation and then sufficient samples had to be taken during peak feeding intensity to sufficiently document individual variability within the population. Simenstad mentioned that the existing data on daily ration illustrates that although considerable variability in ration is evident within individual samples, daily ration estimates generated from 24-hour diel sampling series are usually less variable and only indicate changes in the time of feeding periodicity as a result of light conditions, tides, etc.

Karpov also brought up the problem of sampling design influencing daily ration estimation, citing his attempts to assess daily ration of Pacific mackerel from commercial seine catches over 24 hours where the stomachs never contained anything more than scales.

Given the high proportion of fish with empty stomachs, Chapman attempted to determine how fast individual fish were digesting prey simply by catching and holding fish individually and collecting their feces over consecutive time intervals; this worked until he tried Pacific staghorn sculpins which were feeding on the crab Hemigrapsus and found that after 24 hours they still had as much volume in their stomachs as fish that were caught and killed instantly. La Bolle noted that gut content motility often stops in fishes which are handled or otherwise stressed. Chapman replied that, although that may be true of some fish species, it could hardly be said of staghorn sculpins, which tolerate laboratory manipulations willingly. Sullivan described the use of the variability in feeding rates and growth rates.

Boehlert suggested that it might be appropriate in any future GUTSHOP to include a session on the physiology and biochemistry of digestion in fishes.

Concerning the sample size necessary to measure trophic diversity, M. Crow suggested that measuring stomach content volume or biomass to obtain a daily ration estimate will probably require a lot fewer samples and standard statistical methods for estimating a univariate sample size are appropriate. Boehlert stated that he was more concerned with the variability that there might be on the individual fish level over the longer term, i.e. slow growth characterizing individuals in a population may be more a function of natural variability in individual growth than in food availability. Grossman clarified that use of a food preference or diversity index to ensure that the sample size necessary to tell what a fish is eating at a given time is adequate but should not necessarily be used to address what the daily ration is. Boehlert suggested that while the seasonal variability on a population level is considerable (i.e. Cochran's presentation), the individual variability in growth within the population is seldom addressed. Assuming that, Larson asked if daily growth increments in otoliths could be used to back-calculate growth histories as an indication of individual variation. Boehlert reminded us that you would need to make a number of critical assumptions concerning common physical factors and would best choose early juveniles which had a high probability of growing under identical conditions. Feller asked if fishes didn't always put on daily growth increments regardless of food intake; Boehlert replied that under starvation the fish may cease laying down otoligh layers and even reabsorb calcium carbonate. Ebeling asked why we couldn't just use the Cochran and Rice model to determine daily ration from annual growth, given temperature data. Rice responded by noting that the model in question is based on "average" fish, in that the fish have integrated variations in environmental conditions and consumption over time, and can't really be used to separate out variation in individual growth.

OPEN MICROPHONE SESSION

Seven impromptu presentations occurred during an informal session Monday evening. Following is a list of names of presentors and the subjects of their presentations.

Michael Crow presented a paper with Eric Prince and David Bennett summarizing a study on "food partitioning of rocky-shore fishes in Humbolt Bay, California."

Charles Knechtel discussed "the qualitative sensitivity of some feeding parameters of an age-structured growth and population model of walleye pollock, *Theragra chalcogramma*."

Larry Crowder discussed his studies of "predator-prey interactions in structurally complex habitats."

Mark Hixon summarized some work he has completed since GUTSHOP '78, entitled, "behavioral mechanisms of competition between California surfperches."

Marilyn Varela related her work with the Environmental Protection Agency on "assessment of the ocean disposal option for radioactive wastes" to the need for good studies on the feeding habits and trophic interactions among organisms living in potential ocean disposal sites.

Bruce Robison presented some information on the potential of the underwater deep-sea suit (WASP) to study feeding habits of fishes *in situ*.

In addition to the open microphone session, after the banquet Tuesday night Jay Field narrated a film on the "trophic studies of Alaskan coastal fishes" conducted by he and Rick Rosenthal.

Session III

Competition and Resource Partitioning

SESSION LEADER
Ralph Larson

PARTICIPANTS
Jeffrey Cross
Larry Crowder
Alfred Ebeling
David Laur
Gary Grossman
Peter Moyle
Bruce Herbold
Robert Daniels
James Allen

Resource Partitioning in Three Rocky Intertidal Fish Assemblages

Jeffrey N. Cross
Southern California Coastal Water Research Project

This paper is an investigation into the patterns of resource partitioning in three assemblages of rocky intertidal fishes. I will show first that the functional relationships within the assemblages, ie., patterns of resource utilization, are similar even though the phylogenetic backgrounds and number of species in the assemblages are different. Second I will present evidence that competition for food has played a role in the organization of the assemblages.

Methods

Fishes were collected by hand at low tide from tidepools treated with the anesthetic quinaldine. In Washington and southern California, pools were chosen randomly within vertical strata (upper, mid, and lower intertidal) from the highest pools occupied by fish to the upper subtidal. Data were collected throughout the year for 3.5 years in Washington and 1.0 years in southern California (Cross, 1981, unpubl. data). In France, all pools from as high as possible to as low as possible along a transect laid perpendicular to the water were collected; collections were made during one summer (Gibson, 1972).

Composition of the Assemblages

The assemblages and sources of the data are: Washington (47° N lat; Cross, 1981); northern France (49° N lat; Gibson, 1972; Wheeler, 1969); southern California (33-34° N lat; Cross, unpubl. data). Of the 12 families of intertidal fish in the three assemblages, two families (Gobiesocidae and Cottidae) are shared by all three assemblages, and one family (Blenniidae) is shared by two assemblages (Table 1). Two genera (Gobiesocidae: Gobiesox; Cottidae: Clinocottus) are shared between Washington and southern California.

Table 1. Number of species per family. In parentheses is the number of species that occur emersed beneath rocks at low tide. Washington data from Cross (1981); France data from Gibson (1972) and Wheeler (1969); southern California data from Cross (unpubl.).

Family	Washington	France	California
Gobiesocidae	1(1)	1(1)	1(1)
Gadidae	-	2	-
Sygnathidae	-	1(1)	-
Kyphosidae	-	-	1
Labridae	-	1	-
Clinidae	-	-	2
Blenniidae	-	2(1)	1
Stichaeidae	4(3)	-	-
Pholidae	2(1)	-	-
Gobiidae	-	2(1)	-
Cottidae	8(1)	1	1
Cyclopteridae	1	-	-

While the number of species differs among the assemblages, the proportion of primary residents (species that spend all but their larval life in the intertidal) and secondary residents (species that occur in the intertidal facultatively as adults and/or juveniles, and juveniles of species that occur subtidally as adults) is similar (Table 2). The proportion of beneath-rock species (fishes that occur emersed beneath rocks at low tide) is similar between Washington and France, but lower in southern California (Table 2).

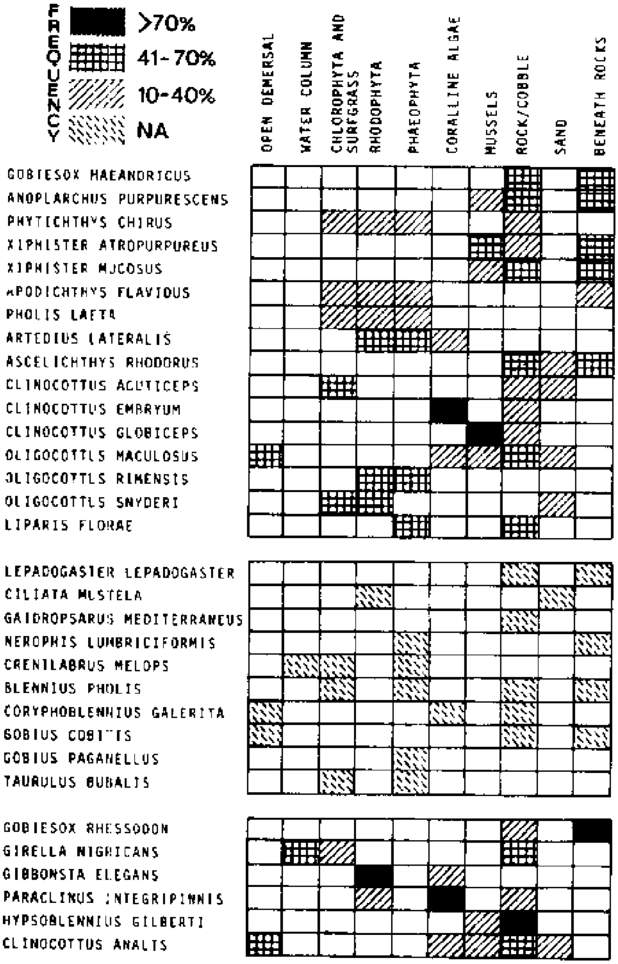
Table 2. Composition of the intertidal fish assemblages (percent of species)

	Washington	France	California
Primary residents	56	60	67
Secondary residents	44	40	33
Beneath-rock species	38	40	17

Microhabitat Separation

Species in each assemblage occupy different microhabitats (Figure 1). Each assemblage is comprised of a few microhabitat generalists (19% of the species in Washington and 17% in California) and more microhabitat specialists. The generalists occur in the widest range of microhabitats, and therefore are more widely distributed and more abundant than the specialists. A corollary of microhabitat specialization is the predictable availability of the microhabitat through time. Suchanek (1979) estimated the life span of mussel (Mytilus californianus) beds on the outer Washington coast to be 8-20 years, or about 4-10 generations of intertidal fish.

The number of species in an assemblage is determined in large part by the presence of absence of particular microhabitats which, in turn, is determined by a complex of environmental and historical factors. For example, fucoids and laminarians are dominant structural features in the intertidal of Washington and France, and several species of fish



FREQUENCY
■ >70%
▦ 41-70%
▨ 10-40%
▧ NA

	OPEN DEMERSAL	WATER COLUMN	CHLOROPHYTA AND SURFGRASS	RHODOPHYTA	PHAEOPHYTA	CORALLINE ALGAE	MUSSELS	ROCK/COBBLE	SAND	BENEATH ROCKS
GOBIESOX MAEANDRICUS								▦		▦
ANOPLARCHUS PURPURESCENS							▨	▦		▦
PHYTICHTHYS CHIRUS			▨	▨	▨			▨		
XIPHISTER ATROPURPUREUS							▦	▨		▦
XIPHISTER MUCOSUS							▨	▦		▦
APODICHTHYS FLAVIDUS			▨	▨	▨					▨
PHOLIS LAETA			▨	▨	▨					
ARTEDIUS LATERALIS				▦	▦	▨				
ASCELICHTHYS RHODORUS								▦	▨	▦
CLINOCOTTUS ACUTICEPS			▦					▨	▨	
CLINOCOTTUS EMBRYUM						■		▨		
CLINOCOTTUS GLOBICEPS							■	▨		
OLIGOCOTTUS MACULOSUS	▦					▨	▨	▦	▨	
OLIGOCOTTUS RIMENSIS				▦	▦					
OLIGOCOTTUS SNYDERI			▦	▦					▨	
LIPARIS FLORAE					▦			▦		
LEPADOGASTER LEPADOGASTER								▧		▧
CILIATA MUSTELA				▧					▧	
GAIDROPSARUS MEDITERRANEUS								▧		
NEROPHIS LUMBRICIFORMIS					▧					▧
CRENILABRUS MELOPS		▧	▧		▧					
BLENNIUS PHOLIS			▧		▧			▧		▧
CORYPHOBLENNIUS GALERITA	▧					▧		▧		
GOBIUS COBITIS	▧							▧		▧
GOBIUS PAGANELLUS					▧					
TAURULUS BUBALIS			▧		▧					
GOBIESOX RHESSODON								▨		■
GIRELLA NIGRICANS		▦	▨					▦		
GIBBONSIA ELEGANS				■		▨				
PARACLINUS INTEGRIPINNIS				▨		■		▨		
HYPSOBLENNIUS GILBERTI							▨	■		
CLINOCOTTUS ANALIS	▦					▨	▨	▦	▨	

Figure 1. Microhabitat separations among fishes in Washington (top), France (middle), and southern California (bottom). Data are frequencies of occurrence. Washington data from Cross (1981), France data from Gibson (1972) and Wheeler (1969), southern California data from Cross (unpubl.). NA = not available.

regularly inhabit them. In southern California, fucoids are small and sparse, and laminarians rarely are present in the intertidal, consequently the brown algal microhabitat does not exist (Figure 1).

Historical differences between assemblages account for some of the differences in microhabitats occupied. For example, there is one laterally compressed, water-column species in the France and California assemblages, but none in the Washington assemblage (Figure 1). The water-column species are from families with tropical affinities (Labridae and Kyphosidae); in fact, the France and southern California assemblages are dominated by species with tropical affinities (60% and 83% of the species respectively) while the Washington assemblage is dominated by species with boreal affinities (94%). The abundance of small, laterally compressed fishes on tropical coral reefs compared with boreal rock reefs may account for the absence of such fishes in the boreal intertidal fauna.

Food Separations

The general food habit patterns of the fishes are similar in the three assemblages (Table 3). Most of the fishes are rather generalized in the foods they consume, although some specializations do exist (Figure 2). Nearly all of the species in each assemblage eat amphipods and isopods, but only a few species eat molluscs and algae. Dentary specializations are required to capture and consume molluscs, and digestive specializations are required to process algae, but relatively unspecialized dentition is required to capture isopods and amphipods.

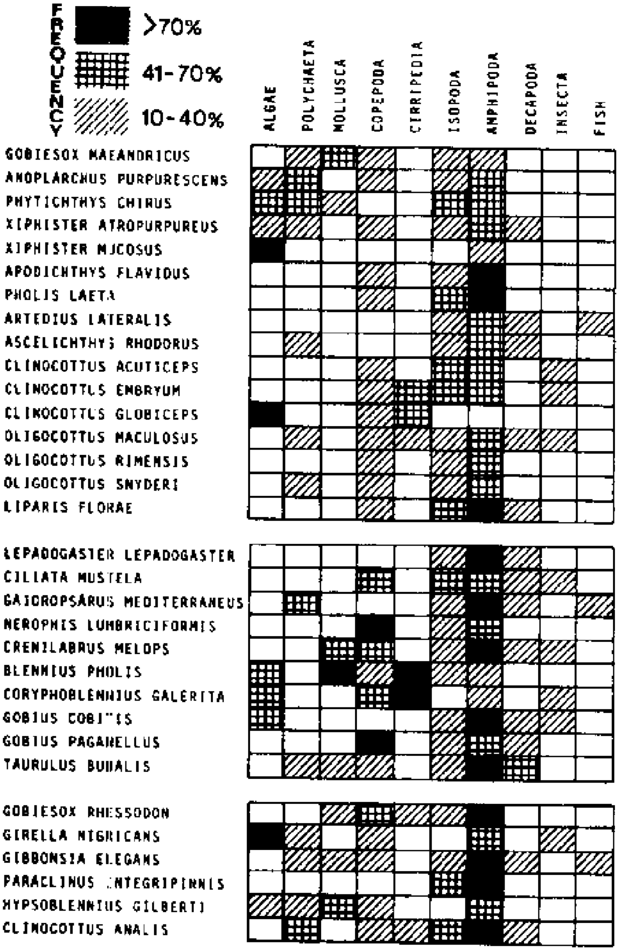
Table 3. Distribution of feeding types. Data are percent of species in feeding categories based on frequency of occurrence of food in the diets.

	Washington	France	California
Carnivores	69	70	67
Omnivores	31	30	33
Carnivores			
Primarily crustaceans	44	40	17
Crustaceans + molluscs + polychaetes	25	30	51
Omnivores			
Algae 50% of diet	19	20	17
Algae 50% of diet	13	10	17

Behavioral Adaptations

In addition to similarities in how they partition resources, members of the three assemblages possess similar behavioral adaptations. On flood tides, several intertidal fishes leave the tidepools and follow the rising water [Washington: *Oligocottus maculosus* (Cross, 1981); France: *Blennius pholis* and *Coryphoblennius galerita* (Gibson, 1972); California: *Clinocottus analis* (Williams, 1957)]. The fish feed on emerging invertebrates during this tidal migration thereby taking advantage of a temporally predictable increase in food availability (Cross, 1981).

Homing behavior has been demonstrated for fish in each assemblage [Washington: *O. maculosus* and *Clinocottus globiceps* (Green, 1971, 1973); France: *B. pholis* (Gibson, 1967); California: *C. analis* (Williams, 1957) and *Hypsoblennius gilberti* (Stephens et al., 1970)]. Because intertidal fish move over a restricted home range (Gibson, 1967; Richkus, 1978), they "know" several pools where they can find shelter at low tide. Homing is advantageous to fish that stray from their pools to feed at high tide; it is also advantageous in an environment where unpredictable changes in habitat suitability can occur over short periods of time.



FREQUENCY
■ >70%
▦ 41-70%
▨ 10-40%

	ALGAE	POLYCHAETA	MOLLUSCA	COPEPODA	CIRRIPEDIA	ISOPODA	AMPHIPODA	DECAPODA	INSECTA	FISH
GOBIESOX MAEANDRICUS		▨	▦	▨		▨	▨			
ANOPLARCHUS PURPURESCENS	▨	▦		▨		▨	▦			
PHYTICHTHYS CHIRUS	▦	▦	▨			▦	▦			
XIPHISTER ATROPURPUREUS	▨	▨		▨		▨	▦	▨		
XIPHISTER MUCOSUS	■						▨			
APODICHTHYS FLAVIDUS				▨		▨	■			
PHOLIS LAETA				▨		▦	■			
ARTEDIUS LATERALIS						▨	▦	▨		▨
ASCELICHTHYS RHODORUS		▨				▨	▦	▨		
CLINOCOTTUS ACUTICEPS				▨		▦	▦		▨	
CLINOCOTTUS EMBRYUM				▨	▦	▦	▦		▨	
CLINOCOTTUS GLOBICEPS	■			▨	▦					
OLIGOCOTTUS MACULOSUS		▨		▨	▨	▨	▦	▨	▨	
OLIGOCOTTUS RIMENSIS				▨		▨	▦			
OLIGOCOTTUS SNYDERI		▨		▨		▨	▦			
LIPARIS FLORAE				▨		▦	■	▨		

	ALGAE	POLYCHAETA	MOLLUSCA	COPEPODA	CIRRIPEDIA	ISOPODA	AMPHIPODA	DECAPODA	INSECTA	FISH
LEPADOGASTER LEPADOGASTER						▨	■	▨		
CILIATA MUSTELA				▦		▦	▦	▨	▨	
GAIDROPSARUS MEDITERRANEUS		▦				▨	■	▨		▨
NEROPHIS LUMBRICIFORMIS				■		▨	▦			
CRENILABRUS MELOPS			▦	▦		▨	■	▨	▨	
BLENNIUS PHOLIS	▦		■	▨	■	▨	▨			
CORYPHOBLENNIUS GALERITA	▦			▦	■		▨		▨	
GOBIUS COBITIS	▦					▨	■	▨	▨	
GOBIUS PAGANELLUS				■		▨	▦	▨		
TAURULUS BUBALIS		▨	▨	▨		▨	■	▦		

	ALGAE	POLYCHAETA	MOLLUSCA	COPEPODA	CIRRIPEDIA	ISOPODA	AMPHIPODA	DECAPODA	INSECTA	FISH
GOBIESOX RHESSODON			▨	▦	▨	▨	■			
GIRELLA NIGRICANS	■	▨		▨			▦		▨	
GIBBONSIA ELEGANS		▨	▨	▨		▨	■	▨		▨
PARACLINUS INTEGRIPINNIS						▦	■			
HYPSOBLENNIUS GILBERTI	▨	▨	▦	▨			▦			
CLINOCOTTUS ANALIS		▦		▨	▨	▦	■	▨		

Figure 2. Food habit separations among fishes in Washington (top), France (middle), and southern California (bottom). Data are frequencies of occurrence. Washington data from Cross (1981), France data from Gibson (1972), southern California data from Cross (unpubl.).

Most intertidal fish are not territorial outside of the reproductive season. Threat displays have been observed in laboratory experiments with stichaeids (J. Jones, pers. comm.), but field and laboratory observations suggest that most species are not territorial (Stephens et al., 1970; Cross, 1981).

Evidence for Competition

The similarities in functional organization among the intertidal fish assemblages suggest a common organizing mechanism. I will present evidence that competition for food has played a significant role in the organization of rocky intertidal fish assemblages.

The most convincing demonstrations of competition are controlled experiments *in situ* (Connell, 1975). The investigator determines the nature of the limiting resource and the potential competitors, and then devises a series of experiments wherein the abundance of the resources and/or competitors are altered, and the consequences are monitored. Experiments such as these work well in systems where the competitors or the resources are sessile or only slightly mobile (e.g. Paine, 1974; Connell, 1975), and have been used productively in fish assemblages where individuals are relatively large and territorial (e.g. Larson, 1980). Intertidal fish assemblages, on the other hand, are comprised of large numbers of small fishes (100 m^2 of rocky intertidal in Washington contains 400-500 fish) that are not territorial, but are highly mobile. Consequently I have relied on indirect methods (natural "experiments" and conformance to model predictions) that are less conclusive. The evidence for competition comes from the Washington assemblage and consists of habitat shifts, reductions in niche breadth with increasing species richness, and complementarity in habitat and food overlap.

In the Washington assemblage, shifts in the vertical distribution of the three most widely distributed fishes (all habitat generalists) were observed with changes in the total number of species found at a site (Figure 3). At sites where the total number of species was low, the three habitat generalists were found from the intertidal well down into the subtidal. As the number of intertidal and subtidal species increased, the lower vertical limit of the three generalists advanced upwards into the intertidal. The addition of suitable microhabitats probably allowed the existence of additional species, assuming that the generalists could have also occupied the additional habitats. Thus I infer that the distributional shifts were due to competitive displacement by more efficient specialists.-

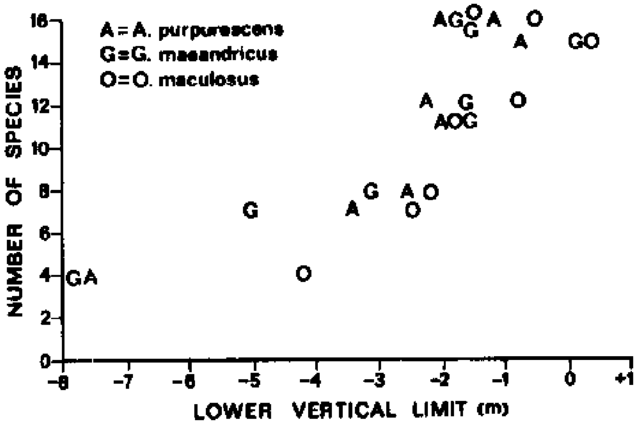


Figure 3. Lower vertical limit of the core species in the Washington assemblage as a function of the number of species at the site.

Decreasing species numbers were also accompanied by increasing microhabitat niche breadths but not food niche breadths. Microhabitat and food niche breadths in the Washington assemblage were measured by:

$$B_s=1/\sum_{k}^{m}(d_{ik}/f_k)^2$$

where k=1,...,m resources, d is the proportion of resource k utilized by species i, and f is the proportion of resource k in the environment. The proportion of each microhabitat in the environment was determined from all collections combined; prey proportions in the envrionment were not determined so f_k was dropped from the equation. As the number of species in the assemblage decreased, microhabitat niche breadth increased (mean increase = 35%, SD = 33, n = 12) while food niche breadth remained about the same (mean increase = 8%, SD = 46, n = 9) (Figure 4). The large microhabitat niche breadth SD was the result of three species whose niche breadth increased more than 70%. The large food niche breadth SD was the result of two species whose niche breadth increased by more than 70%; these species were secondary residents and were more abundant on beaches with fewer species.

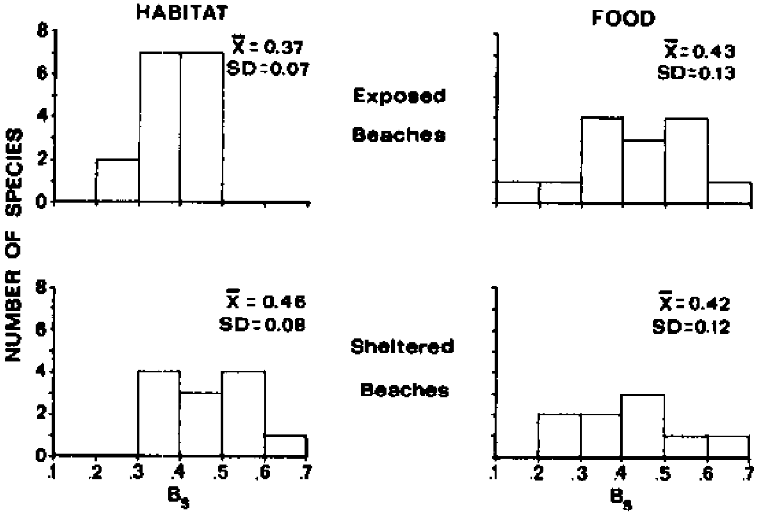


Figure 4. Frequency distribution of microhabitat and food niche breadths of intertidal fishes in the Washington assemblage from exposed beaches (16 species) and sheltered beaches (10-12 species).

Overlap in microhabitat and food resource utilization among the fishes in the Washington assemblage was examined for niche complementarity. Microhabitat overlap was measured by:

$$S_{ij}=\sum_{k}^{m}[W_{ik}(q_{ijk}/q_{ik})] \quad \text{and} \quad S_{ji}=\sum_{k}^{m}[W_{jk}(q_{ijk}/q_{jk})]$$

where S_{ij} is the overlap of species i by species j calculated over k=1,...,m depth strata, q_{ijk} is the number of joint occurences of species i and j in the k^{th} stratum, q_{ik} is the number of occurrences of species i in the k^{th} stratum, and W_{ik} is the relative importance of the k^{th} stratum to the i^{th} species (determined by the proportion of the total density occurring in the k^{th} stratum) such that $\sum_k^m W_{ik}=1.0$ (Cross, 1981). Food overlap was calculated by:

$$A_{ij}=\sum_k^m p_{ik}p_{jk}/\sum_k^m p_{ik}^2 \quad \text{and} \quad A_{ji}=\sum_k^m p_{jk}p_{ik}/\sum_k^m p_{jk}^2$$

where A_{ij} is the overlap of species i by species j, p_{ik} is the proportion of resource k=1,...,m utilized by species i. S_{ij} and A_{ij} are asymmetric, that is, they give two values for each species pair. In general, there were few instances of high microhabitat overlap and high food overlap, and separations between species were greater along the microhabitat dimension than along the food dimension (Figure 5). Several species pairs had low overlaps in both dimensions; these consisted mainly of primary residents that occurred high in the intertidal and ate small crustaceans, and secondary residents that occurred low in the intertidal and ate a variety of foods, especially polychaetes and algae.

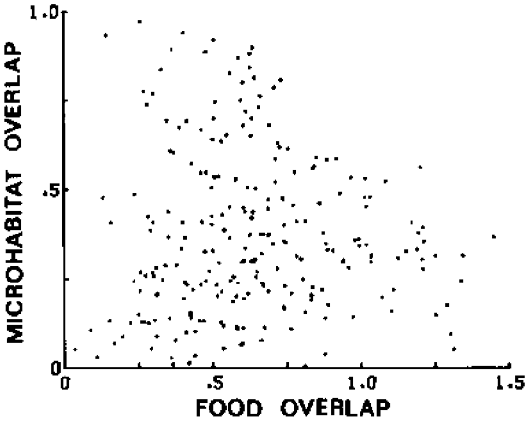


Figure 5. Microhabitat overlap versus food overlap of the intertidal fishes in the Washington assemblage.

Discussion

The intertidal fish assemblages from Washington, France, and southern California exhibit a similar functional organization and, I suggest, have a common organizing mechanism. While the number of species varies among the assemblages, the basic organization consists of a few core species (primary residents) which, in Washington and California, are the most abundant and widely distributed species and have the most generalized diets. They are joined by several microhabitat and, to a lesser extent, food specialists (also primary residents). These two groups dominate the intertidal fish assemblages in Washington and California (approximately 80% of the individuals collected). The remainder of the assemblage is comprised of secondary residents that tend to be specialized in one or more ways. For example, in Washington, one of the secondary residents is a large, solitary ambush predator and two others have the smallest mouths in the assemblage.

Microhabitat and food separations among species in the intertidal fish assemblages could have arisen in sympatry or in allopatry. In sympatry, competition for food would have resulted in microhabitat separations as predicted by optimal foraging theory. In allopatry, niche differences among species would have arisen independently and, when the species became sympatric, the differences would have reduced competition. Since little is known about the evolutionary histories of intertidal fish assemblages, I cannot confidently state that competition for food is responsible for all of the observed niche differences, but the evidence supports the hypothesis that competition for food is responsible for at least some of the separations observed.

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Species Interactions and Community Structure Of Fishes in Lake Michigan

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Introduction

The Lake Michigan fish community has been subjected to a series of manipulations (mostly unintentional) over the past half century which serve as experiments on fish community structure (Smith 1970, Wells and McLain 1973, Christie 1974). Alewives (*Alosa pseudoharengus*) invaded the lake in 1949, uncontrolled by predators, which had been decimated by another exotic species (sea lamprey, *Petromyzon marinus*). Native planktivores declined during the increase of alewife and rainbow smelt (*Osmerus mordax*) which was introduced to Crystal Lake, Michigan in 1912 and subsequently made its way into Lake Michigan. Competition with alewife or rainbow smelt is often assumed to be the mechanism behind these declines, although predation on eggs and larvae also may have contributed to the decline of native species (Smith 1970, Wells and McLain 1973). Once sea lamprey populations were reduced by use of a selective toxicant for ammocetes, piscivores were restocked, beginning in 1965 (Wells and McLain 1973). The results of this series of manipulations may be helpful in interpreting observed fish community dynamics and in inferring mechanisms which underlie those changes.

Resource Use and Competition in Adult Fish

Resource partitioning has often been attributed to competition (Schoener 1974), although predation and other interactions certainly influence resource use. Habitat partitioning is common in fish communities (Sale 1979). Food resource partitioning is probably less common, but it also occurs in fish communities (Werner 1979). Most resource partitioning studies of freshwater fish communities have involved small streams and lakes in which physical structure of the habitat provides a template for habitat partitioning. In larger-scale pelagic systems, temperature may provide this template. In addition, temperature drives physiological rates and thus has important consequences for survival and growth of fishes (Kitchell et al. 1977).

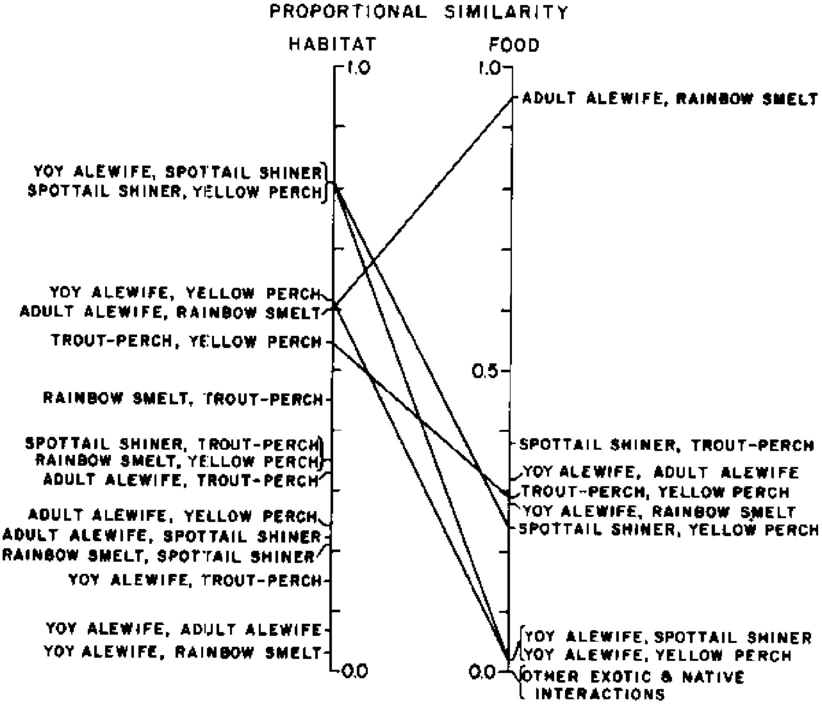

Figure 1. Daytime proportional similarity in food and thermal habitat use by Lake Michigan fishes taken in bottom trawls off Grand Haven, Michigan, September 1977. (Details in Crowder et al. 1981).

We have documented that common adult fishes in Lake Michigan partition the available thermal habitat in a zone where the thermocline intersects the lake bottom (Brandt et al. 1980). In early September 1977, alewife, rainbow smelt, spottail shiner (*Notropis hudsonius*) and trout-perch (*Percopsis omiscomaycus*) segregated along temperature gradients. Most species occupied thermal habitats near their laboratory preferred temperature. Dietary studies of these fishes showed that food use was complementary to thermal habitat use (Figure 1, Crowder et al. 1981). Adult alewife and rainbow smelt had similar diets but occupied different thermal habitats. Young-of-year alewife, spottail shiner and yellow perch used similar habitats, but fed on different prey. These observations are consistent with the idea that competition is important in regulating resource use in adult fishes.

We repeated this survey in 1979, following the increase of a native cisco, bloater (*Coregonus hoyi*). Bloater increased from 0.3% of the catch in 1977 to 41.7% of the trawl catch in 1979. Bloaters were the most abundant species between the 5 C and 16 C isotherms in 1979. Adult alewife have shifted their thermal distribution from near preferred 11-16 C on 1977 to colder 4-8 C in 1979 (Figure 2, Crowder and Magnuson ms.). This shift may have been caused by competition for food or thermal habitat or by predation from salmonid predators. Since

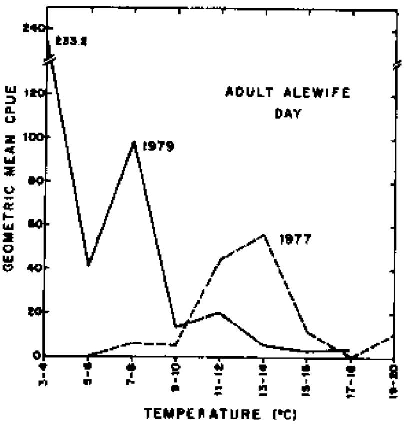

Figure 2. Thermal habitat shift of adult alewife between 1977 and 1979. Fish abundance (geometric mean catch per unit effort) is plotted vs. 2 C temperature strata.

total catch of alewife was not reduced in 1979, and since predation intensity by salmonids did not change drastically between 1977 and 1979 (Stewart et al. 1981), we favor the hypothesis that the altered thermal distribution of alewife resulted from competitive interactions with bloater (Crowder and Magnuson ms.).

Bloaters increased dramatically in the presence of abundant alewives and apparently displaced alewife to a less preferred thermal habitat (Crowder and Magnuson ms.). These observations suggest that the interaction leading to the initial decline of native species was more complex than simple competitive dominance by alewife. Based on available diet data (cf. Crowder et al. 1981), competition is possible at all life stages if resources become limiting. Because adult fish segregate based on thermal habitat, they may avoid direct competition. Young-of-year alewife, bloater and rainbow smelt may occupy similar habitats and consume similar foods (Crowder, unpublished data). It is possible, then, that competition is important at this stage.

Interactions: When and How?

The decline of native fishes during the increase of alewife has often been attributed to competition, though predation has also been suggested (Smith 1970, Wells and McLain 1973). Whatever mechanism we propose to explain these declines should also be consistent with more recent observations, e.g., the bloater increase and the alewife habitat shift.

It is possible that predation by alewife and rainbow smelt on eggs and larvae of native species contributed to their decline (Crowder 1980). Of 21 fish species common in Lake Michigan prior to the invasions of alewife and rainbow smelt, 10 species have pelagic or semi-pelagic eggs or larvae (Balon 1975). After the increase of alewife and smelt, only one of these species, bloater, remained abundant. Pelagic eggs and larvae are obviously more available than demersal ones to pelagic predators such as alewife and rainbow smelt. The eggs of the species which declined are certainly large enough and energetically profitable enough to be included in the diets of alewife and smelt, especially if food were somewhat limited (Crowder 1980).

Emerald shiner (Notropis atherinoides) was probably most affected by alewife predation. Abundant in southern Lake Michigan until about 1960, emerald shiners showed a rapid decline as alewives increased. A congener, spottail shiner, with similar feeding habits, size, predators and distribution has not disappeared, but it spawns over sand and has small, adhesive, demersal eggs (Balon 1975). Emerald shiner has not yet recovered in the open lake.

If alewives were superior competitors during their increase in the 1960s, why is that apparently not true in the late 1970s? What differences in the Lake Michigan system might explain both the apparent alewife dominance in the 1960s and the increase in native species in the late 1970s?

Janssen (1976, 1978) has studied extensively the behavior of alewife and bloater feeding on zooplankton. Both species exhibit non-selective gulping (taking multiple prey) and size selective particulate feeding modes. Alewives can also filter non-selectively. Janssen (1978) argued that while alewives may have an advantage due to a broader feeding repertoire, bloaters are more efficient at feeding near the bottom.

We recently quantified the costs and benefits of feeding on various sizes of prey by alewife and bloater (Crowder and Binkowski ms.). We derived cost curves (sensu Werner 1977) for particulate feeding alewife and bloater and for alewife using all three feeding modes (particulate, gulping, filtering). Costs are lowest for the largest prey normally available in the open lake: Mysis relicta. Costs increase dramatically for small prey. However, if the alewife cost curve is adjusted for shifts in feeding mode as observed by Janssen (1976), the relative costs of feeding on small prey were much reduced (Figure 3). These cost curves indicate that young-of-year alewives would experience much lower costs on small prey (<0.3 mg, ~1.7 mm Daphnia).

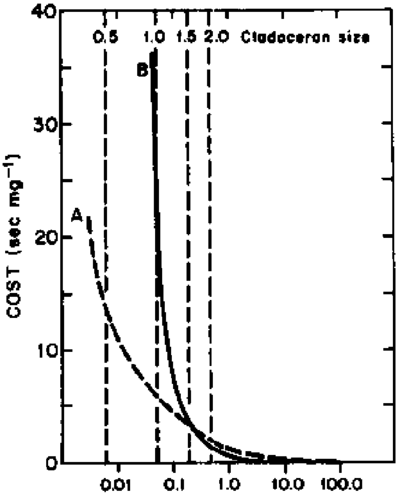

Figure 3. Cost-benefit curves for 5 g young-of-year alewife (A) and bloater (B) assuming all feeding modes are possible for young-of-year alewife. Approximate prey weights for Daphnia are noted with vertical lines for 2.0, 1.5, 1.0, 0.5 mm individuals.

If prey sizes were skewed toward small prey as in the mid 1960s (Wells 1970), young-of-year alewife would have a distinct advantage over bloater due to their ability to filter these prey profitably. This could have contributed to the decline of native species in the 1960s as alewife increased owing to the absence of large piscivores (Wells and McLain 1973). Abundant young and adult alewives probably reduced the average zooplankton size and thus shifted the competitive balance toward alewife.

Subsequent to the stocking of predatory salmonids, which probably consume a substantial portion of the annual alewife production (Stewart et al. 1981), alewife populations have declined, zooplankton sizes have increased over those in the mid 1960s (Wells 1970, Gitter and Crowder, unpublished data) and several native species have increased, including bloater (Crowder and Magnuson ms.).

As long as stocked salmonids reduce planktivore densities and thus permit the maintenance of large zooplankton, native species may compete well with alewife. Intense competitive interactions between alewife and native species are possible but the competitive advantage may well be based on relative foraging abilities which are dependent on the size frequency distribution of available prey. Intensity of competition is also dependent, of course, on the extent to which resources are limiting. Other factors, such as weather or predation on eggs and larvae, may help determine year class strength of Lake Michigan fishes, but these mechanisms are poorly documented at present. The hypothesis of shifting competitive balance may explain the sort of complementary dynamics often seen among Lake Michigan planktivores.

Ontogeny and Resource Partitioning

Unlike many birds and mammals from which the early generalizations and hypotheses regarding competition and resource partitioning were derived (Schoener 1974), fishes do not enter the competitive arena at near adult size. As fishes grow and develop, their diet and habitat preferences shift. Small fishes may experience intense competition with larger fishes and those interactions may well be asymmetrical, favoring large fishes. These interactions may thus create "competitive bottlenecks" for small fishes which result from both intra and interspecific effects (Werner 1979).

Of course, small fishes are also subject to predation by larger fishes including conspecifics. If competition reduces growth rates, then predation effects would likely increase since young fish remain in a vulnerable size range for a longer period of time.

These observations suggest that increasing emphasis must be placed on species interactions and on the early life history of fishes (cf. Steele et al. 1980). Competition probably regulates resource subdivision among adult fishes, but relative abundance of fishes is probably determined earlier in the life history.

Young fishes (larvae and juveniles) may be highly influenced by physical factors, such as weather, as well as predation and competition. Even in the intensively studied northern anchovy (Engraulis mordax), it is difficult to be certain just what rites of passage face potential recruits (Hunter 1980). Ecological theory regarding interactions in size-structured communities is essentially lacking, though optimal foraging theory (Werner 1979) may provide a good start toward interpreting these interactions.

Acknowledgments

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Does Resource Partitioning Have A Descriptive Null Hypothesis?

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Introduction

In the strict sense, "resource partitioning" by members of a feeding guild of fishes implies that the species actively divide up food and/or foraging space, either as a result of coevolved fixed traits or as shifts in usage in direct response to the presence of others (e.g. Schoener, 1974; Benson, 1978). Consequently, the members' diets, feeding behaviors, and/or foraging spaces differ descriptively. The members may have diverged in either or both of two ways to reduce competitive interactions: shifting to different parts of the available resource spectrum and narrowing their choice of items (Abrams, 1981). How are such shifts and specializations that reduce competition in coevolved species distinguished from differences resulting from chance divergences in species that have evolved independently?

All descriptive studies of which we are aware indicate that members of fish guilds differ in diet and/or microhabitat preference. It seems unlikely, in fact, that different species would ever have identical patterns of resource use. Hence, we need an objective method by which to accept or reject the null hypothesis that chance explains the observed differences.

Does resource partitioning have a descriptive null hypothesis? Several have tried to create one by randomizing the degree of resource overlap among guild members to form "null guilds" (Sale, 1974; Pianka et al., 1979; Joern and Lawlor, 1980; Lawlor, 1980). The average overlap among null guilds is used to indicate the degree of difference among guild members that is expected by chance. Relative to this standard, then, average overlap in diet or foraging space among guild members may be significantly smaller than expected, implying that members may indeed partition resources; significantly larger than expected, implying that they "converge" in resource use; or not significantly different from expected (random), indicating that there is no good reason to believe they do either (Sale, 1974).

However, Abrams (1981) discounted the descriptive concept as a hypothetical "catch 22." An unbiased null hypothesis should be independent of the observed data. For example, Lawlor's (1980) "least realistic" randomization procedure is unbiased because it assumes that any species may use any or all resources in proportions (or, better, electivities) varying from 0 to 1. But there is no good reason to assume that each species could ever exploit all resources equally or exploit any one resource to the exclusion of all others. This compels one to derive null guilds more realistically; they should relate to the observed set of species and not to all possible sets. Herein lies the catch. Realistic procedures, which randomly reorder the observed electivities, are biased because they produce null hypotheses that are not independent of the observed data. They test for resource partitioning by dispersion of resource peaks only, because only the observed electivities are used in the model; they cannot test for partitioning by narrowing of niche span (no. of resource items used). Yet in all likelihood resource partitioning may have resulted in the loss of coexploited items from different diets. Metaphorically, Colwell and Winkler (in press) called this bias the "Narcissus effect" because results of past competition are masked by their own reflection in the present "post-competitive pool."

Abrams (1981) concluded that to obtain evidence of altered patterns of resource exploitation in response to competition, one must determine patterns that would occur if there were no competition. This implies a comparison of species' realized and fundamental niches (Hixon, 1980). Thus the null hypothesis would no longer be descriptive (based on original diets or distributions). Instead it would state that mean overlap among fundamental niches does not differ from that among realized niches. But fundamental niches--the species' potential exploitive abilities in the absence of competitors--are usually unknown, because their measurement requires difficult manipulative experimentation (Hairston, 1980; Connell, 1980) and/or extensive comparative studies of species in areas with and without other guild members (Hixon, 1980; Schmitt and Coyer, unpubl. ms.).

Hence a test for anticompetition (partitioning due to evolution to avoid competition) within a foraging guild of fishes by descriptive null hypothesis requires questionable assumptions that: 1) the "neutral model" creating the standard does in fact properly randomize an indicator of resource partitioning; 2) the species' realized and fundamental niches do not differ in response to competition--i.e. their foraging traits are genetically fixed; and 3) observed resources are the most critical ones and are measurable in a biologically meaningful way.

Laur and Ebeling (unpubl. ms.) provided evidence that assumptions 2 and 3 are reasonable when applied to a feeding guild of 5 epibenthic species of viviparous surfperches (Embiotocidae), which coexist in a semi-isolated area of reef and kelp (Naples Reef) off Santa Barbara, southern California. Relative to assumption 3, all exploit the same forage base of small prey inhabiting a "turf" of attached animals and plants covering much of the reef bottom. Thus turf and the space on which it grows are essential resources, because the fish have few if any other sources of food. Since this forage base is concentrated and circumscribed, it is relatively easily sampled in random fashion. Relative to assumption 2, several studies indicate that the foraging behavior characterizing each of the 5 species does not vary appreciably among geographic localities and habitats (Quast, 1968; DeMartini, 1969; Alevizon, 1975; Ellison et al., 1979; Haldorson and Moser, 1979; Laur and Ebeling, unpubl. ms.; Schmitt and Coyer, unpubl. ms.; D. Stouder, pers. comm.). Hence, there is good reason to believe that their feeding traits are relatively fixed.

Consequently the surfperch guild seems to be an adequate subject for examining resource partitioning from a descriptive viewpoint. The purpose of the present study, therefore, is to investigate assumption 1: that the randomization procedure we used produced a meaningful null hypothesis.

Methods

Dietary overlaps among surfperches were computed from electivity values for 10 "items of food value" (worms, bivalves, amphipods, etc.) determined from gut-contents relative to benthic samples of "turf" (prey "availabilities"). Overlap in foraging space was calculated from electivities for the number of bites that fish took of turf in 5 microhabitat categories (reef crest, slope, flat, etc.) relative to areal extents of these microhabitats (foraging-space "availabilities"). Fish samples were of about 30 adults of each species (Embiotoca jacksoni, E. lateralis, Hypsurus caryi, Rhacochilus toxotes, Damalichthys vacca) speared or observed during spring and summer, 1973; turf samples were of 12 randomly placed quadrats of scrapings collected during the same period (details in Laur and Ebeling, unpubl. ms.).

To construct a null hypothesis, we chose Sale's (1974) method for computing random overlap because it is most realistic (details of method in fig. 1). It preserves the observed pattern of each species' resource use, leaving only the positions of these patterns on the availability spectrum (their degree of overlap) to randomize. Percent volumes of prey items are converted into electivities, which are directly proportional to the percentage use of each resource item if all items (foods, microhabitats) are equally available (Schoener, 1974; Lawlor, 1980). The species' dietary and foraging-space spectra are expanded percentage-wise to 100 items based on an equivalent array of hypothetical "equally-available resources." This process was repeated for all 10 pairs of 5 species to construct a null guild of 10 overlaps between randomly placed species arrays of electivities. Then 100 such guilds were computed; mean overlap was determined for each (fig. 1,$\bar{X}$); and observed overlap was compared with the distribution of means of null guilds in Monte Carlo fashion (Jeorn and Lawlor, 1980).

Results

Relative to the null hypothesis of random overlap, the surfperch guild appeared to converge on resources at Naples Reef, in the sense that most members selected the same prey (e.g., fig. 1, items 5, 6, 7, all amphipods) from the same (richest) microhabitats (Laur and Ebeling, unpubl. ms.). For both diet and foraging space, average observed overlap significantly exceeded random, as indicated by its position well beyond 95% of the averages of 100 null guilds.

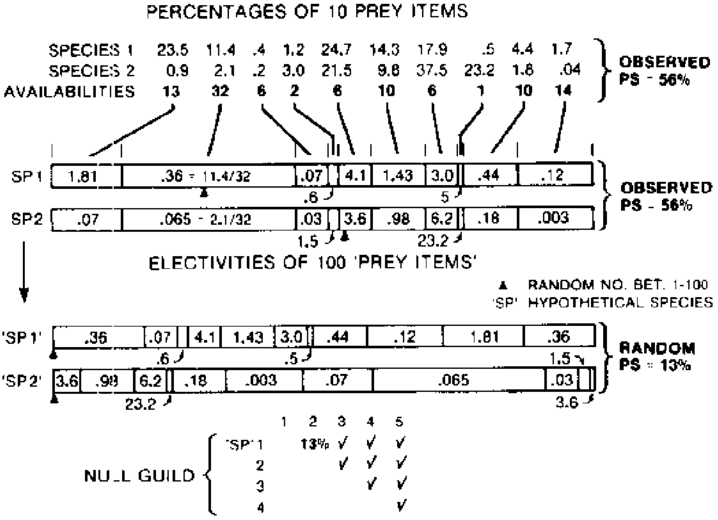

Figure 1. Construction of null guilds of hypothetical surfperches with random dietary overlaps (Sale, 1974), exemplified by observed diets of two species (1,2). As indicated by lines leading from upper columns of numbers to lower rectangles, observed percentages of 10 prey items are converted into electivities of 100 equally-available items by subdividing each (e.g. species 1, second column = 11.4) into the number (32) of equal parts (each = .36) corresponding to the item's availability. The observed overlap (observed PS) is calculated as percent similarity: $\sum_{j=1}^{100}\min(e_{1j},e_{2j})$ where e_{1j} is the jth equal part (electivity) for species 1. From the original arrays of electivities (upper pair of rectangles), hypothetical 'species' are created by choosing an electivity at random (black triangle) for each species and realigning arrays at that point (lower pair of rectangles), and random overlap (random PS) is computed in the same way as observed. Average overlap for a null guild ($\bar{X}$) is obtained from the sum of random overlaps over all 10 pairs of 5 species.

SPECIES 1

A	23.5	11.4	0.4	1.2	24.7	14.3	17.9	0.5	4.4	1.7
B	23.5 +	24.7	11.4	0.4	1.2	14.3 −	17.9	0.5	4.4	1.7
C	37.8	42.5	11.4	0.4	1.2	0	0	0.5	4.4	1.7

SPECIES 2

A	0.8	2.1	0.2	3.0	21.5	9.8	37.5	23.2	1.8	0.04
B	0.8	2.1	37.5 +	23.2	0.2	3.0	21.5 −	9.8	1.8	0.04
C	0.8	2.1	59.0	33.0	0.2	3.0	0	0	1.8	0.04

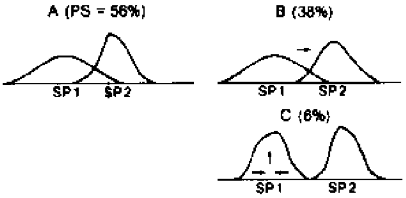

Figure 2. Construction of guilds of hypothetical surfperches with dietary spectra dispersed (B) and then narrowed (C), exemplified by observed diets (A) of two species (1,2). As indicated by arrows between arrays A and B, items with largest percent volumes in gut contents are shifted such that they are juxtaposed within rows (species) but not coincident between rows. After spectra are dispersed (B), diets are narrowed by removing and adding the second largest values (bar, minus, between B and C) to the largest pair (bar, plus) to create array C combining dietary dispersion with specialization. The transformation is depicted by parting but not distorting curves (see text) representing spectra of species 1 and 2 (A to B), which results in a decrease of average percent similarity between the two species from 56% (A1,A2) to 38% (B1,B2); then distorting the parted curves (B to C), which results in a further decrease to but 6% (C1,C2).

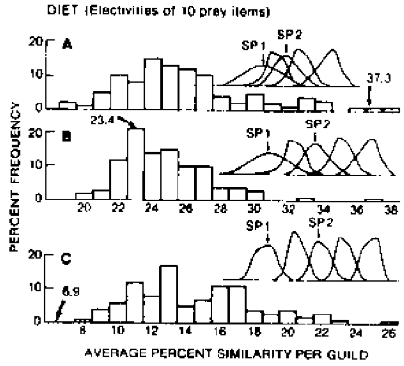

Figure 3. Frequency distributions of average overlaps in diet from 100 null guilds, compared to the observed average (large arrow) of overlaps between all real pairs of surfperches in the guild (A), or between hypothetical pairs whose dietary spectra are altered to represent resource partitioning by dispersion (B) or by dispersion and narrowing (C). Inset curves illustrate the manipulations as exemplified by species 1 and 2 in figure 2.

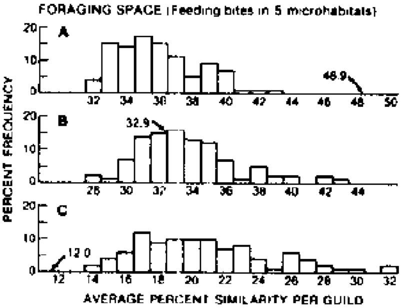

Figure 4. Frequency distributions of average overlaps in foraging space from 100 null guilds, compared to the observed average (large arrow) of overlaps between all real pairs of surfperches in the guild (A) or between hypothetical pairs whose spatial spectra are altered to represent degrees of resource partitioning (B,C) as in figure 3.

Given this observed outcome, therefore, manipulations of the species' arrays of resource usage provided the only means of evaluating the null hypothesis relative to possible outcomes of resource partitioning (details in fig. 2). More or less subjective representations of the observed as well as the two hypothetical outcomes are exemplified as curves of prey usage for species 1 and 2. To simplify, these curves were forced onto a one-dimensional availability spectrum, even though the characteristics of the taxonomically-grouped prey items are multidimensional: size, hardness, distribution (e.g. tube mats for gammarid amphipods, cobbles for crabs and worms, etc.). For the whole guild, this manipulation decreased mean overlap (PS) from the observed 37.3% (fig. 3A) to a hypothetical 23.4% (3B), which simulates partitioning by dispersion of usage only, and further to only 6.9% (3C), which simulates partitioning by specialization as well.

The outcomes were similar when these procedures were applied to foraging space (percentages of total feeding bites taken in different microhabitats). Because microhabitat categories numbered but 5 (compared to 10 prey items), the analogous manipulations were of single values instead of ordered pairs. Even so, decreases of mean overlap in foraging space are of the same order as those for diet: from 48.9% for the observed guild (fig. 4A) to 32.9% for the hypothetical guild simulating partitioning by dispersing usage spectra (4B), and to only 12% for the guild simulating partitioning by dispersing and narrowing spectra (4C).

Discussion

Thus the descriptive null hypothesis may be meaningful if rejected but not if accepted. In addition to the statistical criterion, there is good biological reason to reject the null hypothesis in the real example in favor of the alternative that the surfperches "converge" in resource use. All five species select small prey from turf in most productive microhabitats about the reef crest and slopes. Four of the five species eat mostly gammarid amphipods, and three of the four amphipod-eaters have similar specialized mechanisms for "oral winnowing" and spitting out the amphipod-tube houses and other inedible items (Laur and Ebeling, unpubl. ms.). These three appear to have convergent or parallel adaptations in foraging mode. On the other hand, the manipulation of real guilds to produce hypothetical ones revealed a bias toward accepting the null hypothesis. The statistical model did not distinguish degree of overlap between dispersed spectra with usage peaks positioned at regular intervals from degree of overlap between spectra with peaks positioned at random. Only when specialization was added to dispersion was "observed overlap" significantly less than random.

Besides showing this ambiguity, the descriptive null hypothesis may be partly tautological in that it is generated from observed patterns according to questionable rules of judgement as to what less-structured patterns are (Colwell and Winkler, in press). We only suggest that to completely ignore descriptive outcomes that differ significantly from a reasonably derived random expectation is "throwing out the baby with the bathwater." Such outcomes may be robust. For instance, other lines of evidence substantiate our claim that surfperches with fixed foraging traits do converge on resources at Naples Reef. Instead of diverging in foraging space and/or diet during an extended period of ecological crunch as predicted by partitioning, they have tended to emigrate rather than alter their foraging behavior (our recent observations; D. Stouder, pers. comm.).

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Community Regulation and Patterns Of Resource Partitioning

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Introduction

Since MacArthur's (1958, 1972) and Hutchinson's (1959) seminal work on resource partitioning, many researchers have assumed that this process is the primary mechanism facilitating coexistence in animal assemblages and communities. Numerous empirical studies support this belief (Colwell and Fuentes 1975), including Schoener's (1974) classic review, which demonstrated that species frequently appeared to partition one of three resources: 1) space (i.e. macro - or microhabitat), 2) food, or 3) time of resource utilization (although this can only occur in resources which are non-depletable such as space). These data, combined with considerable, though non-independent, mathematical evidence (MacArthur and Levins 1967; MacArthur 1972; Pielou 1974, 1977; Roughgarden 1979) have enabled the resource partitioning concept to achieve paradigm status (sensu Kuhn 1970) in ecology. Consequently, we now have a large number of completed, in progress, or proposed investigations, whose basic design consists of: 1) an attempt to detect differences in resource utilization patterns of sympatric species, and 2) when differences are found (and they invariably are!) it is generally concluded that such differences are responsible for the coexistence of species within the assemblage. These studies typically last for one or two years and frequently restrict sampling to favorable climatic periods (i.e. late spring, summer, and early autumn). Restricted sampling is not considered to be a problem, however, as an implicit assumption of the resource partitioning paradigm is that communities are at equilibrium (i.e. deterministically regulated, see Grossman 1982). Examples of this approach using stream fish assemblages are: Lotrich (1973) Mendleson (1975), Gorman and Karr (1978) and Baker and Ross (1981), Gatz (1981).

While there can be no doubt that some systems are regulated through resource partitioning (Werner and Hall 1976, 1979; Werner 1977; Brock et al. 1978) the convenience of this paradigm has greatly hindered the acceptance of contrary evidence (Strong et al. 1979; Strong 1980; Sale 1979, 1980; Anderson et al. 1981; Lawton and Strong 1981). In fact, considerable data suggest that coexistence within many animal and plant assemblages is primarily determined by environmental unpredictability, rather than through biologically interactive processes such as resource partitioning (Eggling 1947; Dayton 1971; Sale 1977, 1980; Connell 1978, 1980; Birch 1979; den Boer 1979; Hubbell 1979; Sousa 1979; Grossman 1982; Grossman et al. 1982). If a substantial number of assemblages are strongly affected by environmental stochasticity, then resource partitioning can no longer be viewed as a general mechanism, due to violation of the deterministic assumption (Grossman 1982; Grossman et al. 1982). Consequently, it is necessary to ascertain the processes regulating the structure of an assemblage before any conclusion can be drawn regarding the role of resource partitioning in promoting coexistence (Grossman 1982; Grossman et al. 1982).

It is the purpose of this paper to demonstrate that the resource partitioning paradigm, and its supporting deterministic framework, are incapable of explaining patterns of assemblage and trophic structure observed over a twelve year period in an Indiana stream. The main results of this paper are derived from a more detailed analysis of the effects of stochasticity on structural and functional relationships in stream fish assemblages (Grossman et al. 1982).

Methods

Otter Creek, the stream investigated, was located on an upland-lowland ecotone in Vigo Co., Indiana. The study area consisted of a 120 m long by 23 m wide section of stream located below a small mill dam. The substrate was diverse and consisted of bedrock, rubble, gravel, and in slower areas, sand and silt. This type of habitat is present in many midwestern streams.

Sampling consisted of seining the study site from the lower to upper reaches, until a numerical abundance estimate could be made for each species. To ensure limited bias in collections, one person (J. O Whitaker Jr., Dept. Life Sciences, Indiana State Univ., Terre Haute) supervised all sampling and abundance estimates. A total of 27 collections (four spring, seven summer, and sixteen autumn) were made from 1962-1974. During this time there were no visibly apparent changes in the physiognomic character of the study site. After identification and enumeration, specimens were almost always returned to the stream alive. There is little reason to suspect that sampling had a significant effect on structural or functional relationships within the assemblage (Grossman et al. 1982).

Experimental Design

The resource partitioning paradigm is part of a broader class of ecological theories which can be categorized as deterministic (see Grossman 1982; Grossman et al. 1982). In short, these theories suggest that most assemblages or communities are persistent (i.e. the relative abundances of species comprising the assemblage remain relatively constant). Hence, species must either partition limiting resources or suffer extinction [although other deterministic possibilities occur (Grossman 1982; Grossman et al. 1982) this mechanism is most common]. However, an alternative stochastic theory suggests that assemblages are primarily regulated through stochastic or periodic environmental disturbances (Andrewartha and Birch 1954; Sale 1977, 1980 Connell 1978, 1980; Birch 1979; Lawton and Strong 1981; Grossman 1982; Grossman et al. 1982; Sale and McB. Williams 1982). These purturbations prevent populations from reaching densities at which competition and its consequent, resource partitioning would occur. As a result, species coexistence is not dependent upon the evolution of resource partitioning mechanisms.

These opposing theories make distinct predictions with respect to the stability of assemblage structure. Deterministic theory, as applied to non-successional systems, predicts that assemblage structure will be persistent (Grossman 1982; Grossman et al. 1982) (and this is a necessary condition for resource partitioning studies where limiting resources are not quantified) while stochastic theory predicts that assemblage structure will not be persistent (Grossman 1982; Grossman et al. 1982). I was interested in identifying which model best fit the Otter Creek assemblage and comparing trophic structure patterns with those of assemblage structure. Trophic structure data were examined for two reasons. First, it has been suggested that even if the species composition of assemblages does not stay constant, the trophic structure may remain so (Heatwole and Levins 1972; Moyle and Li 1979). This would produce a deterministically regulated assemblage with respect to trophic organization, even though assemblage structure would appear stochastic. Second, with prior knowledge of the persistence of assemblage structure, I wished to determine whether it would be possible to erroneously classify the assemblage by exclusively using trophic structure data.

To quantify the persistence of assemblage structure I compared the relative abundances of the ten most abundant species from sequential annual collections for a given season. A distribution-free, multisample rank correlation statistic, Kendall's-W was used for significance tests. If an assemblage is persistent, a significant correlation should exist between the relative abundances of species from sequential seasonal collections. If this occurred it would then be appropriate to make inferences regarding coexistence from the resource utilization data. However, the documentation of persistence of trophic structure, would also validate inferences of a coexistence mechanism from resource utilization data. For the test of persistence of trophic structure, species were classified as belonging to one or more trophic groups using published information or unpublished data (see Grossman et al. 1982). Each collection was divided into the percentage comprised by each trophic group and these data were plotted graphically. Due to an inherent inaccuracy in Kendall's-W (i.e. increased chance of Type I error) this statistic was not used for the test of persistence of trophic structure. A visual assessment was used to ascertain whether or not sequential seasonal trophic structures were correlated. A comprehensive discussion of the study site, experimental design and methodology, and statistical procedures is presented in Grossman et al. (1982).

Results

For brevity, only results for Autumn collections are presented here. Results for Spring and Summer collections were identical to those for Autumn (Grossman et al. 1982). The test of assemblage persistence showed that a significant correlation did not occur between Autumn collections from different years (Table 1, $W = .121$, d.f. = 10_r 12_c,

Table 1

Assemblage composition for autumn samples. Data are percent of the community comprised by a species with rank in parentheses. These data are from Grossman et al. (1982).

	11/62	9/63	10 & 11/ 64*	9 & 11/ 65*	9 & 11/ 66*	11/67	9 & 10/ 68*	9/69	9/71	9/72	9/73	9/74
Notropis spilopterus	2 (6)	0 (7)	11 (2)	33 (1)	11 (3)	5 (2)	4 (7)	1 (8)	17 (2)	11 (3)	39 (1)	60 (1)
Pimephales notatus	16 (2)	14 (2)	11 (4)	16 (3)	52 (1)	0 (10)	7 (4.5)	14 (2)	6 (4)	15 (2)	7 (5)	0 (8.5)
Etheostoma blennioides	16 (2)	4 (5)	6 (9)	1 (9)	1 (8)	4 (4)	5 (4.5)	5 (3)	0 (7)	1 (4)	8 (3.5)	2 (3)
Hybognathus nuchalis	0 (9)	0 (9)	0 (10)	7 (5)	2 (7)	2 (6)	18 (2)	7 (4)	42 (1)	23 (1)	4 (6.5)	11 (2)
Notropis atherinoides	0 (9)	0 (9)	8 (3)	17 (2)	0 (10)	73 (1)	28 (1)	1 (8)	7 (3)	0 (10)	8 (3.5)	1 (7)
Notropis chrysocephalus	3 (4)	0 (9)	39 (1)	3 (6)	13 (2)	1 (7)	1 (9)	1 (8)	1 (8)	1 (8.5)	10 (2)	1 (4.5)
Etheostoma caeruleum	16 (2)	4 (5)	1 (8)	2 (8)	2 (9)	3 (5)	16 (3)	17 (1)	3 (6)	2 (6.5)	4 (6.5)	0 (10)
Ericymba buccata	3 (3)	14 (2)	6 (5)	1 (10)	1 (5)	4 (3)	5 (6)	5 (5)	0 (10)	1 (8.5)	0 (9.5)	0 (8.5)
Campostoma anomalum	2 (5)	14 (2)	7 (6)	2 (7)	6 (4)	1 (8)	1 (9)	2 (6)	1 (9)	2 (6.5)	0 (9.5)	1 (4.5)
Notropis umbratilus	0 (9)	4 (5)	4 (7)	5 (4)	3 (6)	1 (9)	1 (9)	0 (10)	4 (5)	3 (5)	1 (8)	1 (6)
Percent of the community made up of the top ten species ($\bar{x}$=76)	59	54	89	88	89	92	84	56	83	64	80	77

*Based on the two samples pooled as including more than one collection per year would increase the chance of Type I error (Grossman et al. 1982).

Table 2

Assignation of species to feeding groups (from Grossman et al. 1982). Included are: 1) seasons of occurrence for species, 2) number of studies utilized in the evaluation, and 3) the quality of the investigations. See Grossman et al. (1982) for further details.

Species	# Studies	Quality of Study	Groups[1] 1	2	3	4	5	6	7	8	Season
Ericymba buccata	5	4			X	X					Sp, Su, Au
Etheostoma blennioides	2	3				X					Sp, Su, Au
Notropis chrysocephalus	8	4								X	Sp, Su, Au
Notropis spilopterus	4	4		X							Sp, Su, Au
Notropis umbratilus	1	3	X								Sp, Su, Au
Sematilus atromaculatus	7	4	X						X		Sp, Su, Au
Etheostoma nigrum	4	3			X	X					Sp, Su
Pimephales notatus	7	4					X				Sp, Su, Au
Etheostoma caeruleum	3	3				X					Sp, Au
Hybognathus uchalis	1	2					X				Su, Au
Hypentelium nigricans	2	1			X		X				Su, Au
Lepomis macrochirus	5	4	X		X	X					Su, Au
Notropis atherinoides	3	4	X								Su, Au
Notropis stamineus	3	3	X								Sp
Etheostoma flabellare	6	4				X	X				Sp
Campostoma ananalum	3	3						X			Su
Noturus miurus	1	3				X		X			Su
Phenacobius mirabilis	2	3			X						Au

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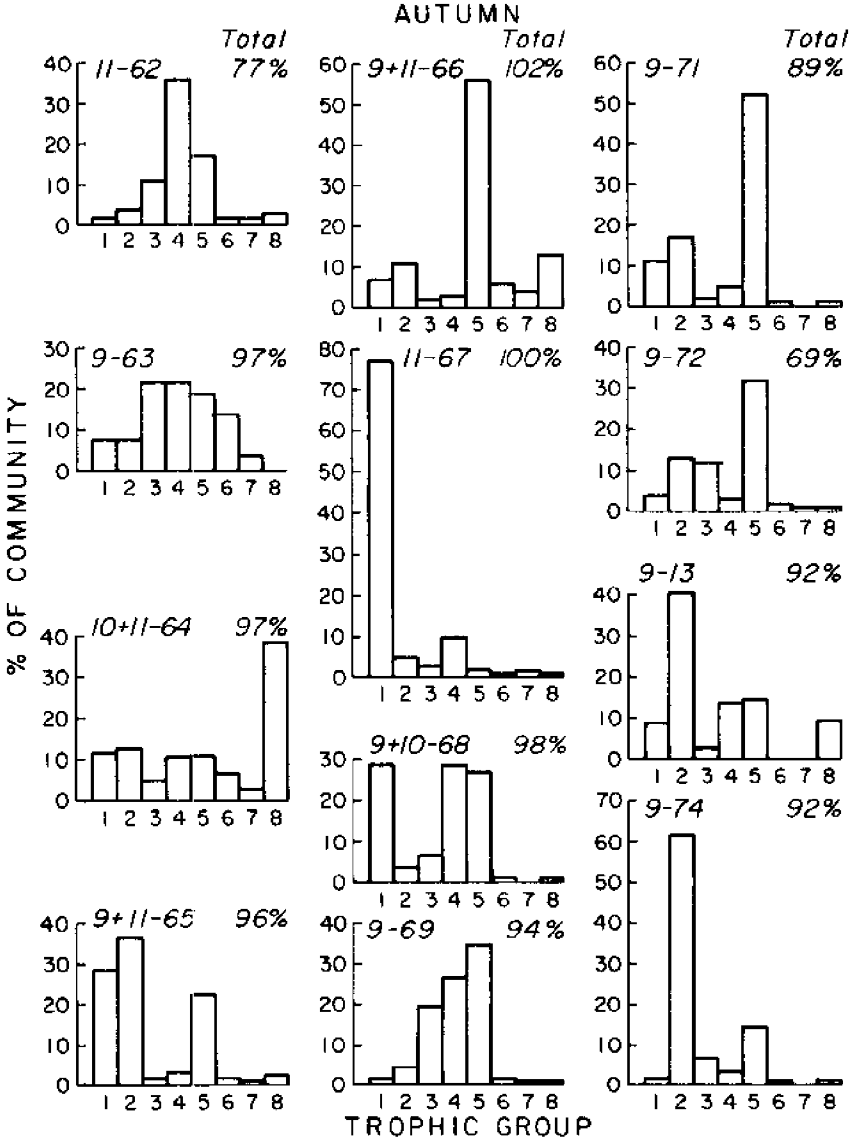
[1] Feeding groups are as follows: (1) Surface feeders, (2) Water column feeders, (3) Small benthos feeders (soft substrate), (4) Small benthos feeders (rocky substrate), (5) Ooze feeders, (6) Algae feeders, (7) Macrocarnivores, (8) Omnivores.

Figure 1: Trophic structure of the Otter Creek fish community for Autumn samples (from Grossman et al. 1982). The percentage of the total community comprised by each trophic group is shown in the histogram. Feeding groups are as follows: 1) surface feeders, 2) water column feeders, 3) small benthos feeders (rocky substrate), 4) small benthos feeders (soft substrate), 5) ooze feeders, 6) algae feeders, 7) macrocarnivores, 8) omnivores. Information on grouping procedures and references used for trophic classification can be found in Grossman et al. (1982).



$.2 > p > .1$). In addition, there was no evidence of multiple equilibria or cycles. This finding is statistically conservative as Kendall's-W is subject to an increased probability of Type I error (Grossman et al. 1982).

Assemblage trophic structure also exhibited no evidence of persistence, multiple equilibria, or cycles (Table 2, Fig. 1). This documents that no conclusions can be reached regarding the role of resource partitioning in the maintenance of assemblage structure. Furthermore, the combined assemblage and trophic structure data imply that resource partitioning plays a negligible role, if any. While this seems unmistakable, it is also clear that if an investigator examined this assemblage's trophic structure in one, two, or even three years, a very different conclusion might be reached. This could occur because almost all feeding groups are present in most samples (Fig. 1). Consequently, a researcher employing the resource partitioning paradigm could easily deduce that this assemblage was regulated through deterministic factors (i.e. resource partitioning), because the coexisting species generally consume different prey (Table 2, Fig. 1). While anomalous years do occur (e.g. 9&11-66, 11-67, 9-71, and 9-74) even these can be explained away; although one species (and as a result one trophic group) dominates the assemblage, the remaining species still rely on distinct food sources (Table 2, Fig. 1). This inexorably documents the dangers inherent in the resource partitioning paradigm.

Discussion

The resource partitioning concept has proven to be a fruitful theoretical construct for much of ecology (MacArthur 1972; Pielou 1974, 1977; Roughgarden 1979). However, this paradigm is sufficiently ambiguous to accommodate most, if not all, sets of resource utilization data, regardless of whether or not resources are actually being partitioned. The results from the Otter Creek fish assemblage demonstrate the following: 1) neither assemblage nor trophic structure were persistent over a 12 year period, and 2) when trophic structure data were viewed alone, it was possible to mistakenly conclude that resource partitioning occurred. These findings are significant because they document violation of deterministic assumptions implicit in the resource partitioning paradigm. While it can be argued that this is a trivial result, peculiar to Otter Creek, this is not the case (Grossman et al. 1982). In fact, many streams appear to be strongly influenced by stochastic factors (Starrett 1951; Larimore 1954; Larimore et al. 1959; Deacon and Minckley 1976; Matthews and Maness 1979; Grossman et al. 1982; Matthews 1982). Thus, it is probably inappropriate to evaluate the role of resource partitioning in the maintenance of assemblage structure without first demonstrating that deterministic regulation occurred. This result may be applicable to other stream taxa (Grossman et al. 1982) as several studies of macroinvertebrates also document a paucity of community-level responses to environmental factors Resh et al. 1975; Friberg et al. 1977; Reice 1980; Grossman et al. 1982).

In descriptive studies of assemblage regulation it is necessary to establish that: 1) the study site either represented a random sample of an assemblage or comprised an entire assemblage, and 2) the time of the investigation was sufficient to detect the effects of bouts of episodic recruitment and catastrophic mortality (Davis and VanBlaricom 1973; Dayton and Oliver 1979). To satisfy the first prerequisite; life history studies by many workers strongly imply that most assemblage members would have spent the majority of their lives within the 120 m by 23 m study site (Grossman et al. 1982). Hence, the study site adequately delimited an assemblage (Grossman 1982). Secondly, with respect to time scale, the twelve year study period was three to four times the mean lifespan of assemblage members (Grossman et al. 1982). Consequently, if episodic recruitment or mortality played a major role in the dynamics of this assemblage it would have been included in our investigation.

The purpose of this paper is to illustrate the inadequacy of deterministic theory, and the resource partitioning paradigm in particular, in interpreting assemblage and trophic structure relationships in an Indiana stream fish assemblage. Such a demonstration is made necessary by investigators who imply that stream fish assemblages are regulated deterministically (Sheldon 1968; Zaret and Rand 1971; Lotrich 1973; Mendelson 1975; Gorman and Karr 1978; Page and Schemske 1978; Gatz 1979, 1981; Baker and Ross 1981). In virtually all of these cases, inferential rather than direct tests of assemblage regulation were utilized. As previously noted, such inferences are not logically valid (Grossman 1982; Grossman et al. 1982). The partitioning observed in these studies may merely represent anatomical, behavioral or physiological, evolutionary constraints which do not involve inter-specific competition (Li 1975; Gould and Lewontin 1979). While short term (one-two year) resource utilization studies can quantify how resources are utilized within assemblages, it is my contention that extrapolation from such data to a mechanism of community regulation is inappropriate. Similar conclusions have been reached by other investigators for related areas of ecological and evolutionary theory (Dayton 1973; Connell 1975, 1978, 1980; Peters 1976; Conner and Simberloff 1979; Dayton and Oliver 1979; Gould and Lewontin 1979; Strong et al. 1979; Levins and Lewontin 1980; Simberloff 1980; Strong 1980; Lawton and Strong 1981; Grossman 1982; Grossman et al. 1982; Sale and McB. Williams 1982).

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Resource Partitioning in a Non-coevolved Assemblage of Estuarine Fishes

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Introduction

An assumption implicit in most studies of the food habits of coexisting fishes is that the different species avoid competition by eating different things. A further assumption is that the differences in feeding habits observed within any group of fishes ("community") will be the result of the coevolution of species and be reflected in their morphological differences. It is not surprising, then, that biologists studying the feeding habits of fishes tend to be impressed by the differences among species, rather than the similarities. In a somewhat circular fashion, they then use these differences as support for interpreting their fish communities as being deterministic in structure (see Connell 1978 for a discussion of the various alternative models). However, recent studies indicate that the structure of at least some fish communities is not highly predictable so that they fit stochastic models of structure, despite the coexistence of presumably coevolved species (e.g., Sale 1977; Grossman, this volume).

An opportunity to test the contrasting views of community structure became available to us when we began a long term study of the fishes of the Suisun Marsh in January 1979. This fish community is made up of a mixture of native and introduced species of both marine and freshwater origins. Although it was obviously not a coevolved community, the wide variety of body morphologies present suggested that it had the attributes of a deterministic fish community. In order to gain an understanding of the community structure we have been intensively sampling the marsh to determine patterns of residency and habitat utilization. We have also been analyzing the feeding habits of the fishes.

Our study is still underway. Nevertheless, the first three years of data allow us to present some qualitative results and to use them as the basis for a discussion of some of the problems involved in the study and interpretation of fish communities.

Study Area

The Suisun marsh is located in the upper reaches of the Sacramento-San Joaquin estuary system, and is adjacent to Suisun Bay which is above the saline San Pablo Bay but below the freshwater delta region. It is the largest brackish water marsh in California and one of the largest in North America. It consists of 34,000 ha of marsh, through which flow many kilometers of shallow tidal sloughs. The depths of the sloughs vary with tidal height and season but in most areas average depths are 1-3 m. Many of the smaller sloughs are completely drained by extreme low tides. Temperatures show a strong seasonal pattern, with lows of 8-10°C in December and January while highs of 22-24°C occur in August and September. During most years salinity also varies with season, from 1-2 ppt in late winter to 8-15 ppt in late summer. Salinities also vary with location. Sloughs closest to Suisun Bay are generally most saline, while those with streams flowing into their upper reaches can be nearly fresh. Turbidity is high all year, with Secchi disk transparencies of 8-45 cm. Although the marsh today is superficially similar to the marsh of 100 years ago, it is in fact a highly modified and managed system. Most of the channels have been dredged at one time or another, or have been confined by levees. The main reason for this has been to prevent uncontrolled flooding of the marsh lands, which are intensively managed for waterfowl. The amount of water released from upstream water projects has an indirect but important effect on water quality in the marsh, particularly in the late summer. Pollution also affects the marsh, most directly in the case of secondarily treated sewage flowing into one of the sloughs from the city of Fairfield.

Methods

The sloughs were sampled with a 4.9 m otter trawl with 3 mm stretch mesh at the cod end. Of 958 trawls all but 25 were made in 20 sampling sites that represented a range of conditions in the marsh. Some collections were also made at selected sites with a 10 m minnow seine. All fish were identified to species and large samples measured (SL). Most fish were returned alive to the water except for those used for stomach content analysis which were either frozen with dry ice or preserved in 4% formaldehyde. Macroinvertebrates, (*Paleamon*, *Crangon*, and *Rhithropanopeus*) taken in the trawls were counted. The abundance of *Neomysis mercedis* was estimated on a 0-5 scale where "0" represented complete absence, "3" moderate abundance (50-100 individuals) and "5" extreme abundance (over 500 individuals).

Samples were taken on a monthly basis through 1979. From January 1980 through June 1981 we sampled on a biweekly basis. Currently we are again sampling at monthly intervals. When possible salinity, temperature, tidal height, water transparency, and turbidity were measured in conjunction with each trawl.

Results

We have collected 39 species of fish from the marsh, of which 16 were abundant enough to make a dietary analysis meaningful (Table 1). Of the 39 species, only two (delta smelt and splittail) are endemic to the Sacramento-San Joaquin estuary. Eighteen of them are introduced

Table 1. Fishes of Suisun Marsh, 1979-1981, ranked by order of abundance in trawl catches, and their percent (%) contribution by number to the catch, their status (S) as residents of the marsh (R = resident year around; SS = spring seasonal; WS = winter seasonal; O = occasional visitor; ? = pattern uncertain) their ecological classification (C) in relation to use of estuaries (TE = true estuarine; EF = euryhaline freshwater; SF = stenohaline freshwater; EM = euryhaline marine; SM = stenohaline marine, A = anadromous), and the region to which the species is native. For introduced species, the data given under the last column is the approximate year they became part of the marsh fish fauna. Species names followed by an asterisk (*) are probably under-represented in the trawl catches.

Rank	Species	%	S	C	Native Region
1.	Striped bass (*Morone saxatilis*)	28	R	TE	Atlantic coast (1880)
2.	Splittail (*Pogonichthys macrolepidotus*)	18	R	EF	Central California
3.	Threespine stickleback (*Gasterosteus aculeatus*)	16	R	EF	Pacific coast
4.	Tule perch (*Hysterocarpus traski*)	9	R	EF	Central California
5.	Longfin smelt (*Spirinchus thaleichthys*)*	8	WS	TE	Pacific coast
6.	Prickly sculpin (*Cottus asper*)	6	R	EF	Pacific coast
7.	Yellowfin goby (*Acanthogobius flavimanus*)*	3	R	TE	Japan (1965)
8.	Sacramento sucker (*Catostomus occidentalis*)*	3	SS	SF	Central California
9.	Common carp (*Cyprinus carpio*)	2	R	EF	Asia (1880)
10.	Staghorn sculpin (*Leptocottus armatus*)	2	SS	EM	Pacific coast
11.	Starry flounder (*Platichthys stellatus*)	2	SS	EM	Pacific coast
12.	Threadfin shad (*Dorosoma petenense*)*	1	WS	EF	Southeast USA (1955)
13.	Delta smelt (*Hypomesus transpacificus*)*	1	WS	EF	Delta
14.	Sacramento squawfish (*Ptychocheilus grandis*)*	-	SS	SF	Central California
15.	American shad (*Alosa sapidissima*)*	-	WS	TE/A	Atlantic coast
16.	Inland silverside (*Menidia beryllina*)*	-	R	EF	Southeast USA (1975)
17.	Goldfish (*Carassius auratus*)	-	R	SF	Asia (?)
18.	Hitch (*Lavinia exilicauda*)	-	WS	SF	Central California
19.	Chinook salmon (*Oncorhynchus tshawytscha*)*	-	SS	A	Pacific coast
20.	Sacramento blackfish (*Orthodon microlepidotus*)	-	SS	SF	Central California
21.	Pacific herring (*Clupea harengus*)	-	WS	EM	Pacific coast
22.	White catfish (*Ictalurus catus*)	-	R?	SF	Atlantic coast
23.	Northern anchovy (*Engraulis mordax*)	-	WS	SM	Pacific coast
24.	Black crappie (*Pomoxis nigromaculatus*)	-	?	SF	Central USA (1910)
25.	Bluegill (*Lepomis macrochirus*)	-	?	SF	Central USA (1910)
26.	Fathead minnow (*Pimephales promelas*)	-	?	SF	Central USA (1950)
27.	Black bullhead (*Ictalurus melas*)	-	?	SF	Central USA (1875)
28.	White sturgeon (*Acipenser transmontanus*)*	-	R	TE	Pacific coast
29.	Rainwater killifish (*Lucania parva*)*	-	R	TE	Atlantic coast (1960)
30.	Brown bullhead (*Ictalurus nebulosus*)	-	?	SF	Central USA (1875)
31.	Pacific lamprey (*Lampetra tridentata*)*	-	?	A	Pacific coast
32.	Sanddab (*Citharichthys sp.*)	-	O	SM	Pacific coast
33.	Surf smelt (*Hypomesus pretiosus*)	-	O	SM	Pacific coast
34.	Green sunfish (*Lepomis cyanellus*)	-	O	SF	Central USA (1895)
35.	Shiner perch (*Cymatogaster aggregata*)	-	O	EM	Pacific coast
36.	Mosquitofish (*Gambusia affinis*)*	-	R	EF	Southeast USA (1925)
37.	Golden shiner (*Notemigonus crysoleucas*)	-	O	SF	Eastern USA (1900)
38.	Warmouth (*Lepomis gulosus*)	-	O	SF	Central USA (1895)
39.	Rainbow trout (*Salmo gairdneri*)	-	SS	A	Pacific coast

species, mostly freshwater species from the eastern United States. Thirteen are native marine, estuarine, or anadromous species. The remaining 5 species are freshwater forms endemic to the Central Valley. Only 11 of the species are present in the marsh all year round, while 14 occur seasonally. The rest occur too infrequently in our samples to say much about the timing of their use of the marsh. The location of the marsh at the freshwater-saltwater interface is reflected in the presence of 23 freshwater species, 7 marine species, 3 anadromous species and 6 true estuarine species. The fact that 11 of the freshwater forms are rare indicates that these fish may have been flushed downstream into the

Table 2. Number of dietary overlap values greater than 0.50 (on a scale of 0.00 to 1.00, where 1.00 indicates complete overlap) among the more abundant species in Suisun Marsh. Values were determined with the Planka (1973) index.

Common Name	Abbre-viation	No. overlaps		Body form**	Feeding Type
		resi-dents	sea-sonals		
Residents:					
Striped bass*	SB	2	4	Rover-predator	Pursuer
Splittail	ST	0	2	Bottom rover	Omnivore
Tule perch	TP	0	0	Deep-bodied	Benthic picker
Prickly sculpin	SCP	0	0	Bottom clinger	Ambusher
Yellowfin goby*	YFG	3	3	Bottom clinger	Ambusher
Threespine stickleback	STBK	2	1	Rover-predator	Benthic picker
Seasonals:					
Longfin smelt	LFS	0	0	Rover-predator	Planktivore
Sacramento sucker	SKR	0	4	Bottom rover	Detritivore
Staghorn sculpin	STAG	2	5	Bottom clinger	Ambusher
Starry flounder	SF	3	4	Flatfish	Ambusher
Threadfin shad*	TFS	0	1	Deep-bodied	Planktivore
Delta smelt	DS	2	4	Rover-predator	Planktivore
Sacramento squawfish	SQ	0	1	Rover-predator	Pursuer
American shad*	AMS	2	4	Deep-bodied	Planktivore
Inland silversides*	MSS	0	1	Surface oriented	Insectivore
King salmon	KS	0	1	Rover-predator	Insectivore

* Introduced species
**From Moyle and Cech 1981

marsh. However, some of these "rare" forms have been abundant enough in the recent past to support fisheries for them. The paucity (3) of native estuarine species presumably reflects the young geologic age of this system (Atwater 1979).

Examination of the diets of the common fishes of the marsh indicates that there is a great deal of dietary overlap (Table 2). A major contributor to this overlap is the opossum shrimp *Neomysis mercedis*, which seems to be "superabundant" seasonally and so not a limiting resource at those times (Brown et al. 1981). The importance of *N. mercedis* is also reflected in the increase in both numbers and species of fish that accompany the annual increase in *N. mercedis* numbers (unpublished data). Other prey types used by several species are planktonic crustaceans and benthic amphipods (particularly *Corophium*). Large crustaceans (*Crangon*, *Paleamon*, and *Rhithropanopeus*) and molluscs are abundant in the marsh but rare in the stomach samples. There appear to be four basic feeding guilds of fishes in the marsh: (1) a bottom-oriented guild eating primarily *N. mercedis* and *Corophium*, (2) an edge-oriented guild feeding on cladocerans and insects, (3) a midwater plankton feeding guild, and (4) a piscivorous guild. Presumably, the potential for competitive interactions are greatest among members of each guild.

When dietary overlaps between species are examined (Tables 2, 3) the

Table 3. Relative usage of prey items by the more abundant fish species. Both prey species and fish species are ranked by abundance. Abbreviations as in Table 2, except Y = young, A = adult.

	SBY	S3A	STY	STA	STBK	TP	LFS	SCP	YFG	SKR	STAG	SF	TFS	DS	SQ	AMS	MSS	KS
N. mercedis	XX		X	X			XX		XX		X	XX		X		XX		
Corophium						XX					X							
Amphipods								XX										
Polychaeta					X													
Chironomidae																	X	
Isopoda						X												
Copepoda:																		
harpacticoid					X					X								
cyclopoid														X		X		X
calanoid													XX	X				
Cladocera										X							X	XX
Other Diptera																	X	X
Fish		XX						X			X				XX			
Substrate and Debris			XX	X		X				X								

XX = 50% of diet by volume.
X = 10-50% by volume.

following patterns can be noted: (1) the lowest number of overlaps occurs among the resident species and those overlaps that exist involve exotic species. (2) The planktivorous species show the greatest degree of overlap, whether native or exotic. However, planktivores also tend to be highly seasonal in occurrence, presumably reflecting seasonal peaks in zooplankton abundance. (3) There is considerable overlap in the diets of seasonal species.

Discussion

From data gathered so far, the fish community of Suisun marsh appears to fit a deterministic model of community structure better than a stochastic one. In the time scale of our study the marsh appears to be a predictable system because: (1) The resident species have shown no shifts in relative abundance that could not be attributed to sampling error. (2) Many species of fish appear to move into or through the marsh on a seasonal basis but do not establish themselves. (3) There is a diversity of body shapes, which is reflected in the high degree of segregation in feeding habits. In addition, the observed dietary overlaps are generally seasonal, especially when *N. mercedis* is superabundant. (4) The structure and stability appear similar to those of other Pacific coast estuaries (e.g., Levy, Northcote and Birch 1979).

On the other hand, there are strong indications that the community structure we have observed for three years is likely to change: (1) Many of the most abundant species are exotic, two of which (inland silverside and yellowfin goby) have been in the marsh for less than 15 years. Most dietary overlap among residents involve exotic species, indicating that competitive interactions may be taking place. (2) Prior to the drought years of 1976 and 1977, during which the waters of the marsh maintained high salinities, exotic freshwater species were more abundant in the marsh, especially white catfish, channel catfish, and black crappie (unpublished data, Calif. Dept. of Fish and Game). The marsh may, thus, be "recovering" from this disturbance. (3) The present community seems to be one that thrives under conditions of predictable annual fluctuations in salinity and temperature. It seems likely that if the marsh receives a more regulated flow of freshwater the dominant fishes will change dramatically. (4) The most abundant species in the marsh, striped bass, appears to have suffered a decline in numbers throughout the Sacramento-San Joaquin estuary (pers. comm., D. Kohlhorst, Calif. Dept. of Fish and Game). The second most abundant species, the splittail, may be declining also, as indicated by the great decrease in its distribution over the last 100 years (Moyle 1980). The splittail may be repeating the history of other endemic fishes, the Sacramento perch and thicktail chub, which are now both extinct in this region. There is thus little definite that can be said about the future of the Suisun marsh fish community except that it is likely to change.

What lessons have we learned from the study so far? (1) General conclusions about the structure of fish communities should be based on long term studies, preferably several times the life spans of the major species. In the case of the Suisun marsh, three years has not been enough time to draw any real conclusions. Because most of the species live 3-6 years, a 10-20 year study is probably necessary. (2) Fish communities cannot just be studied on nice summer days. Seasonal species may provide important clues to the dynamics of the system.
(3) A fish community made up of morphologically divergent forms is not necessarily either coevolved or deterministic in structure. (4) Some apparently desirable prey types may not be utilized by fishes, while others may be eaten by almost every species. It seems to be possible to have a fish community that exists on fewer major prey types than there are abundant fish species. Thus, while extensive overlaps in diet may be an indication of competition, it is more likely an indication of a superabundant prey. (5) The interactions between native and exotic species are not easily predicted. For example, in the Suisun marsh, the most likely competitor of the chinook salmon is the inland silversides, a warm water planktivore. Likewise, the main prey of adult striped bass in the marsh are threespine sticklebacks, which seem to be less available than juvenile striped bass (a major prey in other parts of the system) and the two smelt species (rarely taken anywhere by bass).

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Large-scale Considerations in Studies of Resource Partitioning

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Introduction

In a general sense, studies of resource partitioning are concerned with how a pair of similar species or a group of species in a community or taxocene divide available resources (i.e. food and space). In the strict sense, competition is generally the implied cause of these differences in resource use, and frequently the differences are given evolutionary importance (Schoener, 1974). Although some examples of resource partitioning among a group of species may have an evolutionary basis, others may merely be due to chance. Whether all examples of resource partitioning among species in a community are likely to have an evolutionary basis or not depends largely on the scale of perspective from which the community is viewed. I believe that a failure to recognize this difference in scale of community description often results in conflicting views concerning the occurrence and meaning of resource partitioning among species. This paper examines the differences between large- and small-scale perspectives of the community and how these differences relate to studies of resource partitioning.

Much of the discussion that follows is not new to ecologists. However, some of the ideas relate to studies I have conducted over the last 10 years regarding the organization of the soft-bottom fish fauna of the southern California shelf. Details of these studies will be presented in my Ph.D. dissertation entitled "The functional structure of the soft-bottom fish communities of the southern California shelf."

Although much of the following discussion can be applied to other communities, this fauna has a number of characteristics which may differ from those of communities in other environments (e.g. freshwater, deep-sea, or islands). For instance, a large number of fish species are taken in any given survey and these species are phylogenetically very diverse. The geographic ranges of most species are linear and parallel to the coast (most terrestrial or open ocean geographic ranges have a greater two-dimensional variability in shape). The shelf from 10 to 200m off southern California contains at least three depth or life zones, with taxonomically different but ecologically similar species often occurring in different zones. Few barriers to dispersion exist within the geographic ranges of the species because most species have planktonic larvae and/or wide-ranging adult stages. Except for introductions by man, invasions of the communities by new species are likely to occur only by species with contiguous ranges. In addition, the fauna has probably been strongly affected by Pleistocene climatic changes. These characteristics are probably typical of most coastal faunas.

Large- and Small-scale Perspectives of the Community

For many fisheries or environmentally related problems it is important to know what species feed on different resources. The choice of species for study may be based upon their commercial or recreational importance, their proximity to pollution or other man-related disturbances, or practical considerations such as limited sampling time in seldom-sampled environments. For studies where differences in resource use among species are considered to reflect the process or result of evolution, care must be taken to examine groups of species where such differences may have evolutionary importance. Resource partitioning among congeneric and confamilial species may often be interpreted as an outcome of past evolution that reduces competition. However, resource partitioning among species in any given assemblage may not be the result of such coevolution, because many species in a local assemblage may have their distributional centers elsewhere.

At any scale of investigation, species of organisms coexist with other species of organisms and generally with other species of related taxa. When viewed from the local perspective, each patch investigated will generally differ in species composition from every other patch, but some species will occur more often than others in these patches. When viewed from the large-scale perspective, these commonly occurring species will generally be found living together over a large geographic area. Sale and others (see Sale, 1980) have also made this distinction. For the purposes of this duscussion, I will refer to this large-scale perspective of the community as the biogeographic community and the small-scale perspective as the local assemblage. Both will be restricted to a given taxon, in this case fish. This eliminates considerations of trophic levels above or below those of the taxon of concern and allows one to focus upon the resource partitioning relationships of phylogenetically similar species rather than upon trophic differences among species that are very distantly related.

The biogeographic community

The biogeographic community consists of a set of species with broadly overlapping geographic ranges, depth ranges, and habitat requirements. These species commonly occur together over a broad geographic area and probably have coexisted for a long time. Although not all its members will necessarily be found living together in a particular place at any given time, the community can be described statistically using a cluster analysis or other multivariate technique where the emphasis is placed upon describing species groups as opposed to site groups. I prefer a presence-absence similarity index (e.g. Fager, 1963) because some important community members may not be abundant or may have abundances that are uncorrelated with other members. Alternatively, if sufficient information exists on the geographic range, depth range, and habitat requirements of the species (as might be found in field guides), the biogeographic community can be qualitatively estimated by including all species that broadly overlap in these dimensions. One should remember, of course, that the endpoints of a species' depth or geographic range generally extend far beyond where the species is frequently and abundantly found.

The species in these communities may be phylogenetically different. If this is so, then other life history attributes such as reproductive mode, larval mode, or refuge requirements may be equally or more important than competition-related niche differences such as microhabitat, time of activity, and food or foraging mode (including behavioral, morphological, and size differences; Allen, 1976) in determining which species live together.

If the species are phylogenetically different, the body form was probably developed long ago. Of 44 families of fish collected from 344 otter trawl samples on the southern California shelf for my dissertation study, 40 (91%) are found in the worldwide fossil record (Romer, 1966). The earliest family (Chimaeridae) dates from the Lower Jurassic and the greatest number of families (12, about 30%) date from the Eocene. About 82% of the families fossilized had appeared by the Miocene. All of the 32 fossilized demersal species found in a Pliocene deposit in southern California exist today (Fitch and Reimer, 1967). Hence, niche segregation among phylogenetically different species may be the result of many millions of years of interaction among these species and among their precursors and other extinct species. Keast (1978) recognized this historical contribution to the biogeographic community structure of freshwater fishes in the Great Lakes region.

The local assemblage

The local assemblage consists of whatever species one finds in a small area. It includes some or all of the species comprising the main biogeographic community plus a number of species that belong to other such communities with centers of distribution elsewhere. Of 123 species taken in the aforementioned survey, 30 species (about 24%) comprised seven recurrent groups that were distributed over three depth zones (Allen, 1977). These recurrent groups are regarded as an estimate of the biogeographic community. Of the 93 remaining species, 56 (about 60%) were more common in other geographic areas (north or south), 56 (about 60%) were more common in other depth zones (shallower or deeper), 51 (about 55%) were more common on other habitats (rocky, kelp bed, or pelagic), and 2 (about 2%), the Pacific hagfish (Eptatretus stouti) and the spotted cusk-eel (Chilara taylori), are burrowers that are not well-sampled by trawl while they are beneath the sediment. Note that some species had combinations of the above differences (e.g. more common in other geographic areas and at other depths) which accounts for percentages totaling more than 100%.

Primarily because the presence of incidental species varies from place to place, the species composition of the local assemblage will also vary from patch to patch. Some of the biogeographic species may also be absent due to chance variability, day-to-day movements, and sampling error, or due to unsuitability of the habitat. The difference between the species composition of the local assemblage and that of the biogeographic community and the variability in species composition of the local assemblage should be greatest near the edges of the habitats, biogeographic regions, and depth zones.

Because many of the incidental species forage in a similar way as those species comprising a given biogeographic community, the two kinds of species may overlap broadly in diet. Since incidental species are not commonly encountered by biogeographic community members throughout a large part of their range, they probably do not affect the niche relationships among the biogeographic community members. They may, however, be important in determining the boundaries of the ranges of the biogeographic species. Although they may have less influence on the evolution of the biogeographic community structure, they may depress food supplies locally.

Summary

The evolutionary basis of resource partitioning among species in communities defined from a large-scale perspective may differ from that among species in a local assemblage. Resource partitioning among biogeographic community members may allow them to coexist over large areas for long time periods and hence may be the result of coevolution. Resource partitioning among many members in a local assemblage, however, may simply reflect chance differences among species that happen to be in the same area but which may have evolved independently in different biogeographic communities.

Thus the large-scale geographic range, depth range, and habitat patterns of the species should be considered when choosing species from a local assemblage for a resource partitioning study. Emphasis should also be placed on these spatial patterns when examining resource partitioning among members of a taxocene. In addition, these spatial niche attributes should be considered when interpreting the results of studies where these dimensions have not been considered.

Acknowledgments

I thank Dr. Alfred W. Ebeling, University of California, Santa Barbara, and Dr. Ralph J. Larson, San Francisco State University for reviewing this paper.

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Session III Discussion
Competition and Resource Partitioning

Ralph Larson, Discussion Leader

Questions Following Cross Presentation:

Moyle inquired about the consistency of the intertidal assemblages at given sites from year to year. Cross stated that during his 40 month study, which covered many seasons, the assemblages appeared to be quite consistent or resilient, a term which has recently been applied to rocky intertidal fish assemblages in the Gulf of California. Chapman asked how the terms generalist and specialist were defined and whether they were influenced by competition. Cross defined generalists as those capable of living in many micro- and macrohabitats, whereas specialists appeared more restricted in their distribution. Generalized fishes also had their lower limits shifted upward in the presence of other, presumably more specialized, species. Fishes which entered given habitats sporadically tended to be microhabitat specialists. When such a specialist entered a microhabitat, it outcompetes a generalist that might be occupying that particular microhabitat. Thus, when such shifts in distribution are noted, it can be indirectly interpreted as having resulted from competition. Ebeling asked about one graph relating overlaps in food and microhabitat, which seemed to show resource overlap complementarity for one category of fishes, but also showed another group with smaller overlaps, and perhaps a third group with a tendency toward co-shared, large overlaps. He requested a description of these three groups and wondered about the lack of complementarity in the third group. Cross pointed out that this one figure results from only one site, and mentioned that these overlap results often changed from site to site. The site which produced this figure characteristically had the most species present. One explanation, Cross said, for these categories is that these fishes can be classed as either primary or secondary residents. The primary residents occur mostly in the upper subtidal and are carnivores, while the secondary residents are more common subtidally and are herbivores facultatively inhabiting the low intertidal. Since these separations are quite obvious, it often leads to the kinds of groups noticed by Ebeling. In sites which are less diverse, these separations often do not apply as well since the fish can be separated simply on microhabitat differences. Cross also mentioned that categories based on overlap measures could be influenced by the characteristics of the overlap index used. Ebeling continued the discussion by asking whether these two groups could be equivalent to guilds. Cross replied that he was hesitant to apply this term because there was too much play in the system. For example, one might try to separate cottids and stichaeids into groups which live under rocks and those which live only in tidepools, but species can vary in the amount of time they spend in these various microhabitats, thus making guild distinction based upon microhabitats difficult. LaBolle asked if Cross had measured general food availability or turnover rates. Cross pointed out that this would be very difficult, especially since these fish move about a lot, their food is very patchy, and experiments he has attempted to control the amount of food were difficult to complete. In one example, Cross mentioned that after removal the food recovered faster than the fish could reoccupy the area. Thus, it is obvious that turnover rates of available prey are often high. Regarding food availability, Cross also mentioned that the habits and cryptic nature of the prey make this a hard thing to measure. Utilization of available prey is also difficult to estimate since some species of fish have hind guts which enable them to store their food for perhaps days and even weeks. LaBolle then asked whether Cross felt that food in this habitat could be limiting. Cross replied that he feels that food is often limiting, despite its apparent abundance. Cottids, for example, can eat prodigious amounts of food in a short period and have been observed to completely clean out most of the invertebrates in a given tidepool. Fishes, in addition, are often shoulder to shoulder in these pools. Cross also mentioned that he felt the most generalized fishes are those which can clean out these prey species.

Questions Following Crowder Presentation:

Eggers asked for further explanation for the increase in prey size in Lake Michigan in recent years. Crowder explained that he feels it is due to the increase in stocked salmonids, which act as predators in controlling the major planktivores, the alewives, in this system. Ursin commented that Lake Michigan appears to act like a "bad" model of a marine ecosystem, one which lacks buffering mechanisms. He felt that people who study marine systems tend to overemphasize the variability and need to impose stabilizing schemes. However, he felt that Lake Michigan serves as an ideal subject for an ecosystem model since all stabilizing mechanisms appear to be lacking. Ursin was thus surprised that this system behaves so simply, especially when compared to the literature on marine systems. Crowder added that the manipulations which have occurred in Lake Michigan have been quite influential ones, such as sea lamprey introduction and removal and salmonid introduction, and that this might explain the difference between most studies on marine systems and this study. Grossman asked whether alewives and their prey migrate through the thermocline at night and what the evidence was for this. Crowder explained that they had both acoustic and midwater trawl data supporting this migration for both alewives and rainbow smelt. Moyle, Simenstad, and Crowder discussed in general terms the relationships between both zooplankton prey populations and planktivorous fish populations and the thermal distribution patterns in Lake

Michigan. Crowder suspected that there would be whole assemblages that would roll back and forth in association with these thermal fronts, but that he would not know details until he had completely analyzed all of the samples. Feller asked about the distribution of both zoo- and phytoplankton in relation to the thermocline. Crowder indicated that there was a strong indication of a chlorophyll maximum associated with the thermocline and that zooplankton often tend to stack up there. Some species of mysids, for example, migrate up into the thermocline and feed there at night. Crowder felt that there are a good number of ecological interactions which occur there.

Questions Following Ebeling Presentation:

Larson asked whether the distribution and abundance patterns of the surfperches on Naples Reef after the massive kelp die-off were what Ebeling would have predicted after previous studies. Ebeling responded that those species you would predict to leave first did so. One such example is the rainbow perch, which is a migrant anyway, tending to move off and on the reef predictably. They typically arrive in early May, stay and feed, then leave after about five months, usually in October. After the "crunch," they arrived about the same time, but left in only two months in the first year, but left almost immediately after arrival in the second year. These rainbow perch overlap in diet and microhabitat to a greater extent with the other species than do any of the resident species on the reef. So they have the most sensitive numerical response to the change in the reef. The second most sensitive species is the black perch, which seems to depend on superficial prey living in the turf. Since the urchins now dominate, they graze down all the turf from the base of the reef on up to the crest, and this causes the black perch, usually the most abundant fish on the reef, to dwindle in numbers. Species which seem less sensitive are those which can forage on infauna and have a food refuge, such as pile perch, rubberlip perch, and striped perch. Thus the fish are dwindling in proportion to what you would expect from the changes in their food supply. Chapman asked whether there was any indication of food limitation in the diets through time or any changes in the overlaps among these fishes as their preferred prey were diminished by urchin grazing and lower algal abundance. Ebeling did not feel he could evaluate food limitation, but did point out that there were other areas near the reef where most of these fish could migrate and still survive. So there is little indication of change in diet, but rather that they migrated off the reef before they suffered too much. Crowder asked if this ecological crunch was also affecting other nearby reefs and if there were other areas where they could go. Ebeling pointed out that the crunch was affecting the offshore and nearshore reefs differentially. The kelp beds nearshore are healthy and the urchins are not moving in. Inshore areas are thus good controls since they are not suffering from these problems. The fish could also move further offshore, where the kelp that is broken off moves as drift and eventually becomes detritus. Another concern is that the refuge for the young surfperch has been destroyed since they seek understory algae. Therefore, the young perch either move inshore, are eaten, or move offshore, where predation by kelp bass might also be quite influential. Cailliet pointed out that the importance of the terms "fundamental" versus "realized" niches in these surfperches, since at least three species of surfperch, the black, striped and white surfperches, occupy different microhabitats in different geographical locations. Ebeling responded that this was a valid distinction and that in different environments, these species do act differently. He also considered that there may even be different genetic stocks living at Naples Reef near the coast than at the Channel Islands. LaBolle mentioned that these surfperches are quite similar in their feeding modes and that this might influence their responses to a major change in food available. He asked if it was characteristic to see whole groups (guilds) drop out, or is there some social structure which helps keep some remnants of subdominants still around. Ebeling responded that, indeed, large males tended to defend breeding territories, while smaller males and females had a more peripheral distribution, and that it could be that these less dominant ones would be the first to leave. He proposed that they would like to further study this, perhaps following tagged fish before, during and after such a perturbation. He again mentioned that the least dominant fish, the rainbow perch, was the most sensitive in numerical response to the crunch.

Questions Following Grossman Presentation:

Breitburg maintained that an equally plausible explanation of Grossman's stream fish results might be resource partitioning or competition and that the changes in these assemblages could be a function of the change in kinds of prey available. Grossman countered that the resource partitioning concept assumes persistence, and that this interpretation of his data would violate that assumption. If environmental stochasticity alters the resource base, then one would expect concomitant changes in species which are preadapted to use the resulting resource base. Grossman also claimed that constructing a limiting simularity model would be inappropriate to explain the large "flip-flopping" in resource utilization which he had observed. Breitburg still did not feel that the kinds of data presented for this system were sufficient to discern whether the shifts noted were due to preadaptation or competition. Grossman felt, on the other hand, that his data did disprove both the resource partitioning and deterministic hypotheses, especially since the trophic changes were complete rearrangements and there was no evidence of physical changes in the study site for over 12 years. He contended, therefore, that the major shift from an herbivore-dominated to ooze-feeder-dominated assemblage indicated that the community organization was more stochastic than deterministic. Ebeling asked whether many of these feeding adaptations were the result of evolution toward anticompetition which occurred sometime in the past. Grossman replied that this would require further study, but that he felt such adaptation often were flexible when competition or natural selection is relaxed and that the "ghosts of competition past" approach needed scrutiny.

Questions Following Moyle Presentation:

Chapman asked whether the success of the introduced species could indicate that competition was important in determining the assemblage that is now seen. Moyle indicated that he felt this to be the case, but also pointed out that a number of native species have done quite well, while others have disappeared. Herbold stressed that these assemblages may be the result of competition and resource partitioning but that the evidence does not always support all the underlying assumptions of these two concepts. Larson suggested that one can look at communities as assemblages of coevolved organisms or that colonization, introduction, and the like make these assemblages quite flexible. Moyle then stressed the great adaptability that temperate fishes exhibit in general and how this might influence our interpretation of community or assemblage structure. He felt that this was true also for the stream fish assemblages studied by Grossman. Grossman then made the point that the major question is not whether assemblages are the result of stochastic or deterministic processes but to stress that we should not always follow the tradition of interpreting all assemblages as resulting from resource partitioning. He stressed that community or assemblage structure need not always be interpreted using coevolved characteristics. Often, Grossman contended, these alternative (stochastic) interpretations appear to be at least as good, if not better, than the traditional deterministic approaches.

Chapman contended that he did not feel it would be a unanimous decision by most ecologists that resource partitioning is the only alternative to interpreting community structure. Grossman maintained that the literature indicates the opposite. Cailliet then stressed that we consider scale in these discussions. Small systems that are studied tend to vary some from place to place or season to season. However, when considered on a large scale, one finds the same species commonly occurring together and their trophic composition also appears similar. Therefore, he contended, proposing coevolutionary processes based upon small-scale studies can often lead to misleading conclusions. Larson then mentioned that this discussion of scale was appropriate at this time, since it leads directly into Alan's talk.

Questions Following Allen Presentation And General Discussion of Resource Partitioning:

Crow asked what percentage of the total numbers of all fishes were resolved into recurrent groups, compared to the 24% of the species which were. Allen said he had not calculated this, but that it included most of the abundant species. Cailliet asked if looking at fish from very local areas would give a very different opinion of recurrent groups or trophic function of any given species. Allen indicated that analyzing fish from very local areas often presents a different impression of their groups and feeding habits, and that this was the reason he was stressing viewing their assemblages and their functional organization in a broad perspective, considering perhaps the entire range of distribution of most of the species included. Crowder followed with a published statement by Levin and Paine about the rocky intertidal that seemed pertinent: globally the most predictable thing about it is that it is locally unpredictable. Crowder then proposed that this statement may equally apply to both Allen and Grossman's systems.

Larson stressed that one must be careful in defining groups, especially in partitioning models, and that it is difficult to actually know what kinds of interactions might be occurring among different species in the field without actually measuring them. Allen concurred, but again stressed that much can be learned from the large scale approach, and that considering other aspects of the life history of such fish species (that is, their reproductive habits, the distribution and abundance of their larvae, their growth and mortality) is also essential if one is going to try and make statements about their coevolution, competition, or resource partitioning. Ebeling discussed how some had criticized Peter Sale's work on coral reef fish assemblages because of the small-scale, patch reef approach taken. But he also defended Sale in that there must be some bounds on the scale in order to study a system because if the scale becomes too large, then a good deal of useful information cannot be accumulated. Ebeling then went on to present similar problems encountered when dealing with southern California subtidal, kelp bed fishes. In reefs off the channel islands, which appears to be an ecotone between the southern California bight species and northern species coming around Point Conception, one often finds unusual mixes of fish species. So, locally these systems may vary and therefore appear stochastic, but globally the system almost looks deterministic, if broad weather patterns do not change and influence the species existing generally in the area.

To continue the discussion on resource partitioning and anti-competition mechanisms, Ebeling still contended that character displacement could occur during secondary sympatry for such groups as sanddabs which originally became different species through allopatry, and thus one now sees partitioning remaining either through feeding habits or depth of occurrence. So Ebeling still felt that there is a problem of sorting out possible character displacement features resulting from adaptations over evolutionary time and the simple accumulation and accommodation of whole array of species at a particular cross section over a geographic range where some species are climatically well adapted to an environment and others are more marginally adapted. Allen then mentioned the influence on this coast of the glaciations which have been occurring since the pliocene. These need to be considered, he proposed, since they must have strongly affected the environment in which these species have evolved. For example, one estimate maintains that the amount of bottom area available to demersal fishes may have been as low as 10% of what it is at present, thus influencing heavily the biomass and number of species occupying that region and the interactions among them. Ebeling attempted to summarize the discussion so far by stating that the pardigm of resource partiitioning assumes that one can explain the structure and stability of existing communities simply by measuring the interactions among the members of each guild within these communities at a given time. If in fact a given community is a hodge-podge of species showing character displacement, coevolved species, front runners, etc., then the paradigm simply does not work.

Lea inquired as to the percentage of the assemblages derived in Allen's study were confined by Magdalena Bay on the south to Point Conception on the north. Allen had not calculated this figure, but indicated that a good portion of the shallow assemblages were constricted by these boundaries, whereas the deeper-dwelling forms were not. Eggers returned to the resource partitioning discussion and stressed that the reproductive strategies were an important consideration to make in determining which locations and how broad an area to cover in doing such a study. He felt that this was not as much of a consideration in marine demersal fishes since most have pelagic, widespread larvae, but it certainly would be for such habitats as estuaries or lakes where there are fishes with a whole diversity of reproductive modes. Allen did point that some of the demersal fishes he studies, such as the midshipman (Porichthys notatus), were inshore spawners with demersal eggs, larvae, and postlarvae. Therefore, he felt it important perhaps in all habitats.

Session IV

Feeding Behavior of Fishes and Prey

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Feeding Behavior of the Widow Rockfish (*Sebastes entomelas*), A Diurnally Feeding Rockfish

Peter B. Adams
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Introduction

Prior to 1978, widow rockfish landings were an insignificant component of the Northeastern Pacific Groundfish Fishery, but since then, these landings have grown from below 1,000 mt to an estimated 28,000 mt in 1981. This dramatic increase in the fishery has more than doubled the commercial landings of rockfish in the area off California, Oregon and Washington (PFMC 1981). Now the immediate question is how these people that are in this highly competitive business could have overlooked this vast resource all this time. There are many reasons but the principal one is that the widow fishery is fundamentally different from traditional rockfish fisheries. The traditional rockfish fishery is a daytime bottom trawl operation while the widow fishery is a nighttime midwater fishery. Obviously it is important to understand these differences in behavior of the widow rockfish (a nocturnal aggregating species) from the traditional commercially important rockfish species which aggregate diurnally. Actually this is really the converse of the question since in most fish species that aggregate into schools and disperse, it is the dispersed stage when the fish is feeding that is the driving force of this day-night cycle (Hobson 1973).

Diurnal Feeding

Stomach sample data were taken primarily from commercial landings in the Eureka area, supplemented with other samples from Northern California sport and commercial catches. Most were fish taken in the nighttime midwater fishery. The diet of the widow rockfish consists of salps, fish, (primarily myctophids) shrimp and euphausiids (Table 1). These four groups are roughly equal in the diet and make up over 90% of the total diet volume. The only other commonly occurring prey group is hyperiid amphipods. Phillips (1964) felt that these amphipods dominated the diet of widow rockfish. All these prey groups represent organisms that migrate to the surface at night while the widow rockfish is aggregated near the bottom. So probably these prey are taken during the day in their submerged stage (Adams in prep).

The obvious next step is a directed fishing effort to obtain day and night stomach samples from members of the same population. This data would be used to examine their pattern of gut fullness. This was attempted in conjunction with a NWAFC research cruise that was attempting to make biomass estimates of the widow rockfish population off Oregon. The vessel used in the cruise was the R/V Chapman, a new stern end trawler which is equipped with the most recent electronic and mechanical fishing gear, but even using this boat, we were unable to consistently catch fish in midwater. Midwater fishing is very sophisticated. Besides extensive technological gear, it requires a great deal of fishing experience plus current feedback on the local fishes' schooling behavior. It is questionable whether any research vessel, no matter how suitably equipped, can successfully fish in midwater without extensive prior experience. Nevertheless, we need this type of data to answer the day-night feeding question.

Seasonal Feeding

There are also strong seasonal differences in the diet considering just the four major groups mentioned earlier; euphausiids, shrimp, salps and fish. These four major groups dominate the diet (accounting for between 82 and 97 percent of the quarterly diet volume), but the distribution of diet volume among the four major groups is different during the year (Figure 1). During the fall, fish dominate, while in the winter, the major prey are shrimp. In the summer quarter, the widows are feeding on euphausiids and fish. The spring quarter is the only period when salps are a major part of the diet. This period and summer are the only time of the year when euphausiids are important. The spring quarter is also the period of highest absolute volume of prey per fish and also of the highest number of prey categories per fish.

This pattern is significant since the widows are feeding most heavily just after they have finished partition (release of young) during winter months (T. Echeverria per. comm.). There is a high demand for energy during reproduction, and following this activity stored energy is at its lowest level. In other species, natural mortality is concentrated during this period (Shul'man 1974), and perhaps this is also true for widow rockfish.

Discussion

Random sampling is rarely possible in feeding studies; therefore it is important to understand the relationship between different types of sampling and the error involved. How stomach samples are gathered cannot be considered independent of the intended questions that are going to be asked of that data. Samples used here were gathered both from research cruises (directed sampling) and from commercial port sampling (incidental sampling). Average values of the amount of a particular type of prey item will differ from true population values because of variation and bias. Variation is the spread (or dispersion) of the observed sampled values around the mean. The enormous variation typical of food habitat data is due largely to its patchy or contagious nature. These types of data have sampling distributions which are skewed and have a large proportion of empty sample elements. That is, it it common for a prey item to occur in only a few fish, but for those few fish to be stuffed with them. In order to evaluate the relative importance of this type of variation in both direct and indirect sampling, I looked at the degree of patchiness in a research trawl versus a commercial landing using Lloyd's (1967) mean crowding index. For the different major prey groups, the patchiness indices are very similar, with the commercial data consistently less patchy (Table 2). Essentially this means that the relationship between the mean and the variances is similar, and although neither of these data sets are normally distributed, there is not a great deal of difference in this aspect of the data between these two types of sampling.

The other possible source of error, sample bias is simply when certain individuals in the population have a greater chance of being included than others. Bias is unrelated to variation. Confidence limits can be very narrow, but still strongly biased. Bias usually results when the sample coverage of the population is inadequate in some area. In Figure 2, the large distribution is the lengths of fishes used in all of stomach samples from port sampling; the small distribution is the lengths of all widows taken in midwater hauls during the April research cruise. Even though the research cruise sample represents almost 200 fish versus around 500 for the port sampling, the range of lengths in the research survey data covers only a small portion of the length range of the port samples. Both of these samples are biased in different ways. In common usage, the term bias, in common usage, has negative connotations implying a faulty sampling design. But bias is really a problem only when it is unrecognized. Attempts to identify bias must be independent of attempts to reduce variance.

Of the two types of sampling, port sampling has the advantage of much lower costs. Incidental sampling of this sort can provide descriptive information about the target population, an example being the seasonal distribution of food of the widow rockfish. However, except in unusual circumstances, this type of data is not adequate for hypothesis testing. When data are needed to detect differences between subgroups of the target population to verify hypothesis, a directed sampling effort is needed.

The widow rockfish offers a typical example of the evolution of management of a species. Usually,a fishery develops explosively. As with the widow rockfish, usually little or no previous information is available prior to the onset of the fishery. Management plans based completely on age and growth studies are developed after intense fishing has taken place. Traditionally feeding studies had no impact on these plans. I have thought about why this is so and there are two possible reasons. The first is that feeding is an unimportant aspect of the fishes' biology. My studies and the views expressed at this workshop, indicate this is untrue. This leaves the second reason that feeding studies have failed to provide the kind of information that is necessary for management. If this is so, the obvious question is: What kind of information is needed by management?

My idea of the kind of food habit data needed for management is related to how fish communities are structured. Ecological theory concerning community structure has been dominated by the Hutchinson-

MacArthur school of thought. In its simplest form, this type of theory views a community of animals as a unidimensional resources axis upon which species occupy some area or breath. When there are multiple species, a zone of overlap exists where species co-occur. The underlying assumption of this theory is that direct competition is the principal force in determining community structure and therefore controls these patterns of niche breath and overlap. This view regards feeding studies as simply a means of identifying potential competitors. When the diets of offshore fishes are found to be widely overlapping, direct competition for food, and therefore feeding studies, is considered unimportant in management strategies. In the terrestrial communities for which these concepts were developed, this theory has been widely accepted, but in aquatic communities, predation has been found to be one of the most powerful integrating concepts (Hobson 1968; Lowe-McConnel 1975; Paine 1966). An alternative to the Hutchinson-MacArthur model is to view the community as a lattice, then the vertical connections would represent predation and the horizontal connections would be competition. Using this model, predator-prey relationships can be an important factor in community interactions. If there is ever going to be true multi-species management, feeding studies are going to have to focus more toward these vertical connections both above and below the managed species and the mechanisms which control them.

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Table 1. The diet of widow rockfish from Northern California (Average TL = 464 mm, min. Size = 361 mm, Max. Size = 543 mm, n = 365).

	Number	Volume	Min. Size	Max. Size	Freq. of Occurrence
Hydromedusae	1.28	3.90	1.00	4.00	0.06
Ctenophora	0.10	0.84	0.50	3.00	0.01
Oligochaeta	-	0.27	90.00	-	0.01
Pelagic Polychaeta	0.07	0.56	2.50	2.70	0.01
Pelagic Gastropoda	0.13	0.79	7.00	-	0.02
Cephalopoda	0.14	0.91	50.00	-	0.03
Mysidacea	0.01	0.01	1.00	-	0.01
Isopoda	0.01	0.28	1.50	-	0.01
Gammaridea	0.07	0.34	1.00	-	0.03
Hyperiidea	1.45	3.77	0.70	10.00	0.18
Caprellidea	0.01	0.01	1.00	35.00	0.01
Euphausiacea	30.88	21.05	6.00	36.00	0.37
Natantia	11.78	12.78	0.30	7.00	0.20
Ascidiacea	0.02	0.22	1.50	2.00	0.01
Larvacea	0.11	0.03	0.30	0.68	0.01
Thaliacea	22.98	16.74	1.00	80.00	0.370
Chaetognatha	0.01	0.55	-	-	0.01
Fish	5.38	24.80	1.50	90.00	0.403
Undet. Gelatinous material	-	10.22	6.00	-	0.02
Sand	-	0.91	-	-	0.01

Table 2. Lloyd's (1967) index of patchiness for major prey categories from research trawls versus commercial landings.

Prey Categories	Commercial Landings	Research Trawls
Euphausiids	2.72	2.30
Salps	3.94	1.34
Shrimp	10.15	10.36
Fish	10.71	.24

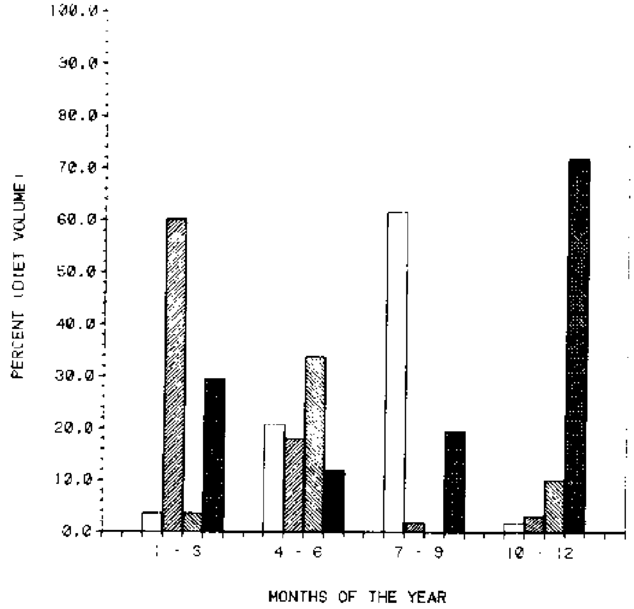

Figure 1. Seasonal feeding of the widow rockfish on salps (clear bar), shrimp (left-hatched bar), euphausiids (right-hatched bar) and fish (cross-hatched bar).

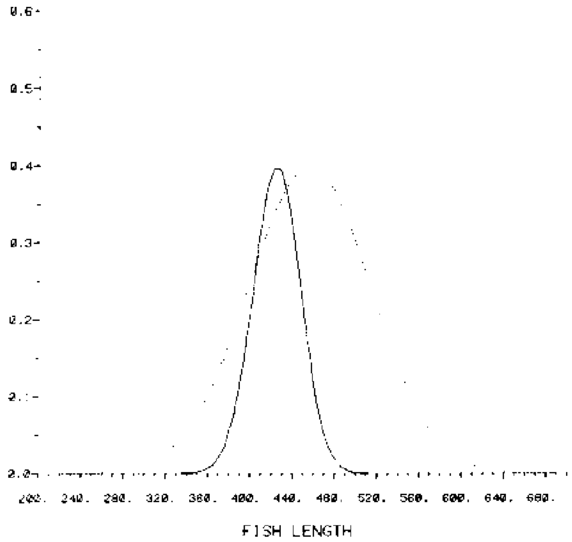

Figure 2. This distribution of lengths of widow rockfish from port sampling (dashed line) and from the April research cruise (solid line).

The Spring Diets of Walleye in the Lower Columbia River, 1980-1981

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Introduction

The walleye (Stizostedion vitreum vitreum) is a highly piscivorous cool-water fish whose native range centers around the Great Lakes region (Scott and Crossman, 1973). During its approximately 40-year tenture in the Columbia River, the walleye has extended its range down river to the edge of the estuary (Durbin, 1977).

The construction of numerous dams has transformed the Columbia River into a series of low current lakes, with somewhat faster currents in the tailrace areas. The John Day pool is the second longest (123 km) reservoir in the Columbia River and, aside from variations in water velocity and bathymetry, it was found to be limnologically homogeneous (Hjort et al., 1981). Thus the Columbia River fits the model for optimum walleye habitat proposed by Kitchell et al. (1977). The change from free-flowing to sequential reservoirs has made the river a less than optimal habitat for salmonids, and has reduced the rate at which juveniles migrate downstream and increased their exposure to predation (Raymond, 1976). It is not surprising that persons interested in salmonid fisheries are concerned about the extent of walleye predation on juvenile salmonids.

In this study, I investigated the diets of walleye collected in the first (upstream) 23 km of the John Day pool in the springs (April-June) of 1980 and 1981, with special interest in the walleye-salmonid interaction.

Methods

All of the walleye obtained in the spring of 1980 were captured in either a 38.1 x 1.8-m multifilament sinking gillnet with variable stretch mesh of 3.81 cm, 5.08 cm, 6.35 cm, 7.62 cm, and 10.16 cm, or a

76.2 x 3.7-m monofilament floating gillnet with 15.25-cm stretch mesh. In 1981 I used the same gillnets but also used an electroshock boat utilizing a 3500 watt generator and a D.C. pulser. All of the gillnet sets were of 1 to 2.5-hr duration to minimize regurgitation and digestion of stomach contents. I sampled walleye between April 2 and June 30, 1980 and between March 30 and June 16, 1981. During each month, I obtained a minimum of 10 walleye for each of four generalized times of day--morning, mid-day, evening, and night.

For each walleye captured, I collected data on fork length (mm), weight (g), and sex and stage of maturity. I collected a scale sample, and removed the stomach and preserved it, with an identification tag, in a solution of 10% buffered formaldehyde. At a later date I examined each stomach for contents and identified each prey item to the lowest possible taxonomic level. I recorded information on each items' volume (ml), estimated standard length (mm), and estimated percent of digestion. The data were put into computer format and was subjected to a nonparametric multivariate test for statistical significance, $L_{N,t}$, which is approximately a Chi-squared distribution with p(v-1) degrees of freedom (Koch, 1969) where p is the total number of prey taxon and v is the number of treatments or populations being tested.

Results

The walleye sample for spring 1980 consisted of 91 fish, varying in length between 230 to 753 mm. There were 141 walleye in the 1981 sample, varying in length between 214 to 764 mm. Table 1 shows the percent volume and percent occurrence for each prey taxon by year. It is evident that fish represent the vast majority of the walleye diet; in fact, if all of the invertebrates for both years are combined, they represent only 0.1% of the total prey volume. All invertebrates are combined in the following analysis.

After the 1981 sampling season, I learned that the National Marine Fisheries Service (NMFS) was collecting juvenile salmonids at the McNary Dam, upstream of the study area and releasing them below Bonneville Dam, approximately 240 km downstream. The NMFS collection facility was improved prior to the spring of 1981 and total spring diversions increased from 1.5 million juveniles in 1980 to 2.6 million juveniles in 1981 (Thomas Ruehle, NMFS, Pasco, WA., personal communication). Hjort et al. (1981) reported that their juvenile seine catch-per-unit-effort (CPUE) of juvenile chinook (Oncorhynchus tshawytscha) in the John Day pool fell from 15.9 in the spring 1980 to 9.5 in the spring of 1981. These data indicate a reduction in the relative abundance of juvenile salmonids in the John Day pool between 1980 and 1981. Unfortunately, Hjort et al. (1981) state that their data cannot be used to estimate interspecific relative abundances due to gear selectivity.

The data in Table 1 suggest that there was a reduction in the dietary importance of sculpins (Cottus asper) and salmonids from 1980 to 1981 and a concomitant increase in the importance of catastomids (Catastomus columbians; C. macrocheilus) and cyprinids (Acrocheilus alutaceus; Mylocheilus caurinus). Despite this apparent change in diets and a change in the relative abundance of salmonids, I found no significant difference in the numbers of prey items between years (P=.50) or in volumes of prey items between years (P=.25).

While examining the stomach contents, I observed differences in the diets of large vs. small walleye. To test this, I combined all walleyes from both years. Initially, I tested between fish <400 mm FL and fish ⩾ 400 mm FL and found no signigicant difference (P=.40) in numbers of prey items. However, when testing between walleye ⩾ 500 mm FL and those <500 mm FL there were significant differences in volumes (P=.005) and numbers (P=.01) of prey items. Table 2 contains the percent volumes and numbers of prey for walleye separated at 500 mm FL. Sculpins are very important to small walleye followed distantly by salmonids and catastomids. Large walleye utilize sculpins, catastomids and cyprinids in almost equal proportions and rarely consumed salmonids. Parsons (1971) found a direct relationship between walleye size and prey size, so one would expect a difference in volumes between large and small walleye. The difference in numbers of prey indicates a difference in prey selection, but may also reflect size preferences. Most of the sculpins and juvenile salmonids in the pool are less than 100 mm FL whereas the catastomid and cyprinid length frequencies extend past 300 mm (Hjort et al., 1981).

Discussion

The walleye has frequently been described as an opportunistic predator, selecting prey primarily based on abundance (Colby et al., 1979). Moreover, the presence of a subretinal tapetum lucidum enhances the walleye's scotopic vision and allows them to successfully feed when the prey are less able to see, i.e. dawn and dusk (Ali et al., 1977). By far the most important walleye prey item in this study was sculpin followed by largescale and bridgelip suckers, chiselmouths and peamouths. All of these prey species are closely associated with the benthos (Wydoski and Whitney, 1979), as are most of the primary prey previously reported for walleye (Ryder and Kerr, 1978).

I propose the following scenario of walleye feeding behavior in the John Day pool. During the day the walleye remains in deep water, avoiding high light intensity (Ryder, 1977) and occasionally encountering prey. At the onset of dusk, the walleye moves into progressively shallower water, encountering abundant prey associated with the bottom, and selecting food items based on size preference. It is not until the end of the initial foraging episode that salmonids are encountered at the surface. Thus, the salmonids are buffered by an abundance of alternate prey, of a wider size range and in a location where predation by walleyes is most likely. It is important to note that this scenario is specific to the current abundances of walleye and prey. If NMFS stops collecting juvenile salmonids or if the walleye population expands and/or reduces the abundance of alternate prey, the predator-prey relationship will change.

Acknowledgements

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Table 1. Percent volume and numbers of prey items found in the stomachs of walleye captured in the John Day pool of the Columbia River, Spring, 1980 and Spring, 1981. Raw data is in parenthesis.

	1980		1981	
	(n=91, 38.5% empty)		(n=141, 40.0% empty)	
Prey Taxon	% Vol. (ml)	% Number	% Vol. (ml)	% Number
Oncorhynchus tshawytscha	2.7 (26)	8.4 (10)	1.1 (14)	2.3 (4)
Salmonidae	2.2 (21)	5.0 (6)	2.5 (31)	2.9 (5)
Cottus asper	44.1 (428)	40.3 (48)	22.9 (282)	28.3 (49)
Catastomus columbians	1.5 (15)	1.7 (2)	10.6 (130)	2.9 (5)
C. macrocheilus	1.6 (16)	1.7 (2)	0.7 (8)	0.6 (1)
C. spp.	27.6 (268)	4.2 (5)	22.3 (275)	6.9 (12)
Acrocheilus alutaceus	0.3 (3)	0.8 (1)	31.9 (393)	6.9 (12)
Mylocheilus caurinus	15.4 (150)	1.7 (2)	0.2 (2)	0.6 (1)
Ptychocheilus oregonensis	-	-	1.0 (12)	0.6 (1)
Cyprinidae	-	-	0.1 (1)	0.6 (1)
Unidentified Fish	4.5 (44)	30.3 (36)	6.6 (81)	37.0 (64)
Ephemeridae	0.03 (0.32)	1.7 (2)	0.2 (2.55)	9.8 (17)
Chironomidae	< 0.01 (0.04)	2.5 (3)	-	-
Talitridae	< 0.01 (0.04)	0.8 (1)	-	-
Gammaridae	< 0.01 (0.05)	0.8 (1)	0.04 (0.05)	0.6 (1)

Table 2. Percent volume and numbers of prey items found in the stomachs of large walleye (≥ 500 mm FL) and small walleye (< 500 mm FL) captured in the John Day pool of the Columbia River, Spring, 1980 and Spring, 1981. Raw data is in parenthesis.

	Large Walleye (n=87, 52.9% empty)		Small Walleye (n=145, 32.4% empty)	
Prey Taxon	% Vol. (ml)	% Number	% Vol. (ml)	% Number
Oncorhynchus tshawytscha	0.3 (4)	2.4 (2)	5.0 (36)	5.5 (12)
Salmonidae	1.8 (26)	1.2 (1)	3.6 (26)	4.5 (10)
Cottus asper	24.3 (361)	18.3 (15)	48.5 (349)	41.4 (91)
Catostomus columbians	2.8 (42)	3.7 (3)	14.3 (103)	1.8 (4)
C. macrocheilus	-	-	3.3 (24)	1.4 (3)
C. spp.	33.9 (503)	11.0 (9)	5.6 (40)	3.6 (8)
Acrocheilus alutaceus	22.6 (336)	9.8 (8)	8.3 (60)	2.3 (5)
Mylocheilus caurinus	10.1 (150)	2.4 (2)	0.3 (2)	0.5 (1)
Ptychocheilus oregonensis	0.8 (12)	1.2 (1)	-	-
Cyprinidae	0.1 (1)	1.2 (1)	-	-
Unidentifiable Fish	3.2 (47)	32.9 (27)	10.8 (78)	33.2 (73)
Invertebrates	0.1 (1.84)	13.4 (11)	0.1 (.76)	5.9 (13)

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Deep Guts
A Shallow-water Solution Using Immunological Methods

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Introduction

Food web descriptions and classical food chain models for aquatic organisms have typically been deduced from visual observations of the stomach contents of specimens collected within a given predator-prey community matrix. Such descriptions evolve slowly as new data for additional taxa are collected and added to the matrix. New data arise most frequently as a result of changes in the temporal sampling scale (i.e., previously unsampled seasons or times of day) or as a consequence of new analysis and collecting methodologies. A new methodological approach is perhaps the more lucrative in providing new information on qualitative aspects of food and feeding habits of target taxa.

Quantitative descriptions of feeding by individuals or among individuals within distinct communities are almost always biased to some extent, either by sampling or methodological constraints. Gut analysis methods have been reviewed recently by Hyslop (1980) who also discusses some of the biases peculiar to particular methodologies. Hyslop concludes correctly that no single method of analysis can adequately depict dietary importance. This is also true for terrestrial food web investigations. Thus our views of food chains and webs and mass and energy flow in the aquatic environment may be seriously biased by methodological constraints and our inability to determine the true magnitudes and directions of predator-prey interactions.

The most common trophic modes in the deep-sea are deposit-feeding, carnivory, and scavenging (Sanders and Hessler, 1969). The gut content examination of carnivores and scavengers has provided most of our information on deep-sea food webs (e.g., Sokolova, 1972; Harding, 1974; Pearcy and Ambler, 1974; Nemoto, 1977; Hessler et al., 1978), whereas the analysis of deposit feeders is information poor. A very large proportion of deep-sea animals collected have no visible gut content remains upon retrieval or else much of the remains cannot be visually identified (especially true for sediment-laden deposit feeders). Deep-sea food web models (e.g., Rowe, 1980) are particularly difficult to formulate for lack of basic data on biological linkages among organisms within our conceptual black boxes. The need to understand functional linkages within and between these modeling abstractions becomes more and more urgent as the ocean depths increase in attractiveness as a final repository for man-made wastes (Hollister et al., 1981). The ability of immunological tracer techniques (see review by Boreham and Ohiagu, 1978) to identify soluble proteins of prey taxa in deposit-feeders' guts or in the fluid remains or intestines of organisms whose guts have everted holds promise for identifying higher-level trophic connections among deep-sea organisms.

Results and Discussion

Based upon comparative immunological cross-reactions between benthic invertebrates from Puget Sound, Washington, and North Inlet, South Carolina, common antigens (soluble proteins) were found among several phylogenetically related taxa (Feller and Gallagher, in press). Since high diversity, small body size, and low numerical abundances of deep-sea fauna precludes preparation of highly specific antisera to every organism there, the existence of common antigens among shallow and deep fauna may allow use of a wide variety of antisera to shallow-water taxa to detect similar taxa as prey in the guts of deep-sea predators and deposit feeders. Antisera to numerous macrofaunal and meiofaunal taxa (e.g., bivalves, gastropods, polychaetes, decapods, amphipods, forams, harpacticoid copepods, nematodes, ostracods, etc.) are currently in use for deciphering food web properties of intertidal communities and are available for use with deep-sea gut contents.

Specificity tests with mid-water organisms using antisera to shallow-water invertebrates were faithful across taxa. That is, antiserum to a shallow-water decapod shrimp reacted extensively and uniquely with mid-water shrimp species but not to the same extent if at all with, for example, euphausiids, calanoid copepods, squid, or myctophid fishes (Feller, 1981). Additional deep-sea specimens are currently in the preliminary stages of immunoanalysis, and specificity tests with a deep-sea lyssianassid amphipod, *Eurythenes gryllus*, show high affinity of this amphipod's proteins with antisera to shallow-water amphipods. The specimens were kindly donated by R. Hessler. The stomach contents of sablefish, *Anoplopoma fimbriata*, have also recently been donated for analysis by J. Young, Battelle Pacific Northwest Laboratories.

Existing or newly-prepared antisera which recognize easily-collected shallow-water organisms may thus be useful in the gross identification of major trophic links among deep-sea communities. Traditional gut analysis techniques have probably inadequately described the complexity of trophic pathways in this remote environment.

Acknowledgements

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A Preliminary Evaluation of Prey Selection By Juvenile-Small Adult California Halibut (*Paralichthys californicus*) In Nearshore Coastal Waters off Southern California

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Introduction

Although many studies of fish feeding exist, few have attempted to obtain the concurrent prey availability data necessary to assess prey electivity. The diversity, clumped distributions, and complex behaviors of prey organisms are factors which have generally complicated prey electivity studies for marine fishes.

Our preliminary data on the feeding habits of juvenile and small adult California halibut (Paralichthys californicus) suggested that this species would be an excellent candidate for such a study since it feeds on only a few types of prey, the abundances of which are being monitored as part of an ongoing impact assessment. In this paper we present data and analyses on the previously undocumented feeding habits of these fishes in southern California coastal waters. We provide a preliminary evaluation of the prey selectivity of halibut based on a comparison of its diet and some approximations of prey abundances based on prior years' data.

Methods

Paralichthys californicus were collected during the period March to September 1981, inclusive, from 6, 18, and 30 m depths along the coast between San Onofre and Oceanside, California. Standard 7.5 m otter trawls with 3.8-cm (stretch mesh) wings and 1.3-cm (stretch mesh) cod-end liner (Mearns and Allen, 1978) were used.

Each halibut was eviscerated immediately after capture and its alimentary tract fixed in 10% formalin. Fish were returned to the laboratory, macroscopically sexed, measured (SL in mm), and weighed (0.1 g). After a minimum of four days fixation, viscera were soaked in tap water for 24-48 hrs and then stored in 70% ethanol for subsequent detailed examination.

Stomach contents only were examined. Fish prey were identified to species, if possible. Major fish prey were assigned "reconstructed" (= undigested) wet weights based on derived SL-wet weight regressions. Fish skeletal remains were identified using Clothier (1950). Partial skeletal remains, identifiable to species, were assigned standard body lengths by comparing dimensions of key vertebrae to the vertebrae of reference specimens. Mysids were identified to lowest possible taxon and sex/maturity class. The weights of mysid prey were reconstructed based on sex and maturity criteria rather than length classes (Bernstein and Gleye, 1981).

The relative abundances of northern anchovy (Engraulis mordax) were estimated from night lampara net (wings: 15-cm stretch mesh; center bag: 1.25-cm stretch mesh) catches made at fortnightly intervals during the period from March to September 1980. Mysid abundances were estimated based on contiguous on-offshore tows of a 1-m^2 epibenthic sled (0.333-mm mesh) made during the period from March to September 1979.

Results

One hundred and ninety-three Paralichthys californicus were collected at 6, 18, and 30 m depths off San Onofre-Oceanside during the period March to September 1981. One hundred and fifteen (60%) had food in their stomachs (Table 1). Of the 14 taxonomic categories of prey

Table 1. Number of California halibut (Paralichthys californicus) trawled at 6, 18, and 30 m depths off San Onofre and Oceanside, California, each month during the period March-September 1981. Number of halibut with food in their stomachs noted in parentheses.

	Number of Halibut (with Food) at		
Month	6 m	18 m	30 m
March	0 (0)	25 (10)	2 (1)
April	3 (2)	14 (12)	10 (5)
May	16 (10)	24 (16)	0 (0)
June	6 (2)	48 (36)	0 (0)
July	4 (0)	3 (1)	1 (0)
August	11 (2)	3 (2)	0 (0)
September	21 (16)	1 (0)	1 (0)
All Months	61 (32)	118 (77)	14 (6)

recognized, only two categories predominated (Table 2). Adult Engraulis mordax were the most important item and accounted for 84% by weight of all prey consumed. E. mordax occurred in 46% of all halibut which contained food. Various mysid species (mostly Neomysis kadiakensis and Metamysidopsis elongata) were also important prey. Mysids were the numerically dominant prey group. Juvenile-adult sciaenid fishes, fish larvae, and amphipods were minor components of the diet (Table 2).

Table 2. Measures of the importance of various prey consumed by juvenile-small adult California halibut (Paralichthys californicus) collected from 6, 18, and 30 m depths off San Onofre and Oceanside, California, during March-September 1981. Weights are reconstructed wet weights (see text). Prey are ranked by Index of Relative Importance (IRI, Pinkas et al., 1971).

Prey Category	IRI	% Freq.	% No.	% Wt.
Engraulis mordax, juveniles-adults	4262	46	8.8	84
Metamysidopsis elongata	957	21	46	.1
Neomysis kadiakensis	827	25	32	1.0
F. Sciaenidae, juveniles-adults	26	1.7	.2	14.9
Neomysis rayii	11.9	3.5	3.3	.1
Acanthomysis costata	9.7	3.5	2.8	.01
Mysidopsis californica	7.7	3.5	2.2	<.1
Engraulis mordax, larvae	7.2	7.0	.8	.2
Acanthomysis sculpta	2.3	2.6	.9	<.01
Mysidopsis intii	.8	2.6	.3	<.01
Acanthomysis macropsis	.6	1.7	.3	<.01
Unidentified juvenile-adult fish	*	12.2	1.4	*
Fish Larvae	*	7.8	1.3	*
Nonmysid Crustaceans	*	5.2	.6	*

*Reconstructed weights not available.

Depth of capture influenced halibut size and mysid abundance. Halibut captured from the 6-m depth stratum were smaller than those from deeper waters (Fig. 1). The mean field abundance of mysids was generally greater (114/m^3) at 6-m depth than at 32 meters (23/m^3) (Fig. 2). Small halibut, most abundant in shallow water, had more frequently consumed mysids at 6-m depth where mysids were most abundant. Larger halibut, more commonly found in deeper water, fed relatively more frequently on anchovies (Fig. 3).

There was also an obvious seasonal influence on prey selection by P. californicus. Halibut collected during March to May were more likely to have consumed mysids, while those examined during June to September fed more frequently on anchovies (Fig. 4). This pattern was independent of depth and only partly confounded by halibut size

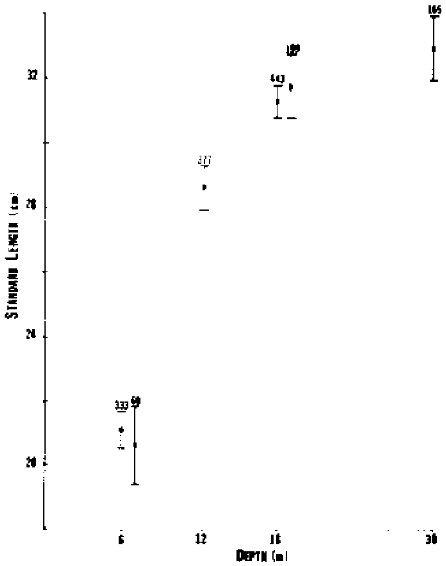

Fig. 1 Mean size of California halibut (Paralichthys californicus) trawled at 6, 12, 18, and 30 m depths at various locations (pooled) in between San Clemente and Oceanside, California. Two standard errors of means and sample size are noted. Dotted lines represent data collected by Lockheed Environmental Sciences during 1978, 1979, and 1980, pooled (Southern California Edison, 1981); solid lines represent data for fish collected by the authors (March 1980-September 1981).

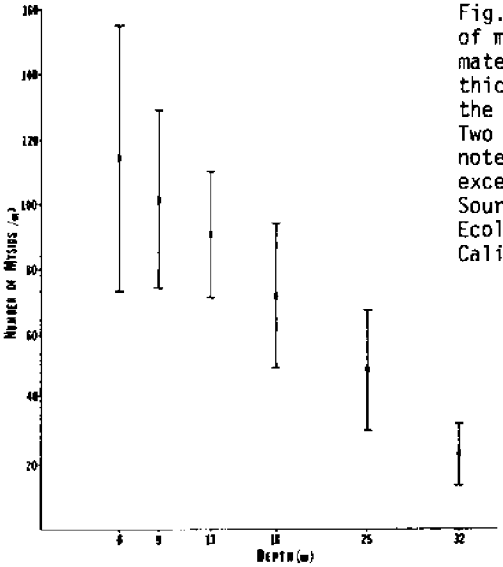

Fig. 2 Plot of the mean density of mysids (all species pooled) estimated from tows of a 1-m^2 epibenthic sled (0.333 mm mesh) during the period March-September 1979. Two standard errors of means are noted; sample size is 13 cruises, except for 6-m depth (11 cruises). Source of data: L. Gleye, Marine Ecological Consultants of Southern California, pers. comm.

(Fig. 3). The relative abundance of northern anchovy in the diet was positively correlated with an increase in the field abundance of anchovy (Spearman's rho = 0.943, N = 6, P = 0.01; Fig. 4). Although there was no significant difference in the size of halibut caught at 18-m depth during March to May as compared to June to September ($t = 1.59$, df = 64,55, $P > 0.1$), there was a significant difference in the proportion of P. californicus that had consumed northern anchovy during these two periods ($\chi^2 = 23.2$, df = 1, $P < 0.001$; Fig. 3).

During the season (March to May) when halibut fed on mysids, fish captured from the 18-m depth stratum appeared to have selected the largest of the two most commonly eaten mysid species. Neomysis kadiakensis (adult weight, 41 mg) was much more abundant in halibut stomachs than in field collections while the converse was true of the much smaller (adult weight < 3 mg) Metamysidopsis elongata. Ivlev's (1961) index of electivity illustrates the apparent preference of P. californicus for the larger mysid (Table 3).

Discussion and Conclusions

A number of interactive factors appear to influence prey selection in P. californicus. Predator size, season, depth, and size and species of prey all play a role. In general, our data suggest that P. californicus feeds in a manner consistent with optimal foraging theory.

Numerous investigations have shown that predatory fishes consume increasingly larger prey as they grow (Nikolsky, 1963). This is mechanically possible because mouth size becomes larger as the fish grows and is necessary due to the increasing nutritional demands of the predator. Dietary habits consistent with such behavior have been described for a diverse array of Pacific coast marine fish, e.g., see the studies by Quast (1968), Hobson and Chess (1976), Ambrose (1976), and Coyer (1979). In conformity with this general rule, small halibut feed on mysids

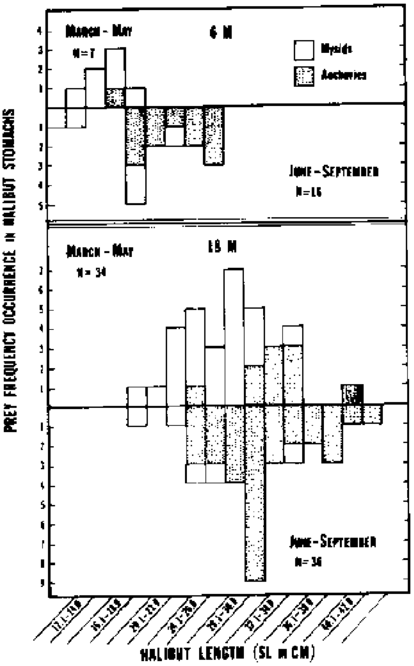

Fig. 3 Comparison of size frequency distributions fo California halibut that had eaten mysids versus northern anchovy (Engraulis mordax) during two seasons (March-May and June-September) at two different depths (6 m and 18 m). Feeding by halibut captured at 30 m is not shown because relatively few halibut were caught at this depth.

while larger P. californicus consume anchovies (Fig. 3). It is noteworthy that queenfish (Seriphus politus) which inhabit our study area exhibit a similar pattern, i.e., consuming mysids when small and anchovies as it grows (Gleye and Bernstein, 1981).

Small halibut may inhabit shallow water because the density of one of their preferred foods (mysids) is greatest in shallow water (Fig. 2; also see Bernstein and Gleye, 1981). With regard to mysids, the three bathymetric zones sampled may be viewed as alternate patches of prey with varying abundance. There are numerous examples of terrestrial, aquatic, and marine predators which forage in patches of the highest prey density (MacArthur, 1972; Krebs, 1978; Hughes, 1980).

Our data are consistent with the prediction that P. californicus elect the largest prey available. In general, predators should select more profitable (larger) prey, not always in proportion to their abundance (MacArthur and Pianka, 1966; Hughes, 1980). This theory has been supported by several experiments in closed systems using freshwater sunfishes (Werner and Hall, 1974; O'Brien et al., 1976). Our results however are merely consistent with theory (Hughes, 1980) and do not rule out the possibility of discriminatory criteria other than size, such as the ability of halibut to differentiate different prey types on the basis of their behavior.

The relatively large size of E. mordax clearly makes them the most profitable prey for medium-sized predators such as juvenile and small adult P. californicus. Mysid abundance peaked nearshore during late spring-early summer (of 1979), in contrast to a later increase in anchovy abundance during summer (of 1980) (Fig. 4). The apparent shift in halibut predation from mysids to anchovies that occurred during June 1981 (Figs. 3,4) was probably the result of an increase in the abundance of anchovies rather than a decrease in mysids. Optimal foraging theory predicts that a larger, more profitable and preferred prey such as anchovies would be chosen over a smaller, less preferred prey such as mysids, regardless of the abundance of mysids. The consumption of mysids during the period of peak anchovy abundance perhaps reflects the fact that both mysids and anchovies have patchy distributions (Clutter, 1969; Huppert et al., 1980). The clumped nature of mysid and anchovy schools may make it difficult for P. californicus to assess the relative abundances of alternate prey types on a short-term temporal basis. It is noteworthy that large adult halibut seem to prefer fishes larger than E. mordax. For example, our largest halibut specimen (69 cm SL) had eaten two adult white croaker (Genyonemus lineatus); casual observations of the diet of large halibut made by ourselves and our colleagues corroborate this. Furthermore, a comparison of the relative incidence of the various mysid species eaten and their respective abundances suggests that, when given a choice between large and small mysids, P. californicus prefers the larger Neomysis kadiakensis even though it is much less abundant than the smaller Metamysidopsis elongata (Table 3). The energetic benefit of such a choice is obvious since individual N. kadiakensis weigh 13 times as much as M. elongata.

In summary, we conclude that juvenile and small adult P. californicus selectively prey on the largest food items available; specifically, E. mordax are preferred over mysids and, among mysids, the larger of two common species is chosen. We emphasize, however, that our data and

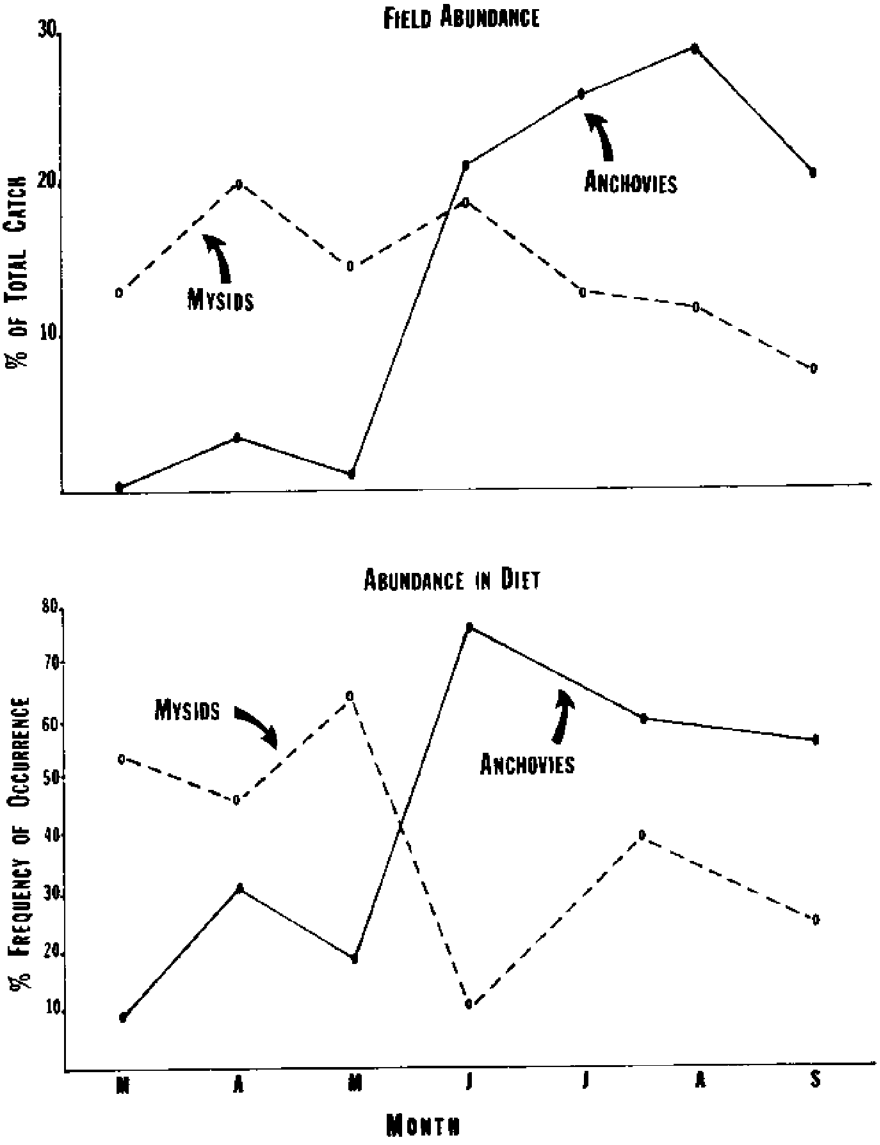

Fig. 4 Relative field abundance (percent of total catch) and relative abundance in halibut diet (percent frequency of occurrence in stomachs) of mysids and northern anchovy (Engraulis mordax) each month during spring-summer. Mysid and anchovy field abundances estimated (see Methods) based on sled tows (6-18 m depths) and lampara catches (5-30 m depths) made during March-September 1979 and 1980, respectively.

Table 3. Estimated field abundances, numbers in *P. californicus* stomachs, and electivity values for mysid prey present in halibut collected at 18 m depth in the San Onofre-Oceanside area each month during the period March-September 1981. Field abundance values (nos./m^3) are based on estimates made during March-September 1979 (L. Gleye, Marine Ecological Consultants of Southern California, pers. comm.).

	March	April	May	June	July	August	September
Neomysis kadiakensis							
Field Abundance	0.5	4.0	8.9	9.1	11.8	3.8	8.5
Nos. in Halibut Stomachs	95	110	137	32	2	0	0
Electivity	+.99	+.90	+.63	+.59	+.74	-	-
Metamysidopsis elongata							
Field Abundance	78.2	80.2	49.7	61.5	47.6	20.6	26.5
Nos. in Halibut Stomachs	7	34	50	42	0	0	0
Electivity	-.86	-.53	-.55	-.13	-	-	-
All other mysids							
Field Abundance	8.4	19.2	4.0	12.5	20.5	8.9	6.7
Nos. in Halibut Stomachs	0	0	31	0	0	0	0
Electivity	-	-	+.38	-	-	-	-

analyses are preliminary. Patterns of prey abundance and their dietary contribution were compared for spring-summer seasons among different years. The fact that changes in the prey composition of halibut can be explained by these data however suggests that the predator-prey system involving halibut-mysids and anchovies is fairly persistent from year to year. The relative abundances of mysid species in the general study area fluctuated from 1976 to 1979 but have remained constant since that time (L. Gleye, Marine Ecological Consultants of Southern California, pers. comm.). Mysid abundances have been consistently greater during the first half of the year in the San Onofre-Oceanside area (Bernstein and Gleye, 1981), whereas the abundance of E. mordax historically peaks nearshore within the Southern California Bight during the second half of the year (Huppert et al., 1980).

Data will soon be available on mysid and anchovy abundances at various depths in the San Onofre-Oceanside area during 1981. At that time we will incorporate these new data into a more accurate reassessment of prey selection by P. californicus.

Acknowledgements

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Variations in the Feeding Habits Of Salmon Caught in Gillnets During a 24-hour Period

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Introduction

Most studies of the daily or diel patterns of feeding behavior of salmon have been conducted on juveniles in fresh water or in coastal waters. These have generally shown that juvenile pink, sockeye, and chum salmon are diurnal or crepuscular feeders (e.g., Doble and Eggers, 1978; Godin, 1981). However, Shimazaki and Mishima (1969) analyzed the feeding habits of maturing pink salmon in the Okhotsk Sea and found peak values for stomach fullness between sunset and sunrise.

This is a study to investigate possible changes in the feeding rate and prey composition of several species of salmon caught over a diel period in oceanic waters of the northeastern Pacific Ocean.

Methods

The study was localized within the region between 54°51.5' and 54°57.9'N latitude, and 144°55.1' to 145°11.3'W longitude. Two gillnets, each 800m long and 6m deep, with 300m of 115mm, 250m of 121mm and 250m of 130mm (stretch) mesh, were alternately fished for about 2-hour periods over 24-hours in the Gulf of Alaska. The first net was set at 1200-hours local time (GMT-9 hours) on July 13; the last set was hauled at 1206-hours on July 14, 1981. The time that each of the twelve sets fished varied from 129 to 150 minutes (from start of set to start of hauling). Five to eight minutes were required to set the nets, twelve to 20 minutes to retrieve them.

Consecutive gillnets were set 1.5 to 3.0km apart to reduce the possibility of one net influencing the catch of another. Gillnets were set along a ship course of 040°, except for the first two nets which have set along 230°. In general, nets drifted 0.4 to 6.5 km northward during the sets.

The vertical location (upper, middle and lower 2m) and species of each gilled salmon were noted as the gillnet was hauled aboard. Fish were removed from the gillnets, identified, measured (fork length) and weighed with a beam balance. Stomachs were removed, weighed to the nearest gram with a beam balance, placed in a tray and cut open with scissors. The fullness of gastric and pyloric portions of the stomach was each estimated visually as: (a) empty, (b) trace amounts (few individual organisms with cumulative weights of a gram or less), (c) <1/3 full, (d) >1/3 full, and (e) full (rugae fully distended, stomach lining thin and translucent). The degree of digestion was estimated as (a) fresh (prey intact, no obvious digestion; fish and squids with intact skin, euphausiids translucent), (b) partially digested (fishes and squids identifiable, with skin, but not flesh, largely digested; euphausiids opaque, appendages often absent, and (c) digested (fish consisting of pieces of white flesh and vertebrae, crustaceans in pieces, euphausiids sometimes identifiable from fragments eyes).

The percentage composition by volume of major prey taxa (euphausiids, amphipods, squids, fishes, salps, pteropods, chaetognaths, medusae, copepods and appendicularians) was visually estimated for the cardiac and pyloric portions of each stomach. Stratification of food taxa in the cardiac portion was noted. Stomachs with diverse prey taxa were flushed into a petric dish to facilitate identifications and estimation of volumes. Samples of prey organisms were preserved in formalin for verification and identification to lower taxa. Stomachs with more than trace amounts of food were then rinsed with water to remove adhering food items, blotted and reweighed to the nearest gram.

All the above estimates and determinations were performed during the two hour periods after setting one gillnet and hauling the other.

Results

A total of 108 sockeye, 68 pink, 49 coho, 44 chum and 6 steelhead trout were caught. Stomach weights of the four species of salmon, calculated as a percentage of body weight for each gillnet set over the 24-hour period, were usually variable, ranging from 0% (empty) to a maximum of 4.0% for sockeye, 2.3% for pink, 3.3% for coho and 3.0% for chum salmon.

Although empty stomachs occurred for all species during most sets, variations of maximum stomach weight: body weight percentages suggest the possibility of diel periodicity in feeding of some species. High values for sockeye, pink and coho salmon (>2%, >1%, >0.7% body weight, respectively) occurred after sunset (2113 hours), and maxima occurred during nighttime sets. However, some high values also occurred in the morning hours for these species. No diel trend was indicated for chum salmon.

Visual estimates of stomach fullness showed similar trends. Full cardiac and pyloric portions of sockeye, pink and coho stomachs were only noted for fish caught between sunset and sunrise.

The average percentage composition of major prey taxa was calculated for the cardiac portions of stomachs containing more than trace amounts of food for each species of salmon and each gillnet set. Distinct trends were apparent in the composition of prey over the 24-hour period. The percentage of euphausiids increased in stomachs of sockeye, pink and coho salmon caught in gillnets that fished between sunset and sunrise. Squids, fishes and amphipods were more important during daytime than nighttime periods for these species. No diel changes were apparent for chum salmon.

Discussion

Changes in stomach fullness and prey composition over the 24-hour period indicate diel variations of feeding behavior of sockeye, pink and coho salmon caught in the upper 6m of oceanic waters of the Gulf of Alaska. Predation by these species of salmon apparently shifted from several types of prey available in upper waters during the day to almost exclusively euphausiids at night, when feeding was very intense. This shift in feeding habits coincided with the migration of a 24-kHz scattering layer into the surface waters after sunset on an overcast night. In addition, total catch rates by the gillnets and the proportion of salmon caught in the upper one-third of the gillnet increased during darkness, suggesting vertical movement of salmon into the upper 2m at night. Salmon are apparently capable of modifying their swimming and foraging activities in oceanic waters to capitalize on abundant prey organisms available in surface waters, even at the low light intensities present during overcast conditions at night.

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Predator-Prey Relationship in a Guild of Surfperches

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SYNOPSIS

Five species of surfperches (Embiotocidae) exploit the small prey in benthic "turf" on a kelp-forested reef off southern California. Turf contained inorganic debris and "items of doubtful food value" (plants, colonial animals, etc.) which fish mostly rejected, and "items of food value" (amphipods, etc.) which they selected. In mode of food handling, two species selected their food by taking careful bites and swallowing all items, either by picking out small amphipods etc. from algae or plucking larger prey and crushing it between strong pharyngeal teeth. The three others selected food by winnowing bites of turf in their mouth and spitting out the cast. All species differed from expected in foraging effort among microhabitats, one noticeably more than the others; they generally preferred microhabitats with highest densities of valued food items. All but one foraged during the day only. Functional morphological specializations may constrain their foraging modes and diets. The presumed most generalized mode is "browser-picker"; "crunching" and "oral-winnowing" are more specialized. The surfperches' elaborate pharyngognathy is a likely basis of these specializations for greater foraging efficiency.

Food Specialization by *Mulloides flavolineatus* (Mullidae) at Midway Islands

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Introduction

The Northwestern Hawaiian Islands (NWHI) is a chain of atolls and volcanic islands stretching northwest from Niihau to Kure. Kure and Midway Islands are under military control and the remaining islands are a national wildlife refuge. The NWHI therefore provide a unique opportunity for the study of predator-prey relationships in fish populations. Inshore commercial fishing may be allowed in the NWHI in the future; there is currently a research program sponsored by Sea Grant and the State of Hawaii to estimate the fishery potential of the shallow waters of the NWHI atolls, islands and shoals.

Goatfishes (Mullidae) are important food fishes in Hawaii and throughout the Pacific. There is a small commercial and subsistence fishery for all goatfish species in the high Hawaiian islands. Opening the NWHI to a commercial fishery would result in considerable fishing pressure on goatfish populations that are presently in their natural state. I have been studying the diet and potential diet of goatfish species at Midway Islands, NWHI. This paper deals with the feeding preferences of one species, Mulloides flavolineatus.

Goatfish locate their prey by means of chemosensory receptors in the barbels. The prey is then disturbed by blowing in the sand (Holland pers. comm.) or digging with the pectoral fins (pers.obs.). Searching goatfish move rapidly over the sand flicking the surface with the barbels; when food is located they stop and dig head down into the sand. Mulloides flavolineatus may dig a hole 5 - 10 cm deep.

Methods

Goatfish and sand samples were collected at the same time from the same locations in Midway lagoon. Station 1 was located at the north end of the lagoon just inside the reef at a depth of 1-2 m. The sand was in a layer 1-2 cm deep overlying consolidated limestone, with very few deep patches. Station 2 was in a similar position relative to the reef with a water depth of 2-4 m. At both stations the sediment was medium-sized sand. Three 2 litre sand samples were collected at each station with corers made from 3 lb. coffee cans. The sand was preserved in 10% formalin and stained with the vital stain, rose bengal, to facilitate sorting of small invertebrates. Twenty-two fish were collected using the Hawaiian pole spear. The gut cavities of the fish were injected with 100% formalin immediately after spearing, and the whole fish were preserved in 10% formalin.

The Proportional Similarity Index (PSI) was used as a measure of preference. $PSI = 1 - \frac{1}{2} (p_{ij} - p_{ik})$, where p_{ij} and p_{ik} are the proportions of the ith species in the guts and sand respectively. Higher values of PSI, to a maximum of 1.0, indicate that resources are being used in proportion to their availability, while lower values indicate dietary specialization (Feinsinger *et al* 1981).

Results

Polychaetes were the most important prey of *Mulloides flavolineatus* and were found in all fish with recognizable gut contents. A wide range of prey, mostly small animals, e.g. isopods, amphipods, crabs were also eaten. Polychaetes were also the most abundant taxon in the sand samples. At Station 1 the mean density of polychaetes was 54 animals/litre with a range of 30-75 animals/litre. At Station 2 the range was 25-280 polychaetes/litre with a mean of 113. Almost all the polychaete species occurring in the sand samples were present in one or more gut contents of *M. flavolineatus*, with a total of 23 species eaten. PSI values for polychaetes were 0.2695 at Station 1 and 0.1167 at Station 2 implying dietary specialization. Two sand dwelling polychaetes, the opheliid *Armandia intermedia*, and the tube dwelling onuphid *Nothria holobranchiata* comprised two thirds of the total numbers of polychaetes eaten (Table 1). An unidentified capitellid species which was very abundant in the benthos constituted a relatively small percentage of the diet. Individuals of the Capitellidae are considerably smaller than *A. intermedia* or *N. holobranchiata*.

At both stations the relative abundance of *Armandia intermedia* and *Nothria holobranchiata* in the diet is greater than their relative abundance in the benthos (Figs 1 and 2). Viven and Peyrot-Clausade (1974) found that the consumption of polychaete species by holocentrid fish at Tulear, Madagascar was directly proportional to their abundance in the benthos. At Midway nereid and dorvilleid species were eaten in direct proportion to their abundance in the sand (Figs 1 and 2). Capitellid polychaetes comprised 73% of the polychaetes in the sand at Station 2 but less than 5% of the diet. At Station 1 capitellids were 45% of the benthos and 6% of the diet.

Discussion and Conclusions

The onuphid polychaete, *Nothria holobranchiata*, builds a permanent tube covered with sand grains. This species has been previously recorded only from deep water habitats in Hawaii; all deep water species of Nothria are sessile (Fauchald and Jumars 1979). Other sessile onuphid species, e.g. Diopatra leuckarti, are gregarious and form mounds of vertically orientated tubes and compacted sediments with an associated community of tanaids, amphipods, and polychaetes, etc. (Bailey-Brock 1980). Onuphids such as Nothria and Diopatra species are surface feeders, and are capable of retracting into their tubes when disturbed (Fauchald and Jumars 1979, Hulberg and Oliver 1978). It is possible that the concentration of animals and/or fecal material around the tubes of Nothria holobranchiata provide a means whereby Mulloides flavolineatus 'keys in' on the presence of potential prey (Holland pers. comm.).

Opheliid polychaetes do not build tubes, but burrow in the sand. Armandia intermedia is active at the sand/water interface, feeding by ingesting sand grains and associated organic matter (Fauchald and Jumars 1979). This behavior would seem to make this species vulnerable to predation by fish feeding within the sand.

Larger species of capitellids, e.g. Notomastus and Dasybranchus species, construct deep burrows and are not active near the surface; Capitella capitata burrows at or near the surface. This small species was eaten by Mulloides flavolineatus more often than the other capitellids. The depth distribution of capitellid polychaetes at Midway is unknown, due to sampling constraints, but it is likely that capitellid species 2, like C. capitata, is active near the surface. Individuals of capitellid sp. 2 are very small and may be energetically 'unattractive' as food.

The gut contents of the goatfishes collected at Midway may contain prey eaten at locations other than those of the sand samples. However, every effort was made to spear goatfish while they were feeding, and species were observed feeding at the same locations where the sand samples were taken.

Heavily ornamented tubes such as those of Diopatra ornata and D. cuprea function as predator defenses for the worms and the fauna associated with the tubes (Brenchley 1976, Woodin 1976,1978). Onuphid polychaetes extend some distance out from their tubes when feeding (Fauchald and Jumars 1979). Regenerated heads of D. leucharti from Oahu, Hawaii, are evidence of predation on the anterior portion of this species (Brock pers. comm.). Whole or large sections of Nothria holobranchiata were found in the gut contents, indicating that the sand grain covered tube is less protective than the more ornamented tubes, or that the active digging of Mulloides flavolineatus within the sand causes the worms to leave their tubes.

Infaunal species that live in tough tubes and/or deep within the sediment, and can quickly retract exposed body parts, are less affected by fish predation than species that are active close to or on the surface (Virnstein 1979, Hulberg and Oliver 1978). The apparent negative selectivity of Mulloides flavolineatus on the surface active capitellids is a result of the very small size of these animals. It is likely that M. flavolineatus is eating polychaete species as encountered, but that prey size, behavior and habitat preference make some species more available than others.

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TABLE 1

Polychaete species in the diet of *Mulloides flavolineatus*
Percent of total numbers of polychaetes in gut contents
All stations pooled. N (fish) = 22

TAXA		%N
Opheliidae	*Armandia intermedia*	34.98
	Polyopthalmus pictus	1.08
Onuphidae	*Nothria holobranchiata*	33.44
Nereidae		7.09
Syllidae		4.93
Eunicidae	*Nematonereis unicornis*	3.39
	Eunice sp.	.46
	Lysidice sp.	.62
Capitellidae	*Capitella capitata*	2.46
	Dasybranchus/Notomastus sp.	.77
	capitellid sp. 2	.77
Spionidae		2.16
Dorvilleidae		2.00
Amphinomidae	*Linopherus* sp.	2.00
Chaetopteridae	*Spiochaetopterus vitrarius*	.46
	Phyllochaetopterus verrilli	.31
Cirratulidae		.46
Glyceridae	*Glycera tesselata*	.46
Arabellidae	?*Notocirrus* sp.	.31
Hesionidae		.31
Polynoidae		.15
Paraonidae		.15
Phyllodocidae	*Phyllodoce* sp.	.15
unidentified polychaetes		1.08

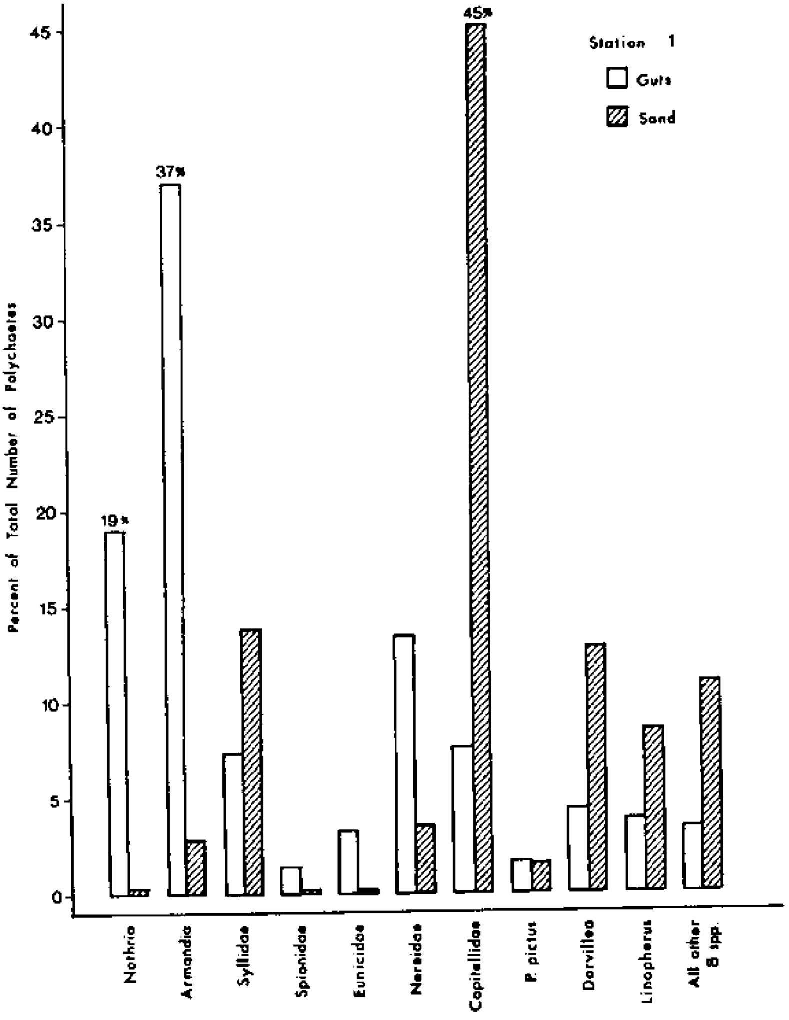

Fig. 1 Polychaetes in the guts of M. flavolineatus and sand Station 1

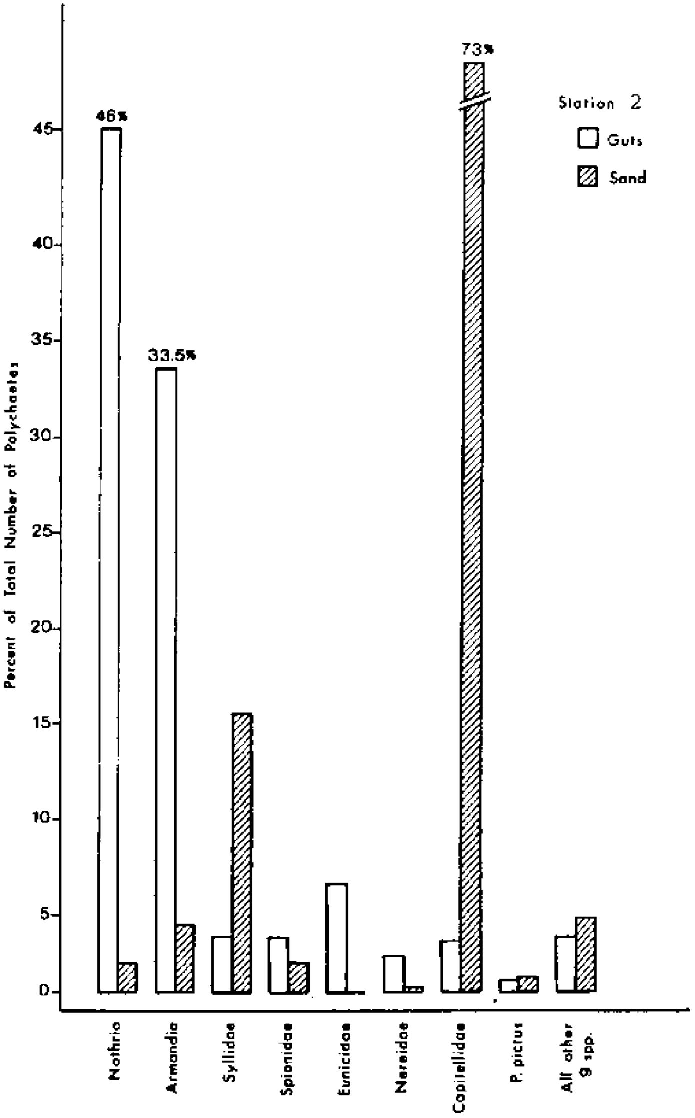

Fig. 2 Polychaetes in the guts of M. flavolineatus and sand Station 2

Session IV Discussion
Feeding Behavior of Fishes and Prey

Ted Hobson and James Chess, Discussion Leaders

Questions Following Adams Presentation:

Cohen discussed the phenomenon of predation by adults on subadults and juveniles of the same species and stressed that information on feeding habits should be incorporated more often into management schemes. Feller asked why Adams felt that their samples taken at sea were less biased than those taken through port sampling. Adams pointed out the non-random nature of the fishing industry and indicated there were other problems associated with the handling of the port-sampled fish. Karpov asked how Adams identified prey items that were gelatinous or easily digested from port samples. Adams agreed that this was a problem. Hobson commented on the unusual behavior of the widow rockfish in that it schooled by night to prey, rather than during the day like most fishes.

Questions Following Maule Presentation:

Moyle asked what the size and age of maturity of the walleye was and whether there was a shift in food composition with size. Maule said the size range he studied was from 200 to 750 mm TL, but did not know for sure what their ages and stages of maturity were. He noted a slight difference in the percentage of empty stomachs between smaller and larger individuals, but did not think it was of any significance.

Questions Following Feller Presentation:

Prior to the talk, someone was recorded as saying: "Here comes the rabbit killer." Van Blaricom asked whether gut contents could ever reach such an advanced state of digestion that this immunological technique would not work. Feller responded affirmatively since proteins are digested. Some of his experiments at room temperatures using grass shrimp fed nematodes and sacrificed over time indicated that his techniques could detect nematode protein for up to 48 hours, but that nematode remains would virtually disappear in three hours. This indicates that the signature stays around a considerable amount of time. Cailliet asked how long it takes to run one analysis. Feller said that the time is short once the laboratory is set up, and the antisera are available. All antisera need to be checked for cross reactions with each other. The actual process of sucking up a portion of the stomach fluid and placing it on the microscopic slide, then running it through the antibodies for all potential prey antisera, and waiting for the response takes about 48 hours. But Feller said that he could do about 500 of these tests per day. So, building the panel of antisera takes a long time, but processing the guts is relatively swift. Sakanari asked if you could quantify the antibody. Feller responded that he could measure the concentration of antibodies of different kinds in the blood collected. Feller responded to a question by Herbold by saying that he had not tried to analyze fecal matter in this way, but he said it could be done, but it would probably be pretty well broken down and only portions of the fecal matter could be recognized. Grossman asked if only information on the kinds of prey consumed could be gathered with this technique, or could the amount of each prey item be estimated. Feller then stated that he could, with a bit more work, estimate the relative proportion of each kind of prey by comparing the amount of total sample processed versus the amount that responded to the panel of antisera. However, problems occur here, primarily due to different digestion states, and the results do not indicate what proportion of each prey item actually was consumed by the predator. Also, if prey were macerated by the predator, then this would be extremely difficult. Cowen asked how well this technqiue can discriminate cannibalism from intestinal or stomach lining tissue. Feller mentioned he could detect cannibalism only if the concentration of that tissue was high. Naughton asked for an estimate of the cost per sample. Feller pointed out that it depends on how many antibodies would be needed. It costs him about $200 to make an antiserum. This takes him two rabbits spread over two months, which require feed, care and maintenance. This figure does not include any salaries. If one went to a professional immunological company and provided them with the tissue or fluid, it would cost about $10 per ml. An average rabbit can provide about 100 ml of antiserum. Therefore, that is about $1000 done that way. Feller has now found a firm that will do it for about $150 a rabbit. Of course these are rough figures, but Feller only intended it to give everyone an understanding of the cost.

Hixon asked whether this technique had been used on herbivorous fishes. Feller said that he was now working on this, especially to distinguish whether fish eat plants like Spartina for the plants themselves or for the detritus, bacteria, or epiphytes on them. Knechtel inquired if there were other types of donors which would be any cheaper than rabbits. Feller replied that rabbits were a good size and that we already "stick it to white rats enough." LaBolle asked what level of identification is obtainable using this technique. Feller pointed out that it depends upon the the specificity of the immuno-response of the rabbit. So far, he can distinguish families and sometimes down to genus and species. He first looks at the contents visually and identifies all that he can, then uses the remaining fluid for the immunological analysis. LaBolle then asked what the minimal percent of the gut contents that he would do this analysis for. Feller said that since most fish he studied had 90% gorp in their stomachs, it was usual to use this technique. Pearcy suggested that this approach be used on macrourids, since these deep-dwelling bentho-pelagic fishes often come up with the alimentary tract evert and many of the contents lost. Feller said that he intended to. Ursin mentioned a different possibility for identifying unrecognizable material in the gut. A suggestion was made by some geologist colleagues that the unsaturated fatty acids be analyzed, much in the way they are studied in fossil deposits. It requires knowing the molecular weight and therefore is some guesswork involved. Feller was familiar with work by Perry Jeffries at the University of Rhode Island, who is trying to trace food web relationships using this technique. Since it is not very specific, it has been difficult to work with, but it is under investigation by Feller's colleagues.

Questions Following Roberts Presentation:

Cailliet stressed the importance of using the frequency with which a particular prey item occurred in predator guts as well as the percent by number or biomass. This was in reference to Roberts' comment that seldom in an individual gut were both of the major dominant prey items found. Simenstad inquired about the relationship between potential feeding periodicity in the California halibut and the cycles of their prey. Roberts replied that the data on the fish prey and mysid abundance were taken both day and night and that this information was being analyzed. Chapman inquired about the large variation in mysid abundances and Roberts related this to the patchiness of both the mysids and euphausiids. Simenstad asked about the incidence of large epibenthic crustaceans in the large trawls, such as crabs and Roberts stated that such organisms were extremely rare. Cailliet asked if the halibut and queenfish were indeed eating the same kinds of food items. Roberts replied that they were but that they were probably not competing since they were eating different size classes of these prey and that this overlap was not common at all locations. Chess asked if the anchovies in the diet of halibut were more frequent at night or during the day. Roberts had tested this using fullness indices and concluded that there was no difference in day- and night-caught halibuts, so they pooled the stomach samples for this presentation.

Questions Following Pearcy Presentation:

Eggers inquired about the density of euphausiids in surface waters and Pearcy replied that they would be getting these estimates from Isaacs-Kidd midwater trawl samples. Van Blaricom asked whether the eye structure of the salmon would allow it to feed in low light levels. Pearcy responded that salmon have a normal vertebrate eye and could easily use dark-adapted night vision to pick out some of these food items. Karpov asked whether they had used their data to compile an estimate of a daily ration or meal. Pearcy said that they had not, since it was difficult to do with the high variability in the data gathered. Karpov and Pearcy discussed the possibility of doing so, given that percent fullness indices may not be entirely accurate and the fish appeared to be feeding over a large portion of both day and night. Cohen asked if it were possible that euphausiids were more vulnerable due to their own bioluminescence which is usually thought to be for counter-shading. Field asked whether water clarity differed among the areas sampled and Pearcy said he did not think so. Feller thought that euphausiids were more easily caught in nets which were fishing downward rather than horizontal or upward and wondered if salmon fed on euphausiids that way. No one knew. Simenstad recalled that sonic tagging results showed that salmon could undergo rapid and extensive vertical movements, suggesting that they might be able to go deep during the day to pick up squid and myctophids. Pearcy responded that fishermen never fish for them below 20 or 30 meters and Simenstad recalled that the deepest recorded by Ichihara and Nakamura was 80 meters, so it was not likely. Also, Pearcy found some myctophids in their stomachs which had never been collected shallower than 200 m.

Questions Following Laur Presentation:

Cailliet asked whether other fishes ever follow the oral winnowers around to pick up what they discard, or do they ever reingest what they have discarded themselves? Laur said that this happens very rarely, and that when it does, they end up discarding the remains again since little of food value is left in it. A discussion between Chapman and Laur followed concerning mouth width, oral activity volume and prey size.

Questions Following Sorden Presentation:

Ebeling asked if these goatfish foraged mostly at night and what kind of behavioral mechanisms they used to capture their prey. Sorden could not accurately determine periodicity of feeding since she speared her fish during the day foraging over open sandy areas, but she thought that some species fed both during the day and at night. In the sandy areas, they searched over the substrate, and once they found a likely area, they excavated holes in the sand and removed whatever organisms they could from these holes. Ebeling also asked whether some of the worms eaten were more available during the night and Sorden mentioned that she understood some errant polychaetes were nocturnal, but that she did not have this kind of information on most of the prey species in her study. Van Blaricom asked what other kinds of predators were seen commonly feeding on prey in this sandy area. Sorden suggested that perhaps gobies and blennies did, but that they most likely consumed smaller prey items and that the goatfish were definitely the most common predators in that microhabitat. She had not noticed any benthic feeding sharks or rays there. Herbold asked if all the goatfishes appear to have been feeding in these sandy areas as solitary individuals or in groups. Sorden replied that they usually fed individually or in small groups, but not in schools.

Session V

Fish Feeding as a Structuring Force on Prey Communities

SESSION LEADER
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John Chapman
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Millicent Quammen
Edward Cohen
Marvin Grosslein

The Importance of Behavior in Plant-Herbivore Interactions
A Case Study

Gail V. Irvine
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Consumers have been demonstrated to have a dramatic influence on the composition of communities in a number of both terrestrial and marine habitats (Paine, 1966; Harper, 1969; Irvine, 1973; Lubchenco, 1978; Robles and Cubit, 1981). The effects are usually ascribed to selective feeding and often feeding observations and gut analysis are used to make inferences about the effect of a consumer. However, other behaviors of consumers in addition to selective feeding can have important effects on community structure (VanBlaricom, 1976). Interference interactions and other specialized behaviors are often ignored in the analysis of interactions which "structure" communities. Awareness of these interactions should affect the design of experiments and the care with which inferences concerning causation are made.

In this paper, methods used in assessing the impact of a consumer on other species in the community will be discussed, then a study of the coral reef damselfish, *Eupomacentrus planifrons*, will be used to illustrate the effectiveness and limitations of some of these methods.

Various methods are commonly employed to determine the impact of a species or group of species on community structure. Although the specific questions addressed are of primary importance in determining which methods should be used, the nature of the environment and the organism in question may limit which methods *can* be used. Methods often used include: manipulation of the numbers of individuals of the species in question via addition, removal, inclusion or exclusion experiments, gut analysis and controlled behavioral experiments in the lab and/or field. These methods have both advantages and disadvantages, but used in combination, their results may more strongly elucidate the mechanisms determining community structure.

In caging studies, consumers may be either excluded or included in areas to assess their effects on community structure. Observations on the manipulated community are compared to control areas and causative mechanisms are usually inferred. Such inferences are subject to error from a variety of sources (Dayton, 1973). It is difficult to adequately control experiments; slight changes in physical conditions inside cages may dramatically affect the results and thus our interpretation of the experiment (Hulberg and Oliver, 1980; Virnstein, 1978). In addition, exclusion and inclusion experiments may be qualitatively different (Connell, 1975; Peterson, 1979). Exclusion/inclusion experiments have great potential for suggesting mechanisms responsible for the observed distribution and abundance of species, but without further experimentation, causation is only being inferred from comparisons of community structure in manipulated and controlled areas.

Analysis of prey in the digestive tracts of consumers is another technique which is used to: 1) document what the consumer is eating, 2) suggest the relative preferences of various prey items, and/or 3) make predictions about the effect of the consumer on the distribution and abundance of other organisms. Although the technique has a number of limitations, in some environments it is the only feasible method. Limitations of this method include:

1. Prey may have different relative digestibilities, so what is observed inside the digestive tract, especially at different points along it, may not reflect ingestion. Rapidly assimilated items may be relatively more important in the consumer's diet, and the presence of these items in the gut may be underestimated.

2. Quantitative comparisons of items in the gut can be misleading because of difficulties in determining biomass or in reconciling numbers with biomass. When items vary greatly in size, errors in measurement may be significant. In addition, point-intercept methods bias in favor of certain shapes, making it difficult to accurately translate numbers into volume or biomass.

3. Items in the gut may not reflect active choice; some items may be ingested incidentally with other more preferred items. Predators may be keying in on epiphytes or epizoites, but parts of the substrate plant or animal may also be ingested. This point is significant if one is attempting to determine preference, but less so if the primary interest is the effect of the predator on the relative abundance of its prey.

As an alternative, or in addition to caging experiments and gut analysis, behavioral studies can be conducted in the lab or field. Observed behaviors may provide direct information on mechanisms which affect community structure (Glynn, 1976; VanBlaricom, 1976). These observations can be incorporated into the design of lab or field experimentation.

In lab experimentation, conditions can be controlled more readily than in the field, and, in some cases, animals can be observed more closely. Numbers of individuals can be manipulated to look at the effect of number or density on foraging. Combinations of individuals can also be manipulated to examine the effect of social interactions on foraging behavior. Although there may be many advantages to lab experimentation, the single greatest criticism is that the behavior of the animals may be altered by bringing them into the lab. This difficulty can be reduced by doing experiments in the field, or combining lab and field experimentation.

Field experiments, since they are conducted in the complex milieu of biological interactions and the physical environment an animal deals with naturally, offer opportunities for observing and assessing the importance of more complex behaviors. However, since it is extremely difficult to control conditions, the complicating effects of social behavior, spacing patterns, group foraging behavior, etc., come into play. Problems may also exist in controlling the effect of prior experience, the similarity of physiological state, perhaps even distinguishing male from female. In spite of the difficulties, field observation and experimentation often provide insight into potentially important interactions and their effects (Glynn, 1976; VanBlaricom, 1976; Dayton, 1973).

A case in point is the interaction of the coral reef damselfish, E. planifrons, with organisms in its territories. In my study of damselfish territories, behavioral observations and experimentation in the field were essential to determining the mechanisms structuring the community. Damselfish are abundant on tropical coral reefs, and both male and female damselfish hold interspecific territories which form a mosaic over the hard substrate of the reefs. Within the coral framework of the territories grows an algal turf which is both fed upon and protected by the damselfish. The territories form microcosmic communities within the larger community of the entire reef.

The study was carried out in the western end of the San Blas Archipelago on the Caribbean coast of the Republic of Panama. Most observations were made on patch reefs at depths of less than five meters, during 1978 and 1980. The major questions addressed in this study were the following:

1. Is there any correlation between the pioneer versus persistent status of plants and preference by E. planifrons? For example, are plants characterized by good colonizing ability and rapid growth rate preferred by damselfish over slower-growing, more persistent species?

2. Can E. planifrons maintain preferred plant species in its territories, or does selective grazing on preferred species necessarily result in territories becoming dominated by less preferred species?

First the patterns of algal succession in the presence and absence of grazing were determined. Then, on the basis of differences observed, certain algal species were chosen for use in preference experiments.

The patterns of algal succession were determined by putting paired sets of clay settling plates ($\sim$6.5 cm diameter), one caged and one open to grazing, in a series of twelve damselfish territories, removing these plates at different time intervals and assessing algal composition. A grid of 25 random points was placed over each tile, and the algae beneath each point were counted using a dissecting microscope. After counting, the tiles were returned to the territories. The ages of the sampled tiles were 2, 4½, 15 and 34 weeks.

The pattern of algal succession can be divided into two stages, an early one encompassing assemblages from one week to 15 weeks old, and a later stage from 15 weeks to 34 weeks of age. In the early stages of the development of the algal assemblage, both grazed and caged surfaces were dominated by diatoms, filamentous green algae, and *Polysiphonia* spp. (filamentous red algae), although these groups of algae differed in their abundance in the two treatments. As algal assemblages became older, different algal species replaced the earlier ones, and the disparity between caged and grazed communities became greater. Some species of algae found in one treatment were either never or rarely found in the other treatment. In the early stages of succession, grazing speeded the process of species replacement, whereas in older assemblages the mechanisms responsible for the different patterns were not clear. If the study had stopped here, the conclusion would have been that grazing altered the speed and pattern of algal succession. If selective grazing were assumed to be the major mechanism determining this pattern, then the logical inference would have been that those algae most abundant in cages and rare in grazed communities, *Jania* spp. and *Dictyota* spp., were selectively eaten by damselfish and thus effectively removed from grazed algal assemblages. However, further experiments were devised to examine the mechanisms involved.

Certain algae were chosen for use in preference experiments on the basis of the observed differences in grazed and caged algal assemblages. Diatoms, filamentous green algae and *Polysiphonia* spp. were chosen because of their predominance in young assemblages of both grazed and caged treatments. *Coelothrix irregularis*, a red alga, was chosen because it is abundant in established damselfish territories and in older, grazed treatments. Finally, *Jania adherens* and *Dictyota bartayresii* were chosen because they were present in older caged experiments, but rarely found in grazed assemblages.

Monocultures of each algal group were used in the preference experiments. These monocultures were produced by growing desired algae on dead branches of the coral, *Acropora cervicornis*, under different conditions, or collecting types that couldn't be grown and attaching them to dead *A. cervicornis* branches. All but the desired species of alga were weeded from each branch to produce monocultures. The six types of algae were presented to damselfish in the field in all pairwise combinations. A single pair was presented to a fish at one time and all activities of the fish were recorded for a 15 minute period. Ten to twelve replicates were conducted for each pair of algae tested.

During these observations, the fish demonstrated both positive and negative responses to the algae. Positive responses, observed as simple bites taken by the fish, were interpreted as feeding activities. Negative responses were quite distinct from feeding and had the effect of weeding algae from territories. The weeding behavior consisted of a fish taking a bite of an alga and then releasing it, or taking a bite, swimming and then releasing it. Both the feeding (+) and weeding (-) activities of the fish were incorporated in a Preference Index, which then enabled comparison of the fish's responses to different algal species. The number of weeding responses of a fish to an alga were subtracted from the number of positive responses to give the Preference Index, which if greater than the index for the other species presented at the same time was taken to indicate greater preference.

For example:

$PI_i = f_i - w_i$

PI_i = Preference index for species i

f_i = number of feeding bites of species i/ 15 min. observation period

w_i = number of weeding events of species i/ 15 min. observation period

If $PI_1 > PI_2$, then species 1 is preferred.

The results of each pair-wise replicate test were compiled, and the reaction to different pairs of algae were tested statistically using the Wilcoxon signed-rank test (Siegel, 1956). On the basis of the statistical results, a preference hierarchy was erected. The general form of the hierarchy was, in order of highest preference:

$$\begin{tikzcd} \text{\textit{Polysiphonia} and diatoms} \arrow[r, phantom, ">"] & \text{\textit{Coelothrix}} \arrow[r, phantom, ">"] \arrow[dr, phantom, "\approx"] & \text{filamentous green algae (short)} \arrow[d, phantom, "\vee"] \\ & & \text{\textit{Jania}} \arrow[r, phantom, ">"] & \text{\textit{Dictyota}} \end{tikzcd}$$

The highly preferred alge were basically fed upon and not weeded, and the least preferred species were weeded and rarely fed upon. In between, *Coelothrix* was both fed upon and weeded occasionally and short *filamentous green* algae were largely ignored (Table I).

TABLE I: Mean number of feeding or weeding observations/15 min. trial

Feeding		Weeding	
Polysiphonia spp.	48.2	Filamentous greens - long	26.0
Diatoms	35.4	*Dictyota bartayresii*	13.3
Filamentous greens - long	3.5	*Jania adherens*	2.7
Coelothrix irregularis	3.2	*Coelothrix irregularis*	1.7
Filamentous greens - short	1.7	Diatoms	0.3
Dictyota bartayresii	0.7	*Polysiphonia* spp.	0.1
Jania adherens	0.2	Filamentous greens - short	0.0

Thus, the most highly preferred species were pioneer species (*Polysiphonia* spp. and diatoms), but not all pioneer species were preferred (e.g., filamentous green algae).

Several other experiments tested whether preference between two items was affected by biomass. Since some algal species are larger than others, branches of coral of similar lengths but different algal monocultures will have different algal biomasses. Therefore, in three experiments, biomass was manipulated in order to test its effect. The results of unmanipulated pairs from the preference experiments (e.g., approximately equally-sized long branches of *Polysiphonia* spp. and diatoms) were used as standards for comparison to manipulated pairs. In the preference experiments, long branches with *Polysiphonia* spp. were significantly preferred by damselfish over long branches with diatoms. In one manipulation, *Polysiphonia* plants were mowed down to a height of 4-5 mm and were presented to fish at the same time as branches with intact diatoms. There was no significant difference in preference for these two groups. When shortened branches of unmowed

Polysiphonia plants were compared to long branches of diatoms, again there was no significant difference in preference. Thus, the manipulations of branch length and mowing, designed to reduce the biomass of the larger Polysiphonia, indicate that biomass did have an effect on preference ranking. In another set of experiments, the responses to Polysiphonia plants and filamentous green algae were compared. In the standard preference experiment, long branches of Polysiphonia spp. were highly preferred over long branches of short filamentous green algae. In the manipulation, long branches of Polysiphonia species were mowed and presented to fish with long branches of short filamentous green algae. There was no shift in preference ranking; both intact and mowed Polysiphonia plants were preferred over filamentous green algae. The results in these experiments demonstrate that between the two most preferred algae, Polysiphonia spp. and diatoms, altering biomass did affect results, but between Polysiphonia spp. and filamentous green algae, reducing the biomass of Polysiphonia did not significantly affect the results (Polysiphonia spp. remained highly preferred).

In a separate trial, branches with Polysiphonia spp. were compared to branches with long filamentous green algae several centimeters in length. The fish clearly preferred the Polysiphonia plants and quite vigorously weeded the long filamentous green algae (Enteromorpha spp.). The response of the fish was quite different to these long filamentous green algae than it had been to short filamentous greens; the long filamentous greens were consistently weeded by damselfish, whereas the short filamentous greens were largely ignored. This suggests that biomass or size considerations may greatly affect the type and vigor of the fish's response.

The results of the preference experiments are compatible with the findings of the caging experiments. From comparisons of caged and grazed surfaces we might easily have inferred that Jania and Dictyota were selectively eaten by damselfish since they were both more abundant inside cages. However, the preference experiments demonstrate that this is not the case, rather, Jania and Dictyota are selectively weeded by damselfish from territories. These results demonstrate that caging experiments must be combined with behavioral experimentation in order to determine the actual mechanisms responsible for the observed patterns.

The second question posed was whether damselfish could maintain preferred algae in their territories. A survey of 144 territories on 3 patch reefs indicated that the most higly preferred species, diatoms and Polysiphonia spp., were each present in 99% of the territories surveyed.

Possible mechanisms for maintaining preferred algae in territories include:

1. the weeding out of less preferred algae, which opens up space for settlement and growth by preferred species,

2. the killing of coral, which opens up new substrate for algal colonization, and

3. the exclusion of other herbivores, who are potential grazers on preferred algal species.

Observations have indicated that all three mechanisms are utilized by damselfish. The importance of weeding was demonstrated in the preference experiments. Also, territories which showed evidence of recently-dead coral were noted during the survey. Sixty-four percent of the territories had coral damage of the type which *E. planifrons* inflicts. Thus space is frequently being opened up, though usually at relatively slow rates. This would tend to increase the abundance of preferred species since they are rapid colonizers. Finally, observations and experiments indicate that *E. planifrons* removes small invertebrate grazers from territories, including snails, crabs and sea urchins (Irvine, 1975, pers. obs.; Williams, 1979). Damselfish chase other herbivorous fishes from territories and nip the spines of the sea urchin *Diadema antillarum*, which often results in the rapid departure of these animals from territories. In this way, damselfish enhance the abundance of preferred algae in their territories.

The understanding of this network of interactions might have been quite different if different methods, or combinations of methods had been used.

If study of established algae in territories were combined with gut analysis of *E. planifrons*, electivity indices for the different prey items could be computed. These results might have indicated that diatoms and *Polysiphonia* spp. were preferentially eaten, but problems with the quantification of gut samples might have occurred since preferred algae often exist as epiphytes in territories and the substrate plants might have been ingested incidentally. Since the substrate plants are considerably larger than the preferred plants, the relative preference for *Polysiphonia* spp. and diatoms might be underestimated. This combination of techniques provides no understanding of how succession is affected, and no suggestion that weeding occurs.

If only caging experiments excluding *E. planifrons* were conducted, the effect of the damselfish on the pattern of succession could be described. The mechanism would be unknown, but probably selective grazing would be invoked to explain the differences between caged and grazed treatments. The conclusion, that *Jania* and *Dictyota* are preferred by *E. planifrons*, and their removal through selective grazing accounts for the observed differences, would be incorrect.

If caging studies had been combined with gut analysis, the result might have been confusing. From the results of the caging studies, the inference would probably have been that *Jania* and *Dictyota* are preferred by damselfish. Gut analysis would not have supported this conclusion, since *Jania* and *Dictyota* are probably rare or non-existent in the fish's digestive tract. This approach would be unable to separate other alternative mechanisms, such as:

1. The differences are due to weeding by the fish.

2. Competitive interactions of algae are altered by grazing.

3. Grazing is non-selective, and the increased disturbance on grazed surfaces, due to the action of grazing, arrests algal succession at an earlier stage.

I used a combination of caging studies and field preference experiments in this study. The effects of damselfish on the pattern of succession were determined and then preference experiments demonstrated that both selective grazing and selective weeding behaviors were important in producing the patterns observed. The preference experiments enabled a ranking of the prey items tested. A number of important behavioral observations were made either during the preference experiments or while observing the animals in the field (such as, selective weeding of algae from territories, the killing of coral and removal of other grazers from territories). A further advantage of the direct approach in the preference experiments was that behaviors could be examined quantitatively.

The use of multiple experimental methods certainly increases the ability to make inferences or conclusions regarding the effect of a consumer on community structure. Behavioral approaches often provide more direct evidence for which mechanisms are operating and significant. The case of *E. planifrons* is but one example of how a complex set of behaviors can affect the pattern of species abundance in space and time. If this situation had been examined only via indirect means, erroneous interpretations of causation could easily have been made.

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Differential Fish Grazing and Benthic Community Structure on Hawaiian Reefs

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Introduction

Numerous field experiments have demonstrated the predominant role of herbivorous fishes in determining the local distribution and abundance of benthic algae on shallow tropical reefs (e.g., Stephenson and Searles, 1960; Randall, 1961; Earle, 1972; Vine, 1974; Day, 1977; Wanders, 1977; review by Ogden and Lobel, 1978). Intense grazing by parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) is known to result in most exposed coral-rock surfaces being covered by crustose coralline algae (e.g., Vine, 1974; Littler and Doty, 1975; Wanders, 1977; Brock, 1979). By aggressively excluding other fishes from their territories, certain herbivorous damselfishes (Pomacentridae) maintain filamentous algal mats of relatively high biomass and diversity (e.g., Brawley and Adey, 1977; Lassuy, 1980; Lobel, 1980).

The potential impact of fish grazing on benthic communities is similar to that of any other form of ecological disturbance. The "intermediate disturbance" hypothesis predicts that as the intensity or frequency of such disturbance progressively increases from zero, the species diversity of the affected community will initially increase then subsequently decrease (Connell, 1978). At low levels of disturbance, a few dominant competitors are capable of locally excluding most other species, and at high levels, many local extinctions occur. Diversity thus peaks at an intermediate disturbance level, where the coexistence of many species is maintained because their population densities are kept below levels where resources are limiting. This hypothesis has been supported by observations and experiments in several benthic marine systems subjected to physical disturbance (e.g., Connell, 1978; Sousa, 1979). "To our knowledge, however, only Tansley and Adamson's (1925) study of grazing by terrestrial herbivores and Lubchenco's (1978) study of grazing by intertidal snails have experimentally demonstrated this effect occurring as a result of biological disturbance."

This paper summarizes the results of a field experiment designed to test the intermediate disturbance hypothesis for Hawaiian reef benthos subjected to differential grazing by fishes. Our prediction was that, because grazing intensity would be negligible within fish-exclusion cages, moderate inside damselfish territories, and intense outside territories, the benthic communities which developed on settling plates subjected to these three treatments would exhibit relative species diversity patterns similar to those presented in Figure 1. Our results, which will be detailed in a subsequent publication, confirmed this prediction. The data presented here are part of a broader study designed to investigate benthic succession on shallow coral reefs, the preliminary results of which have been presented elsewhere (Hixon and Brostoff, 1981).

Methods

Our study site was located along a 600-meter section of the subtidal windward reef crest off Coconut Island, located in Kaneohe Bay, Oahu, Hawaii (21°26' N Lat., 157°47' W Long.). Water depths at this site average about one meter. The substrate consists of a flat bench of dead *Porites compressa* coral rock, upon which damselfish establish, maintain and defend algal mats measuring less than a meter in diameter. The dominant grazers here are the damselfish *Stegastes fasciolatus* (= *Eupomacentrus fasciolatus* = *Pomacentrus jenkinsi*), several surgeonfish species (especially *Acanthurus triostegus*), and juveniles of various parrotfishes, which are the most abundant fishes on this reef (see Brock et al. 1979). Sea urchins are rare at this site.

To minimize the bias associated with using a single artificial substrate, we followed benthic succession on three types of settling plates: (1) roughly sanded grey polyvinyl chloride plastic (PVC), which had the advantages of being nearly chemically inert and allowing virtually complete removal of attached organisms, but the disadvantage of being

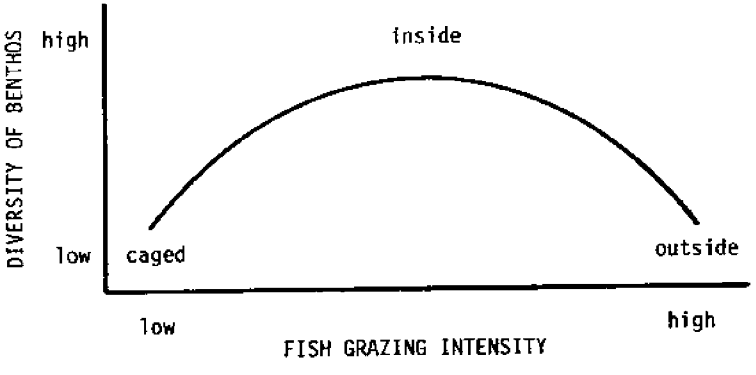

Figure 1. Predictions of the intermediate disturbance hypothesis for the maintenance of local benthic diversity as a function of three levels of fish grazing intensity: within fish-exclusion cages, inside damselfish territories, and outside territories. See text.

an unnatural substrate; (2) flatly cut Porites coral rock, which had the advantages of being the natural substrate and allowing removal of nearly all attached organisms, but the disadvantage of being unnaturally flat; and (3) naturally contoured Porites coral rock, which had the advantage of being the natural substrate in both composition and relief, but the disadvantage of irregular contours precluding exact area measurements. The PVC plates additionally provided a measure of relative fish grazing intensity, since individual bite marks, although present on all three substrates, were clearly visible and countable on this substrate alone. The area of each PVC and flat coral-rock settling plate was 50 cm^2. This area, and the sample sizes described below, were chosen from species-area and biomass-area curves obtained during a preliminary study.

A total of 1344 settling plates were mounted horizontally and coplanarly on 112 concrete blocks, each measuring 18 cm x 18 cm x 10 cm and supporting four of each plate type. In September 1980, 96 of these blocks were distributed simultaneously and evenly among three field treatments: inside territories (exposed nearly exclusively to damselfish grazing); outside territories (exposed mostly to parrotfish and surgeonfish grazing); and within cages (protected from fish grazing). Blocks were arranged in sets of three, such that a given territory contained one exposed block, with one exposed and one caged block located several meters outside the territory at approximately the same depth and degree of wave exposure. (The presence of a block within a territory did not appear to disturb the resident damselfish, but a cage caused obvious disturbance. Hence, all cages were necessarily placed outside territories.)

The cages were constructed of 1.3 cm x 1.3 cm galvanized wire mesh and were 60 cm x 60 cm x 30 cm in volume, so no plate was mounted closer than 15 cm from the wall of a cage. Exterior cage surfaces were prevented from fouling by the intense grazing activity of fishes, while interior surfaces were periodically cleaned by divers. (The effects of the cages on water motion and light penetration were measured with dissolving plaster-of-Paris "clod-cards" [Doty, 1971] and comparative photometer readings, respectively. A cage-control experiment, involving 16 settling-plate blocks and including wall-only [no roof] and roof-only [no wall] cages, tested these and other potential secondary effects. These data will be reported in detail elsewhere.)

During the succession experiment, 63 settling plates (3 treatments x 3 substrates x 7 replicates) were sampled without replacement each week for ten weeks, then each month for six months, with a final sample (reported here) at the end of one year. Thus, a total of 1071 settling plates were sampled during the one-year duration of the experiment (September 1980 to September 1981).

After being photographed, each plate was rinsed free of loose detritus and sediment (which were analyzed separately), and all macroscopic animals were removed, counted, and identified. The relative abundance of crustose coralline algae was estimated visually as percent cover. The remaining algae were then scraped from the plate, wet weighed, examined microscopically, dry weighed, and ash weighed. The naturally contoured coral-rock plates were examined microscopically only, since accurate area measurements were impossible.

For microscopic examination, the algae from a single plate were spread uniformly within a glass petri dish and scanned to determine the total number of species present. A total of 100 randomly selected points within the dish were then examined under 100-power magnification, and the alga occupying the central point of each ocular field was recorded. The total number of species per plate observed by this method was almost invariably identical to that determined by complete scanning, indicating that we had adequately sampled the local species "universe" (see Peet, 1974). This method thus provided an estimate of the proportional relative abundance of each algal species (excluding corallines), and accounted simultaneously for both the number and size of different plants (see Jones, 1968; Montgomery, 1980). Coralline algae could not be removed effectively from the plates; however, no more than two coralline species occurred throughout our study site (see also Littler and Doty, 1975).

The measurement of species diversity has always been a controversial topic because each proposed index contains inherent bias (Hurlbert, 1971; Peet, 1974). To minimize this problem, we analyzed our relative abundance data using seven different diversity measures: (1) the total number of species found on all plates within one treatment and (2) the mean number of species per plate within one treatment, both of which are the only truly objective measures of diversity (Poole, 1974); (3) the Shannon-Wiener index (H'), a traditionally popular measure for which statistical analyses have been derived (Pielou, 1966; Hutcheson, 1970); (4) the exponentiated Shannon-Wiener index and (5) the reciprocal of the Simpson index, which are most sensitive to changes in the proportions of rare and common species, respectively, and which are related by Hill's (1973) unifying notation; (6) Pielou's (1966) evenness index (J), which measures the equitability of relative abundances among species; and finally (7) dominance, which is simply the proportional abundance of the most common species, an inverse measure of evenness advocated by May (1975).

Results

Table 1 summarizes the results of the final sample of 63 settling plates after a one-year exposure to the three field treatments, along with previous data on relative grazing intensities. For simplicity and brevity, these results are pooled for all three types of settling plates (except where noted below). The "approximate t-test" of Sokal and Rohlf (1969), which assumes and compensates for unequal variances, was used for comparisons of mean parameter values between treatments. Diversity (H') comparisons were calculated according to Poole (1974). The results of the cage-control experiment, which will not be detailed here, revealed no substantial secondary effects of caging.

Comparisons of uncaged PVC plates during the first ten weeks of the succession experiment revealed that the mean number of fish bite marks per plate outside damselfish territories was significantly greater than that inside. Thereafter, bite marks on plates outside territories became too dense to count accurately. No bite marks were found on caged plates. Thus, fish grazing was most intense outside territories, intermediate inside territories, and nonexistent within cages.

Inversely correlated with this pattern of grazing intensity, the mean ash-free dry-weight biomass of noncoralline algae on the PVC and flat coral-rock plates after one year was significantly greatest within cages,

Table 1. Summary data on the benthic communities that developed on settling plates after a one-year exposure to the three field treatments (n = 21 each, except for invertebrates per plate and ash-free dry-weight biomass, for which n = 14 each). The data on fish bites per plate were gathered during the first 10 weeks of the succession experiment (n = 63 each). Significance levels are given for comparisons of adjacent means (approximate t-tests). Species diversity (H') comparisons were calculated according to Poole (1974). See text.

	Outside Territories		Inside Territories		Within Cages
Primary Grazer:	Parrotfishes		Damselfish		None
Bites / Plate:	269.6	***	14.9	***	0.0
Inverts / Plate:	1.7	*	34.3	ns	48.8
Algae--					
Biomass (g/m^2):	6.2	***	28.6	***	10.3
Species Total:	13		20		17
Species / Plate:	3.8	***	7.9	**	5.3
Diversity (H'):	1.16	***	2.19	***	1.85
Evenness (J):	0.45		0.73		0.65

***: P<0.001, **: P<0.01, *: P<0.05, ns: not significant (P>0.05).

moderate inside territories, and low outside territories. Correspondingly, the mean number of invertebrates per plate after one year was greatest within cages and inside territories, and negligible outside territories. By rank abundance, these invertebrates included mostly holothuroidean and stomatopod postlarvae, as well as small polychaete worms, harpacticoid copepods, and several rarer taxa.

All seven indices indicated that the diversity of noncoralline algae was significantly greatest inside damselfish territories compared to that either within cages or outside territories. Because of this, only the values of four representative measures are presented in Table 1. Thus, the treatment subjected to intermediate grazing intensity exhibited the greatest diversity of algae.

By rank mean proportional abundance, the dominant erect algae on settling plates located inside territories included the filamentous species Centroceras clavulatum (C. Agardh) Montagne, Ectocarpus indicus Sonder in Zollinger, and Polysiphonia rhizoidea Meñez, which together accounted for only 29.9% of the algae present. On the other hand, plates within cages were stongly dominated by Tolypiocladia glomerulata (C. Agardh) Schmitz, which alone accounted for 47.5% of the algae present. Plates outside territories were covered mostly by crustose coralline algae.

Discussion

The results of this experiment suggest that fish grazing does indeed control the local distribution and abundance of benthos on flat coral-rock surfaces of at least one shallow Hawaiian reef. Grazing intensity increases progressively from surfaces within fish-exclusion cages to those inside damselfish territories (subjected to grazing mainly by a single damselfish) to those outside territories (subjected to intense grazing by numerous parrotfishes and surgeonfishes). With increased grazing, the biomass of erect algae and the abundance of associated small invertebrates expectedly decreases, while the coverage of crustose coralline and prostrate algae increases.

These results also support our prediction that differential fish grazing has intermediate disturbance effects on algal species diversity in this system (see Figure 1). The diversity of algae by seven different measures was significantly greatest at intermediate grazing intensity within damselfish territories.

What are the mechanisms that produced this pattern? Outside territories, intense nonselective grazing by parrotfishes and surgeonfishes simply eliminates most erect algae and associated fauna, leaving only a low-diversity assemblage of grazer-resistant prostrate and crustose forms (see also Brock, 1979; Lobel, 1980). Within cages, where fish grazing is effectively prevented, algal succession proceeds without interruption as prostrate and crustose forms are overgrown. This results in an initial relatively rapid increase in both diversity and biomass, such that after six months algal diversity is actually greater within cages than inside territories (Hixon and Brostoff, 1981). However, following this intermediate stage, diversity characteristically decreases as several late-successional species become dominant (review by Connell, 1978). The ultimate result is that, within one year, the diversity of algae within cages falls below that inside damselfish territories.

Inside territories, grazing by a single resident damselfish apparently maintains the relatively high algal diversity characteristic of intermediate successional stages (see Connell, 1978). Lubchenco (1978) provides data suggesting a possible mechanism by which damselfish might accomplish this effect. Her series of experiments on intertidal snails and algae suggest that intermediate disturbance effects on algal diversity occur where herbivores selectively consume or otherwise remove competitively dominant species. Previous studies suggest that territorial damselfishes are often selective grazers (Lassuy, 1980; Lobel, 1980; Montgomery, 1980), and may additionally "weed-out" undesirable species from their algal mats (Foster, 1972; Lassuy, 1980; Irvine, this volume). Ongoing paired comparisons of the gut contents of our local damselfish relative to the species composition of their algal mats will determine whether or not similar mechanisms occur in our system, although many hours of field observation have revealed no evidence of weeding behavior (Hixon, unpublished).

In any event, it is apparent that territorial damselfishes are capable of enhancing and maintaining the local diversity of reef algae through intermediate disturbance effects. Other studies have also determined that these fishes are able to control the local abundance of living coral (Kaufman, 1977; Potts, 1977; Wellington, 1981) and sea urchins (Williams, 1979, 1980, 1981). Thus, territorial damselfishes may be considered true "keystone species" (sensu Paine, 1969) for their ability to regulate benthic community structure on tropical reefs.

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Effects of Piscivorous Predator Removal On Coral Reef Fish Community Structure

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The role of piscivorous predation in reef fish communities is poorly understood. Sale (1980) noted the lack of data about this problem. Here I examine the possibility that predation controls reef fish abundances. One predator model predicts that reduced predation would allow prey populations to increase (Paine, 1966; Menge and Sutherland, 1976). Eventually, increased competition should occur and then the best competitors should increase in abundance relative to poor competitors.

Here I compare an experimental reef that has small piscivorous predator populations with two control reefs with abundant predator populations. Spearfishing was primarily responsible for differences between predator populations on experimental and control reefs. Results reported here show that (1) piscivorous predator populations are significantly smaller on reefs impacted by spearfishing and (2) the abundance of some remaining species on the experimental reef differs significantly from control reefs.

Study Area

The experimental reef was Looe Key Reef (LKR), located on the outer reef tract (Lat 24° 33' N and Long 81° 24' W) south of Big Pine Key, Florida. LKR is a large reef with well developed spur and groove formations which provide high vertical relief. Antonius, Weiner, Halas and Davidson (1979) reported that most large piscivorous predators were conspicuously absent from LKR because of spearfishing pressure. Spearfishermen particularly concentrate on the larger predator species and individuals because of their greater food and sport value. Spearfishing was legal at LKR until April, 1981.

Molasses Reef (MR) and French Reef (FR), located on the outer reef tract in the Key Largo Coral Reef Preserve, were selected as control reefs because they have been protected from spearfishing since 1960. They also represent two extremes in major reef development in Florida. MR (Lat

25° 1' N, Long 80° 23' W) is a large reef with high relief similar to LKR. FR (Lat 25° 2' N, 80° 21' W) is smaller and less well developed. Divers commonly visited all reefs. Hook and line fishermen visited much less frequently.

Methods

I used two types of visual census methods with SCUBA gear. I censused all observable fishes at random points with one method. With the second method I only censused piscivorous predators during 15 minute search periods. Clear waters made visual censusing ideal for coral reef fishes. The methods were non-destructive and provided data suitable for statistical treatment. Traditional sampling techniques utilizing ichthyocides, trawls or blasting were not possible or were undesirable because of potential damage to the reefs. Data were collected between June 1979 and June 1981 between the hours of 0930 and 1630 (Table 1).

Table 1. Summary of random point census results.

	LOOE KEY REEF	MOLASSES REEF	FRENCH REEF
Total Species Observed	105	102	92
Total Individuals Observed	35,500	19,422	8,382
Mean Species/Sample (± s.d.)	21 ± 4	24 ± 3	21 ± 5
Mean Individuals/Sample (± s.d.)	273 ± 145	309 ± 164	212 ± 133
Number of Samples	130	63	40
Boat Activity Index ($\bar{X}$ ± s.d.)	19 ± 11	19 ± 7	9 ± 4
Number of Samples	13	9	5
Fishing Effort Index ($\bar{X}$ ± s.d.)	0.52 ± 0.81	0.74 ± 0.91	0.40 ± 0.71
Number of Samples	126	58	40

Random Point Censuses

At random points on each reef, I recorded all species observed in five minutes within an imaginary cylinder extending from the surface to the bottom with an 8 m radius from the observer. Numbers of observed individuals of each species were counted and the mean and range of fork lengths were estimated for each species. A ruler held out perpendicularly at the end of a meter stick aided in making size estimates by reducing parallax errors. Size estimates of large fishes were made relative to the meter stick. Bohnsack (1979) found a high correlation ($r = 0.99$, $p < 0.01$) between estimated and measured fish lengths.

A rigorous sampling regime was used to avoid bias and prevent counting the same individuals more than once. All sample points were selected using a table of random numbers. I began each sample by facing seaward and listing all species within the field of view in the sample radius. When no new species were noted, new sectors were scanned by rotating to the left. New species were listed as observed. This process was continued for five minutes. Several complete rotations usually were made for each sample. Individuals were counted and size estimated immediately for species with few individuals (e.g. pomacanthids, chaetodontids, scarids) or for species not likely to remain in the sample area (e.g. carangids and *Clepticus parrai*). Species that were always present in the sample area (e.g. *Thalassoma bifasciatum* and *Abudefduf saxatilis*) and species not likely to leave the sample area (e.g. damselfishes) were initially listed as observed and counted later after the five minute sample period. At the end of the five minute sample period I would make one 360° revolution for each species in the latter two groups, during which data were collected. To avoid bias I would always work back up the list treating each species when reached. This procedure eliminated the tendancy to count each species when it was particularly noticeable and abundant. With the addition of the last procedure, each point census took approximately 20 minutes to complete. Data collected should be considered a relative index of abundance and probably underestimate the true abundance of most species.

At each sample point bottom features were recorded and an index of fishing effort was made by counting the number of lost leaders observed in the sample area. A boat activity index was made by counting the maximum number of boats observed at any one time during each day on each reef. Divers accounted for most of the boats observed at all sites.

Predator Censuses

In addition to using community data described above, piscivorous predator populations were sampled independently during 15 minute search periods. Only piscivorous predators were censused. Each search covered a different area of bottom while swimming speed was held constant as much as possible. Unlike random point samples, likely hiding places for particular predators such as caves and ledges could be closely examined. Members of the following observed groups were considered piscivores: Aulostomidae, Belonidae (genus Tylosaurus), Bothidae, Carangidae (genus Caranx), Centropomidae, Elopidae, Lutjanidae, Muraenidae, Pricanthidae, Scombridae, Serranidae (genera Epinephelus and Mycteroperca), and Sphyraenidae. Designation of a piscivore was based on stomach content analysis and on published reports (Randall, 1967; Starck, 1970). The effect of predation varies with the species of predator, the size of the individual, and the size of the prey items (See Starck, 1970).

Data Analyses

The null hypothesis being tested is that reefs subject to spearfishing are no different in fish composition from protected reefs. A nonparametric Kruskal-Wallis test (Sokal and Rohlf, 1981) followed as necessary by Dunn's multiple comparison procedure (Hollander and Wolfe, 1973) was used to analyze the boat activity index and the index of fishing effort (Table 1). Community structure of the sampled reefs was analyzed on the basis of similarity indicies and abundance distributions.

Results and Discussion

Although this study deals with spearfishing, it is not intended nor should it be construed as a recommendation for a particular management policy.

Looe Key Reef, Molasses Reef and French Reef had a similar number of species (Table 1). Boat visitation was significantly less ($p < 0.05$) on FR versus LKR and MR. No statistical difference in boat visits was observed between LKR and MR. Sightings of lost fishing gear did not differ significantly among reefs ($p > 0.05$).

Total piscivorous predator populations were significantly different on the three reefs ($p < 0.001$) (Table 2). Significantly fewer predators were observed at LKR ($p < 0.05$) than on either control reef. However, the two control reefs were also significantly different from each other ($p < 0.05$) with more predators observed at MR. I interpret this last result as a reflection of the difference in the physical structure between the control reefs.

Table 2. Analysis of variance of predator abundance. Data were normalized by a $\log_{10}$ transformation.

Source of Variation	df	SS	MS	F-ratio	Significance
Among Reefs	2	11.803	5.902	33.26	($p < 0.001$)
Within Reefs	59	10.468	0.177		
Total	61	22.271			

The relative abundance of predator families was similar on all three reefs (Table 3). The lutjanids alone accounted for nearly 76% of all predators censused. Carangids and lutjanids comprised approximately 92% of all observed predators.

Table 3. Composition of all potentially piscivorous predators censused during predator searches.

Predator Group	Looe Key Reef	Molasses Reef	French Reef	Combined Total
Lutjanidae	67.60%	75.53%	92.53%	76.01%
Carangidae	26.19%	23.05%	4.04%	21.32%
Sphyraenidae	2.25%	0.67%	1.10%	1.06%
Serranidae	2.25%	0.19%	1.18%	0.67%
Aulostomidae	0.64%	0.44%	0.86%	0.53%
Other	1.05%	0.12%	0.29%	0.33%
Total Individuals	4,093	12,871	2,449	19.413
Mean Individuals	124	757	204	308
Total Species	24	21	21	28
Total Samples	33	17	12	62

Species composition within the lutjanids differed between experimental and control reefs (Fig. 1). The largest species were much rarer at LKR relative to control reefs, which I attribute to spearfishing pressure. Within a species, mean predator size was generally smaller at LKR, especially for intermediate sized species. Time and lack of space prevent statistical treatment of size data here.

Individual abundance of the serranid *Epinephelus cruentatus* was significantly greater at LKR than on control reefs ($p < 0.05$, mean = 0.58 ind./sample at LKR, 0.11 at MR, and 0.28 at FR). This species is usually too small to spear. The greater abundance of this species at LKR may be due to the reduced populations of other predator species. Thompson and Munro (1978) have shown the same pattern of increased abundance on reefs where populations of larger grouper have been reduced by trap fishing. Unfortunately, it is not clear from the data whether the density increase of *Epinephelus cruentatus* is in response to reduced predation or reduced competition from other predator species.

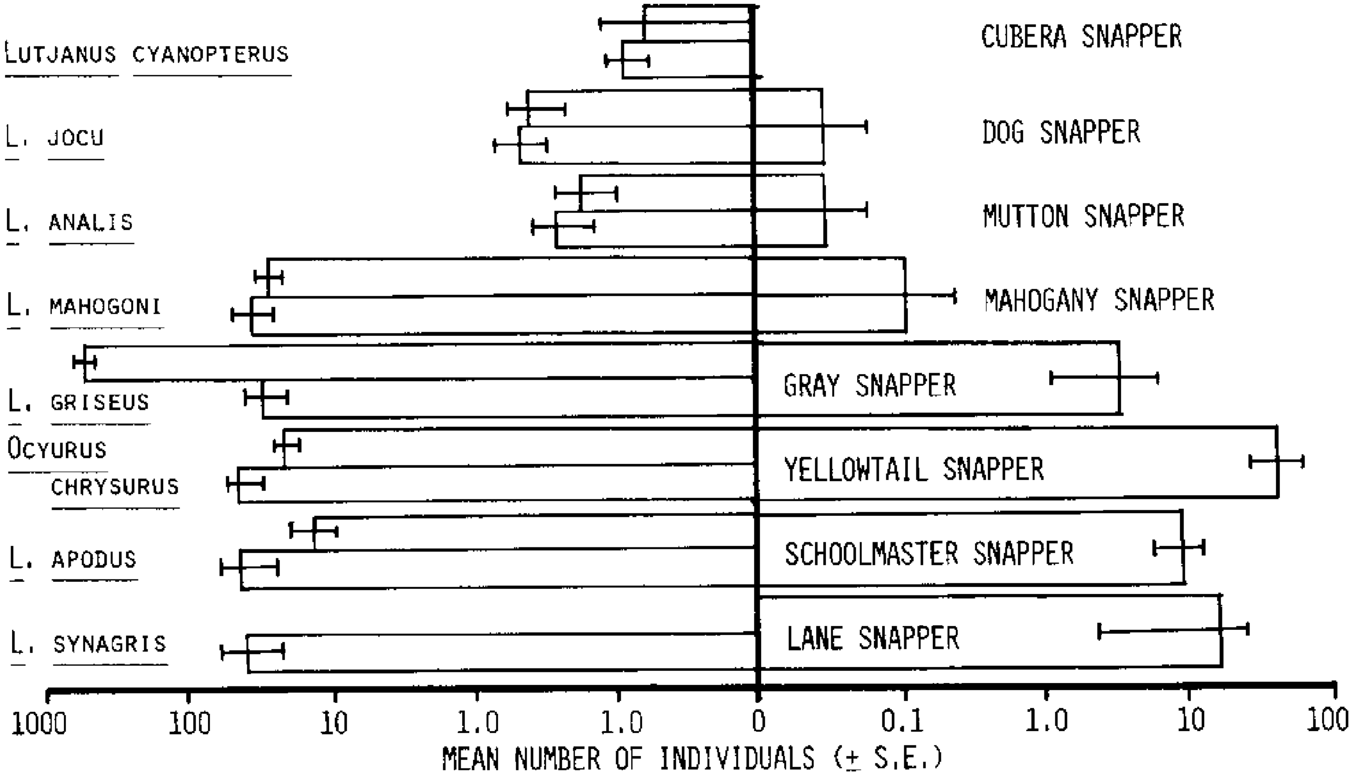

Figure 1. Abundance of snapper (Lutjanidae) compared on the experimental reef, LKR (right side), and control reefs, MR (left side, top bar) and FR (left side, bottom bar). Species are listed from top to bottom in approximate order of decreasing size. Species tend to be increasingly piscivorous from bottom to top. Sample size: 33 at LKR, 17 at MR, 12 at FR.

Community percent similarity indicies show that the three reefs were broadly similar in terms of composition of individuals. Percent similarity indicies were calculated based on the total individuals observed at each reef (Brower and Zar, 1977). The two control reefs were the most similar (65.8%). LKR was most similar to FR (63.5%) and least similar to MR (53.3%).

The total distribution of all species was analyzed using the G-test for goodness of fit (Sokal and Rohlf, 1981). Data were the number of species in different abundance categories (M. E. Crow, in prep.). The abundance patterns were not significantly different between reefs (Table 4). Although fewer species were found in the higher abundance classes at LKR, the G-statistic was not significant ($p = 0.22$). These results do not imply that each species was similarly distributed between reefs.

Table 4. Distribution of species into abundance categories.

ABUNDANCE CATEGORY	NUMBER OF SPECIES		
Percent of Total Individuals	Looe Key Reef	Molasses Reef	French Reef
Greater than 5%	5	6	6
1.0% to 5%	9	10	12
0.5% to 1.0%	5	7	12
0.1% to 0.5%	21	22	23
0.05% to 0.1%	13	11	10
Less than 0.05%	52	46	29
Total Species	105	102	92
$G = 10.38$	$\chi^2_{(0.05)} = 14.07$		

The 25 most abundant species out of 132 total censused species accounted for over 91% of all censused individuals on all reefs (Table 5). The abundances of nine of these species (including six of the eight most abundant species) were significantly different ($p < 0.05$) between control and experimental reefs. The abundances on the two control reefs were similar ($p < 0.05$) for six of the nine species. The abundances for the three remaining species were different on all three reefs ($p < 0.05$), however, LKR was at one end of an extreme.

Among non-piscivorous species, the Haemulidae were examined (Fig. 2) because they were the most important family considering total biomass, number of species, and abundance. Their distribution (Fig. 2) is similar to that found in the Lutjanidae in that the largest species are rarest at LKR. This pattern is most easily explained as a consequence of spearfishing. However, smaller individuals of many of the missing species are not normally speared because of their small size. Their absence could be due to any of numerous autecological causes or it could be in part because of competition from the tomtate (Haemulon aurolineatum) which achieves great density at LKR. At present I cannot support or refute either possibility. Note also (Fig. 2) that H. aurolineatum almost completely replaces H. chrysargyreum at LKR. Interspecific competition may be an important factor for these two species considering their similarity in taxonomy and appearance, or it may be of no importance. Only carefully designed experiments can critically test such an hypothesis.

Table 5. A comparison of the distribution of the twenty-five most important species among reefs. Importance was based on mean proportion of individuals among reefs. Data were analyzed species by species using the Kruskal-Wallis test (Sokal and Rohlf, 1981). Dunn's multiple comparison procedure (Hollander and Wolfe, 1973) was used when appropriate. Data for five species that could be normalized by a log (x + 1) transformation were analyzed by analysis of variance (Sokal and Rohlf, 1981).

Species Ranked According to Decreasing Abundance	Percentage of Total Observed Individuals	Mean Individuals/Sample			Significance	
		LKR	MR	FR		
Thalassoma bifasciatum	18.11	68.88	29.81	35.28	**	1
Eupomacentrus partitus	17.10	46.13	58.60	32.30	n.s.	1
Haemulon chrysargyreum	8.56	0.17	57.21	15.50	*	
Abudefduf saxatalis	8.34	21.31	20.41	21.83	n.s.	1
Haemulon aurolineatum	6.06	72.66	0.00	0.00	**	
Eupomacentrus planifrons	5.35	19.33	12.11	10.58	**	1
Lutjanus griseus	2.89	0.04	25.05	1.15	*	
Haemulon sciurus	2.89	0.67	13.84	8.25	*	
Caranx ruber	2.17	3.06	16.06	0.33	a	
Inermia vittata	2.13	0.00	0.16	13.30	b	
Ocyurus chrysurus	1.92	4.00	6.29	4.75	**	
Microspathodon chrysurus	1.58	6.05	4.87	2.88	a	1
Chromis multilineatus	1.52	3.75	2.00	5.30	n.s.	
Haemulon flavolineatum	1.49	2.69	8.62	1.43	b	
Acanthurus bahianus	1.34	3.49	4.29	2.60	b	
Halichoeres garnoti	1.26	5.48	1.56	2.63	**	
Clepticus parrai	1.18	4.00	4.41	2.23	n.s.	
Mulloidichthys martinicus	1.06	0.90	5.81	2.40	+	
Halichoeres maculipinna	1.06	2.98	1.90	3.03	n.s.	
Scarus croicensis	1.00	3.35	1.37	2.80	n.s.	
Sparisoma aurofrenatum	0.96	1.35	3.46	2.63	**	
Lutjanus apodus	0.87	0.69	1.06	3.43	n.s.	
Pempheris schomburgki	0.81	0.81	1.54	3.38	+	
Acanthurus coeruleus	0.81	0.91	2.29	2.83	+	
Sparisoma viride	0.80	1.20	3.24	1.93	a	

** LKR differed significantly from control reefs ($p < 0.05$) and control reefs were not significantly different ($p > 0.05$).
* All reefs were statistically different ($P < 0.05$) with LKR at one extreme.
+ LKR differed significantly from one control reef ($p < 0.05$) and the two control reefs were not statistically different ($p > 0.05$).
a LKR differed significantly from one control reef ($p < 0.05$) and the two control reefs were statistically different ($p < 0.05$).
b LKR did not differ significantly from either control reef ($p > 0.05$) although the two control reefs differed significantly ($p < 0.05$).
1 Analyzed by analysis of variance.

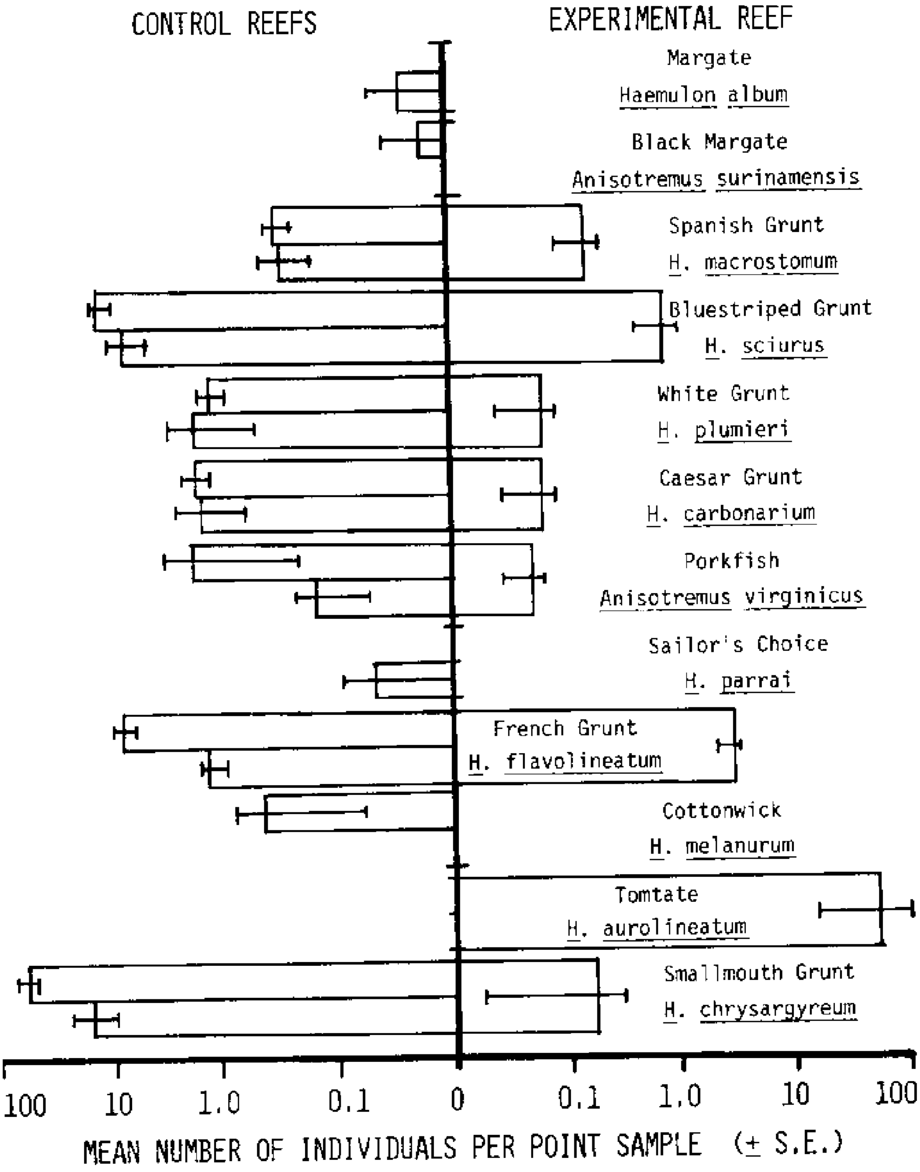

Figure 2. Abundance of grunt (Haemulidae) compared on the experimental reef (LKR, right side) and control reefs (MR, left side top bars: and FR, left side bottom bars). Species are listed from top to bottom in approximate order of decreasing adult size. Larger species are much more rare on the experimental reef. The tomtate, the most abundant grunt on the experimental reef, is absent in samples from control reefs. Sample size: 130 at LKR, 63 at MR, 40 at FR.

Results reported here are suggestive but not conclusive concerning the role of predation in determining relative abundances of reef fishes. The fact that the most abundant species, Thalassoma bifasciatum, was twice as abundant in samples from LKR (Table 5) appears to support the predator model. Likewise two very abundant and similar species of grunt, Haemulon aurolineatum and H. chrysargyreum, show complimentary distributions between control and experimental reefs (Fig. 2) which could be interpreted as support for the model. The same arguments could be made for other observed differences between experimental and control reefs. However, reduced predation or some other unrecognized factor or factors associated with LKR may be responsible for observed differences. Stating that piscivorous predation is an important factor controlling community structure of reef fishes based on present evidence would be premature. I expect ongoing monitoring of control and experimental reefs to help settle these alternative possibilities because in April 1981 LKR was designated the Looe Key Reef National Marine Sanctuary and spearfishing was prohibited. If predator populations increase on LKR and the observed differences between control and experimental reefs diminish, then the importance of predation will be supported. Otherwise other factors should be examined to account for differences between reefs.

Conclusions

Results showed that the total numbers of piscivores were smallest on the reef subject to spearfishing. Within the Lutjanidae, the largest species and individuals tended to be absent. One small species of grouper, Epinephelus cruentatus, showed greater density on the experimental reef which was apparently a response to the absence of larger predators. Community similarity indicies and the distribution of species in abundance categories suggested broad similarities existed in community structure among reefs. However, several non-piscivorous species had significantly different abundance patterns between experimental and control reefs which could be interpreted as support for the importance of predation in structuring reef fish communities. Present data, however, are not sufficient to substantiate the predation model. Ongoing monitoring should help resolve this problem.

Acknowledgments

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The Effect of Sheephead (*Semicossyphus pulcher*) Predation on The Abundance and Microhabitat Utilization of Sea Urchins

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Introduction

Substantial interest has been directed towards the importance of predation in controlling sea urchin populations (see review by Lawrence, 1975). Predators that are capable of eating adult sea urchins include sea otters, various sea stars, crustaceans (e.g. crabs and lobsters), and fish. High sea urchin densities have been found in the absence of such predators. When predators are present, sea urchins are usually found within crevices and often have diel foraging patterns which coincide with the inactive periods of their predators (Ebling et al., 1966; Fricke, 1971; Nelson and Vance,1979; Bernstein et al., 1981). When sea urchins are not in crevices they become vulnerable to predation.

Along the California coast, sea otters are absent south of Point Conception, yet relatively few urchin dominated areas exist. This suggests that other predators may be important in controlling sea urchin abundance along the southern California coast. Likely candidates for this role are the spiny lobster, Panulirus interruptus, and the sheephead wrasse, Semicossyphus pulcher. Both of these predators have similar ranges, occuring from Point Conception to Punta Asuncion, Baja California, though their relative abundance may vary within this range.

The main purpose of the work reported in these preliminary findings is to assess the importance of sheephead predation on sea urchins, Strongylocentrotus franciscanus. To do this, I have set up experiments in an area essentially free of lobsters. Three basic questions are considered. First, how important are urchins in the diet of sheephead? Second, do sheephead affect the density of adult sea urchins? Third, do sheephead affect the spatial distribution of sea urchins, i.e. do they restrict the sea urchins to protective microhabitats?

Methods

This study was done in a Macrocystis pyrifera forest located at Dutch Harbor on the south side of San Nicolas Island (Fig. 1). The kelp forest grows on a bilobed rocky reef (54,600 m^2) surrounded by sand. The reef has extensive vertical relief and deep crevices; depth ranges from 6 to 18m. The western lobe of the reef (12,700 m^2) was designated as the experimental site and the eastern lobe as the control site. Sand separates the two lobes except in the shallow inshore portion of the reef.

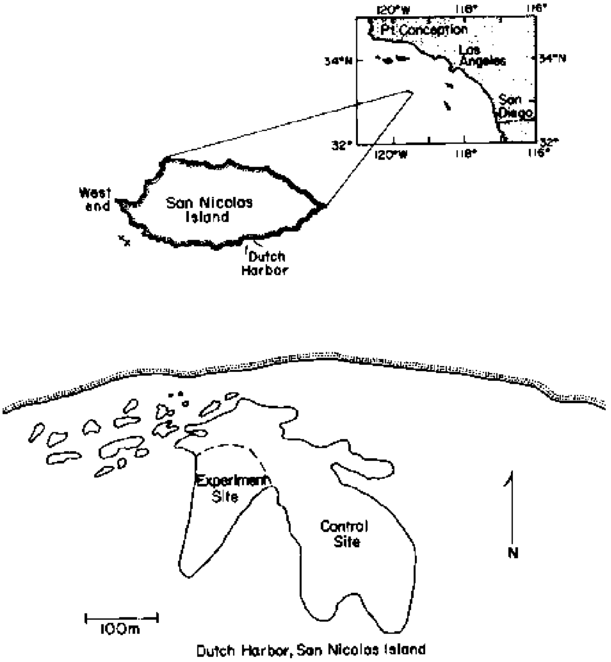

Figure 1. Map of study site on San Nicolas Island, California.

In September, 1980, all sheephead seen within the experimental site were removed by spearing (N=220). Sheephead tend to be curious and are attracted to activities such as divers spearing fish, therefore it is likely most sheephead were seen and hence successfully removed from the site. Following the initial clearing, any sheephead seen within the site were removed at bimonthly intervals (generally 10-20 fish).

Standard lengths and weights were measured on all collected fish. Dorsal spines were removed and frozen for age determination (Warner, 1975), and the coelomic contents were fixed in 4% formaldehyde and then transferred to 70% isopropanol. The prey contents within the tubular digestive tracts were removed and identified to the lowest possible taxa and the proportion that each prey type contributed to the total volume of the gut contents was estimated. Sheephead crush their prey extensively, occassionally requiring the actual number of prey items to be estimated from various identifiable parts (e.g. eye stalks and telsons) or presence as a bolus (e.g. urchins).

Change in the number of sea urchins was assessed by the establishment of five, 5m long transects along crevices in both the experimental and control sites. Total counts of all urchins seen in the crevices and within 1m of the crevices were made without disturbing any of the urchins. The microhabitat utilized by each urchin was also noted. Three microhabitats were designated: 1) crevice - urchin within a crevice and/or in contact with two or more planes of the substratum, 2) pocket - urchin within a rounded depression, and 3) open - urchin away from any crevice and only in contact with one plane of the substratum. Based on field observations, any urchin in a crevice or pocket microhabitat was considered to be sheltered from sheephead predation.

I also contrasted sheephead densities with the proportion of sea urchins in the open microhabitat (i.e. exposed to predation) at three areas around San Nicolas Island and one area in Baja California. The areas surveyed were: 1) East Dutch Harbor (control site), 2) a kelp forest area on the west end of San Nicolas Island, 3) an urchin dominated area on the west end of San Nicolas Island, and 4) the northern headland of Thurloe Bay, Baja California (34km south of Punta Eugenia). Sheephead densities were estimated from 50 X 5 m transects swum by a diver who recorded all observations on an underwater tape recorder. This method allows the diver to keep his eye on the fish and swim quickly enough to observe and identify the fish before they have time to repond to his presence, thereby minimizing bias. Urchins were counted as above on 5m transect lines placed along haphazardly chosen crevices.

Results

For the present study, the digestive tract contents of 87 sheephead were examined (four of which were empty). The sample was from collections made in September, 1980, December, 1980, February, 1981, and April, 1981, and includes all sizes of fish (170-620mm S.L.). The sheephead were found to feed on a broad array of prey types, none of which were extremely dominant in their diet. The ten most important prey types (out of 26), based on index of relative importance values (Pinkas *et al.*, 1971), are shown in Figure 2. The most important prey type was small brachyuran crabs (8-12mm carapace length). Barnacles (*Balanus tintinnabulum*) ranked second overall, but were particularly common in the fish collected during September, 1980. Sea urchins ranked only seventh based on relative importance and third based on volume. Though usually one urchin (and at most two) would be eaten by a given sheephead, it usually constituted a large proportion of the volume of the food in that fish. Another prey item of interest is the mole crab,

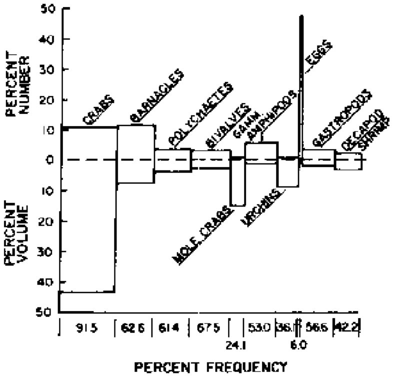

Figure 2. The ten major prey types of the sheephead, *Semicossyphus pulcher*. See text for explanation. N=83.

Lepidopoda californica, which was fifth in overal importance and second by volume. These are large animals (carapace length to 50mm) which live in the sand surrounding the reef.

Even though sheephead are not specializing on sea urchins, they do appear to have an impact on them. Following the removal of sheephead from the experimental site, there has been an increase in the number of urchins on each transect, but in the control site, the number of urchins has remained the same or decreased slightly (Fig. 3). Regressions fitted to each transect and tested with an analysis of covariance (Snedecor and Cochran, 1967) showed no significant differences of slopes and variances within each site, but the slopes between sites were significantly different ($p<0.01$).

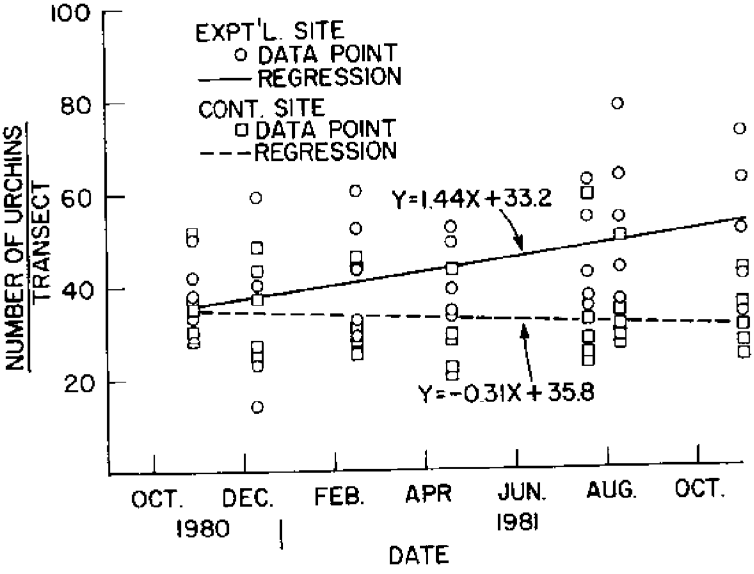

Figure 3. Data and regressions of the number of urchins, *Strongylocentrotus franciscanus*, per permanent transect (5m) in both the experimental and control sites. Regressions are of all five transects in each site.

In addition to a change in the abundance of sea urchins, an increase in the utilization of the open microhabitat occurred at the experimental site (Fig. 4). Prior to sheephead removal, no urchins were counted in the exposed microhabitat at either site. Throughout this study all urchins in the control site have been in sheltered microhabitats. However, in the experimental site a low percentage of the urchins were found in the open microhabitat, beginning about six months after the initial clearing. Although relatively few urchins are in the open, their presence there indicates a lack of predation.

The comparison of sheephead densities with the proportion of exposed urchins in different geographical locations supports the above findings that sheephead affect sea urchin spatial distribution. The two areas on the west end of San Nicolas Island had low sheephead densities

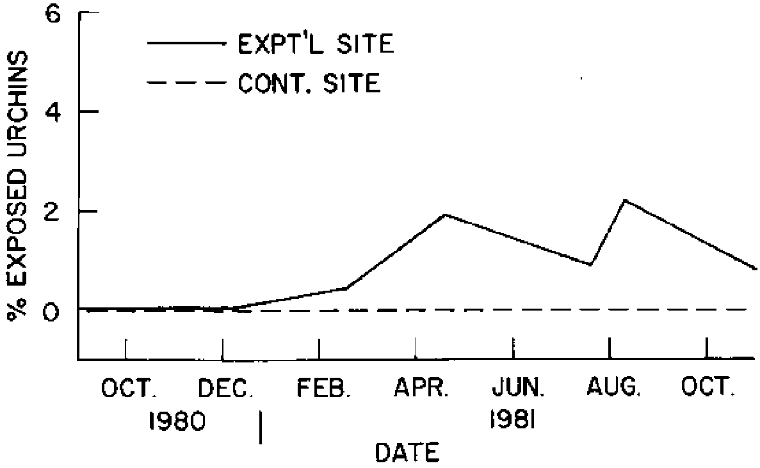

Figure 4. The percent of urchins in the open (exposed) microhabitat in the experimental and control sites.

(kelp area - 28 per hectare, urchin dominated area - 38 per hectare), and both of these areas had a high proportion of exposed urchins (12% and 31%, respectively). The other two areas had high sheephead densities (East Dutch Harbor, SNI - 200 per hectare, Thurloe Bay, B.C. - 510 per hectare) and no exposed urchins.

Discussion

The above data suggest that sheephead may be capable of controlling sea urchin populations, even though urchins do not dominate the sheephead's diet. By eating exposed sea urchins, the sheephead restrict urchins to crevices and pockets and limit urchin density. However, the extent to which sheephead eat sea urchins may not have been as great in the evolutionary past as it is today. Prior to intensive hunting by fur traders, sea otters ranged as far south as Morro Hermoso, Baja California (Kenyon, 1969). By reaching within crevices, sea otters are capable of preying on urchins which would be protected from sheephead, it is therefore doubtful that sheephead ate many urchins when otters were foraging in the same area.

Besides being general predators, the sheephead appear to be flexible enough to utilize alternate food resources as they become available, whether due to loss of a "competitor" (i.e. sea otters) or seasonal and/or geographical variation of prey availability. These preliminary observations show an episodic (possibly seasonal) occurrence of barnacles in the diet of the sheephead which probably reflects barnacle availability. The presence of mole crabs in the Dutch Harbor sheephead is probably unique to those fish which live near sand. Hence, a predator such as the sheephead will exert a different effect in each community it occupies due to differences in availability of prey items and their prey's relative importance within the community.

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Effects of Fish Predation on Peracarid Crustaceans In Mugu Lagoon, California

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Introduction

The effects of fish predators on benthic peracarids in the eastern arm of Mugu Lagoon were studied as part of a larger investigation of the natural resources of the area. One measure of the importance of predation for a prey species is whether the frequency of mortality due to predation is sufficient to affect prey abundances. However, even in the absence of large numerical responses of a prey population to a predator, predation is important if it has resulted in adaptations by the prey that make such numerical effects inconsequential. Both possibilities are addressed in this study by relating changes in peracarid abundances to predaceous fish abundances at corresponding times and by relating the temporal pattern of peracarid vertical migration to the temporal pattern of feeding by potential predators.

Site Description and Methods

Mugu Lagoon is located within the U.S. Naval Air Station at Pt. Mugu, California (34° 06' N, 119° 05' W). The eastern arm of Mugu Lagoon covers approximately 50 ha and is connected to the ocean by a narrow sand channel which varies in length in different years from 0.5 to 1.5 km. One quarter of the eastern arm is permanently covered by water; one quarter is intertidal sand and mud flats and the remaining half is emergent marsh dominated by Salicornia virginica. The deepest part of the eastern arm at low tide is less than 1 m.

The four common peracarid crustaceans of the eastern arm are the gammaridean amphipods Pontogeneia opata and Corophium acherusicum, the caprellid amphipod Mayerella acanthipoda and the cumacean Oxyurostris pacifica. The peracarid populations of the eastern arm are apparently not greatly affected by migration to or from outside areas since the sand channel is a barrier of unsuitable habitat over which peracarid dispersal does not occur. Few peracarids were found in two 24 hour plankton surveys and several benthic surveys of the sand channel. Chenges in peracarid abundances in the eastern arm therefore, were due to local factors. Benthic peracarid populations were sampled at approximately monthly intervals from 1978 to 1981 using a 15 cm length of 4.3 cm ID stainless steel tubing. The sharpened cutting edge and thin walls (0.9 mm) allowed the corer to slice through all substrata encountered, even macrophytes, unlike heavier walled conventional coring devices.

In each sample period, six core samples 2 to 4 cm in depth were collected randomly from areas distributed at approximately even intervals along five transects 60 m in length. Transects were evenly spaced across a subtidal area of the eastern arm either perpendicular or parallel to the shore line. Samples were washed on a 0.5 mm mesh screen to remove fine sediments. Peracarids retained on the screen were preserved in buffered formalin. All peracarids in the samples were identified, counted, measured and transferred to 70% ethanol in the lab.

Fish abundance estimates were based on monthly collections (Onuf and Quammen, MS). A beach seine was used to sample an approximately 10 x 40 m transect adjacent to the study site. All fish collected were identified, measured, and counted. Those not kept for gut analyses were then released.

Three species accounted for 90.8% of all fish caught at the site: topsmelt, Atherinops affinis (35.8%), shiner surfperch, Cymatogaster aggregata (39.4%) and staghorn sculpin, Leptocottus armatus (15.5%). Peracarids were not found in A. affinis stomachs, therefore, monthly estimates of fish consumption of peracarids were based on the latter two species. The average number of peracarids per fish of a given length was estimated from 83 L. armatus and 86 C. aggregata stomachs. A monthly predation estimate was derived from the average number of peracarids per fish of a given length times the number of fish per length summed over the entire length frequency distribution of each month. The sum of L. armatus and C. aggregata predation rates divided by the area collected (@ 400 m^2) provided a monthly estimate of relative predation per m^2.

Plankton samples were collected using a modified centrifugal pump. Water samples of 750 l were collected hourly at each of two stations within the site. Each plankton sample was collected in a 3 minute period and washed over a 0.5 mm mesh screen. Material remaining on the screen was preserved in buffered formalin. All invertebrates from each sample were later identified, counted and transferred to 70% ethanol.

Hourly predation rates on peracarids in the water column and on the benthos were determined by using peracarids as bait. Individual peracarids were placed on #28 and #32 fish hooks which were suspended in the water column or placed on the benthos. All hooks were checked at regular intervals over two 24 hour periods during each sampling period. The percentage of the bait removed was used to estimate relative predation rates through time.

The cumacean, O. pacifica, was used almost exclusively as the bait. The caprellid, M. acanthipoda, was too thin to be threaded onto hooks while the amphipods. P. opata and C. acherusicum were more readily removed from hooks by mechanical disturbance and less readily threaded onto hooks

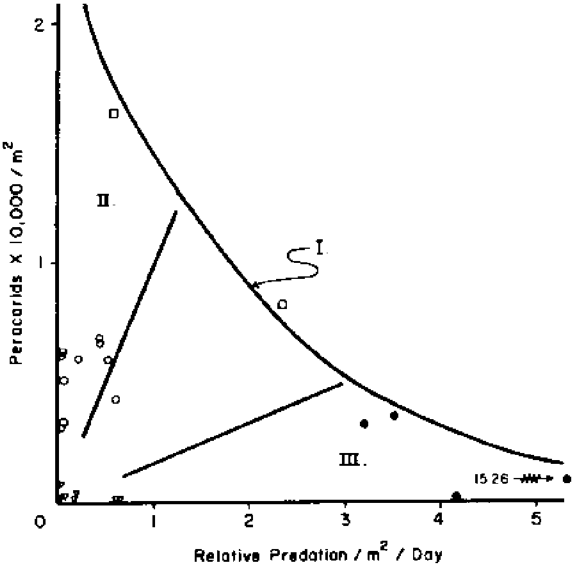

Fig. 1. Relative predation rate vs. peracarid density. Triangles represent sample periods in which peracarids were not reproducing. Open circles, solid circles and open squares respectively represent samples classified as exposed to minimum predation, maximum predation and prevented from increasing in number due to predation. The curved line (1) indicates an estimated boundary of maximum peracarid density for given predation rates and regions II and III respectively indicate conditions of relatively low and high predation per peracarid.

than O. pacifica. Baits were inspected at each check period and all damaged or worn baits were replaced or removed. During a period of low predation, a few baits which were kept in use for 24 hours remained in good condition. Bait loss is, therefore, inferred to have resulted almost entirely from predation.

Results

Two possible types of numerical responses by peracarids to predation by fish were considered. First, peracarid abundances could respond continuously to fish predation. In this case, a negative correlation between peracarid densities and predation rates through time would result. Data from all collections were included in this analysis and no significant correlation was found (all peracarid samples indicated in figures 1 and 2, $r = -.13$, $p < .9$). Peracarid abundances could be affected by fish predation only part of the time or the effects could be delayed resulting in the absence of a negative correlation between predation and peracarid abundance when all sample data are included in the analysis. We therefore considered, in two ways, a second type of numerical responses by peracarids in which abundances could be limited by fish predation discontinuously. Sample periods in which peracarids were not reproducing (triangles in figures 1 and 2) were not included in these analyses because their abundances could not increase.

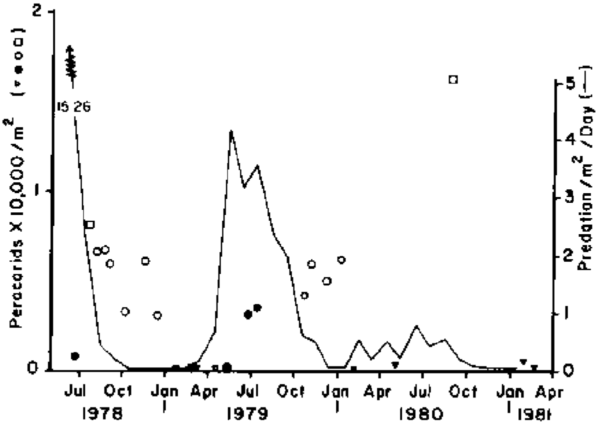

Fig. 2. Peracarid densities (left scale and all symbols) and relative predation rate (right scale and solid line) by sampling date from June 1978 to April 1981. Symbols correspond to those in figure 1.

In one case, a maximum peracarid density would be expected for each given predation rate. This condition is indicated by the curved line (1) in figure 1 which was drawn by eye to fit the six points farthest from the origins (open squares and solid circles). Peracarid densities represented by symbols near the curved line (1) in figure 1 were expected to change little or decrease in the next sample interval due to predation effects. Peracarid densities represented by open circles below and to the left of the line were expected to increase in the next sample interval due to the absence of predation effects. Peracarid densities did not change as predicted if maximal observed densities for each predation rate were near limitation (Fig. 2, Table 1a). Discontinuous limitation of peracarid densities by fish predation was tested a second way by comparing conditions in which predation and peracarid densities occurred in different proportions. This condition is indicated by regions II and III in figure 1. In this analysis, peracarid densities were predicted to decline when there were few peracarids per predation rate (region III, Fig. 1) and peracarid densities were predicted to increase when there were many peracarids per predation rate (region II, Fig. 1). We tested these predictions by determining the direction of population change to the next sample period (Fig. 2). Samples represented by points outside regions II and III (22.5°-67.5°) were not included in order to provide clear dichotomies for the analysis. Peracarid densities represented by solid circles in region III of figure 1 increased in 4 of 4 cases (Table 1b) when they were expected to decrease and densities represented in by open circles in region II decreased in 7 of 10 cases (Table 1b) when they were expected to increase. Changes in peracarid abundances therefore appear not to have resulted from changes in prey-predation ratios.

In addition to fish predation effects on peracarid abundances, fish predation effects on peracarid vertical migration behavior were investigated. At night, benthic peracarids from shallow water migrate

Tab 1. Analyses of observed vs. predicted peracarid density changes to each following sampling period ude to fish predation with results of X square tests of significance (Sokal and Rohif, 1969).

A. Peracarid density changes in response to presumed limitation by fish predation

Condition	Population Changes		
		Increase	Decrease
Population near limitation by predation	Observed	4	2
	Predicted	0	6
Population below limitation by predation	Observed	4	6
	Predicted	10	0

$X^2 = 6.25$, $p < .02$

B. Peracarid density changes in response to differential prey: predation ratios

Condition	Population Changes		
		Increase	Decrease
Many prey per predation rate	Observed	3	7
	Predicted	10	0
Few prey per predation rate	Observed	4	0
	Predicted	0	4

$X^2 = 8.64$, $p < .01$

into the water column (Corey, 1970; Williams and Bynum, 1972; Hobson and Chess, 1976, 1978, 1979; Alldredge and King, 1977, 1980; Jansson and Kallander, 1968; Anger and Valentin, 1976; Bregazzi, 1973; Fish, 1925). The occurrence of this behavior only at night has been hypothesized to be adaptive for avoiding diurnal visual predators, particularly fish, (Kallander and Jansson, 1968; Williams and Bynum, 1972; Hobson and Chess, 1978 and Alldredge and King, 1980). Nocturnal vertical migration is common to the four predominant peracarid species of the eastern arm of Mugu Lagoon. Estimated densities per 0.75 m^3 from one plankton sample collection period are presented in figure 3 as an example.

To test whether vertical migration by Mugu Lagoon peracarids was adaptive for predator avoidance, hourly relative predation rates were estimated from bait-loss rates from hooks in April and August 1981. The same responses to baited hooks as to live prey by predators are unlikely, therefore these methods reveal only relative predation rates. Vertical migration is adaptive for avoiding predators if it occurs when planktonic predation rates are lower (relatively or absolutely) than benthic predation rates.

Results of the bait-loss assessments of planktonic vs. benthic predation rates were very different in April compared to August (Fig. 4 a and b respectively). In April, planktonic bait-loss exceeded benthic bait-loss in the morning while the reverse was true in late afternoon. At night they were similar. Over entire 24 hour periods, there was little difference between planktonic and benthic bait loss rates (Fig. 4a). In contrast, bait-loss in August was predominantly benthic and only in late afternoon did planktonic losses exceed benthic losses (Fig. 4b).

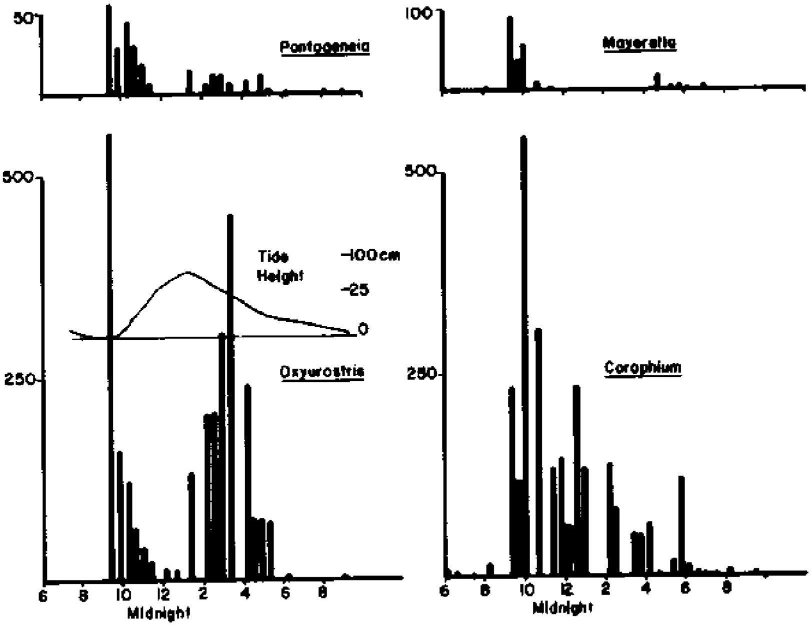

Fig. 3. Plankton samples collected at approximately hourly intervals on 7-8 August 1978. Tide height was measured from low water in the eastern arm. Reduced abundances between 10 PM and 2 AM correspond to increased tide current velocities.

The April results do not support the prediction that vertical migration will occur when planktonic predation is lowest relative to benthic predation. The August results are consistent with that prediction.

Because of these contradictory results, whether vertical migration is timed in a way that minimizes predation by fish is unclear. However, it is possible to resolve the contradiction between outcomes, at least partially, and to suggest which is the more indicative of fish predation effects. Benthic predation was proportionately (Fig. 4a vs. 4b) and absolutely (Fig. 5a vs. 5b) higher than planktonic predation in August compared to April. Also, benthic predation was mainly diurnal in April but mainly nocturnal in August (Fig. 5a vs. 5b) and is correlated with planktonic predation in April (Fig. 5a, $r = .726$, $p < .01$) but not in August (Fig. 5b, $r = .031$ $p < .9$). This suggests that a diurnal and crepuscular predator was responsible for both benthic and planktonic losses in April but that a nocturnal predator was also important for the benthos in August.

We believe that the mud crab Hemigrapsus oregonensis was the new and different predator in August. Hemigrapsus oregonensis usually occurred in low numbers in five years of sampling in Mugu Lagoon. It became very abundant in the summer and fall of 1981, coincident with a dense bloom of Ulva which was unprecedented in our five years of experience for its long persistence. We subjectively estimate that crab densities were more than an order of magnitude greater in August than in April.

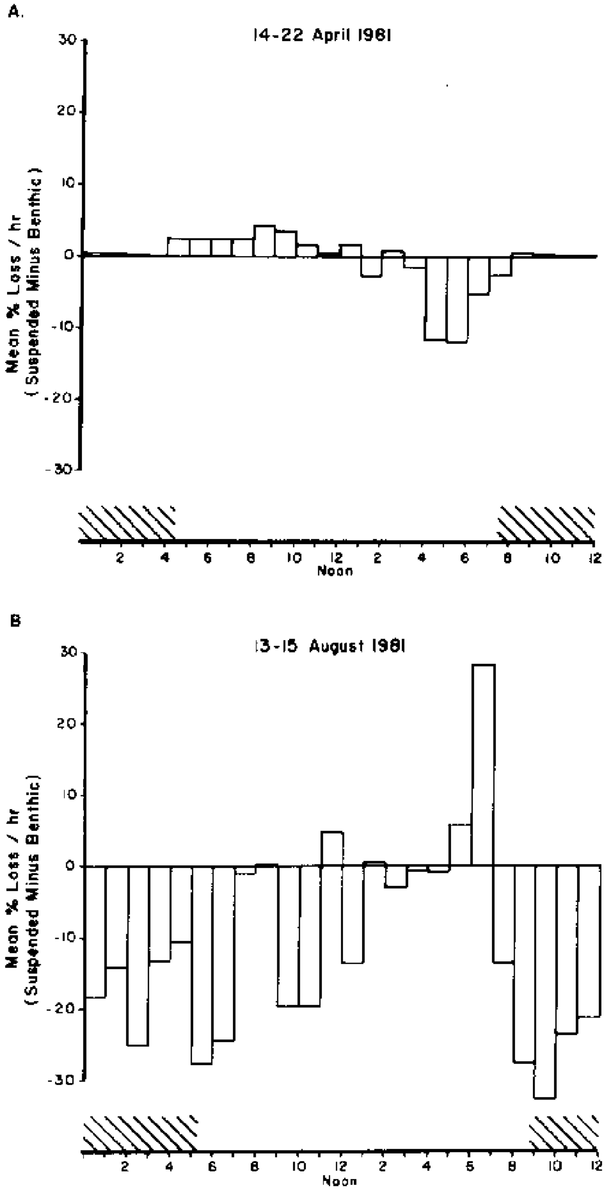

Fig. 4. Average relative bait loss rates over 24 hours (midnight to midnight) 14-22 April 1981 (A) and 13-15 August 1981 (B). Crosshatching.

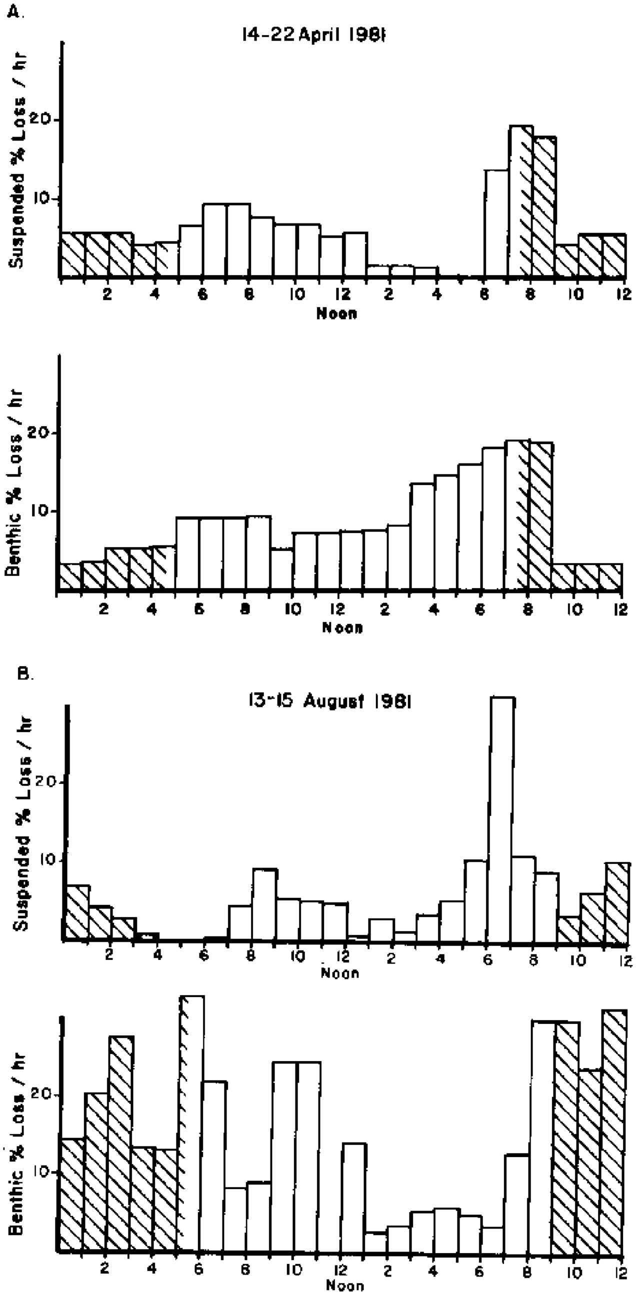

Fig. 5. Average absolute bait loss rates over 24 hours (midnight to midnight) 14-22 April (A) and 13-15 August 1981 (B). Crosshatching indicates period without sunlight.

In field trials, H. oregonensis consumed every peracarid presented on a hook, but in aquaria, they were never successful in capturing free swimming individuals. In contrast, the fish tested in the field, staghorn sculpin L. armatus, diamond turbot, Hypsopesetta gluttulata and arrow goby, Clevelandia ios required averages of 3, 4 and 10 strikes, respectively, to remove bait from hooks. In lab observations L. armatus and C. aggregata captured free swimming peracarids on every strike. Since swimming invertebrates large enough to remove bait from suspended hooks were not observed in the course of this study, suspended bait-loss was apparently due entirely to fish predation. Benthic predation on bait was due primarily to fish and crabs.

Benthic and planktonic bait-loss in April may have been correlated because of minimal effects of H. oregonensis predation on benthic bait then. Since H. oregonensis is nocturnal, the nocturnal increases in bait loss in August (Fig. 5b) would be expected if H. oregonensis was the major predator on benthic bait. This source of benthic bait-loss would provide an over-estimate of benthic predation rates relative to planktonic bait-losses caused by fish. Thus benthic predation rates that live peracarids experienced in August may have been similar to those in April. The opposite results in April compared to August may have resulted from an over-estimate of benthic predation caused by crabs in August. At present, vertical migration by peracarids in the eastern arm of Mugu Lagoon does not appear to be adaptive for avoiding fish predation.

Discussion

Although large effects were expected, the results of this study do not indicate that predation by fish has an important effect on peracarid populations in contrast to the conclusions of Van Dolah (1978) and Nelson (1979 a and b) working in Atlantic estuaries. The sources of this contradiction are not clear at present. Nevertheless, the tests of observed changes in peracarid populations against those expected if predation by fish were limiting their populations spanned 2 years and included 24 observations encompassing a wide range of predator and prey densities. Therefore, the absence of predicted patterns in the analyses performed is unlikely to change with additional observations. Unless other analyses, such as those including population age structure, are warranted, the conclusion that fish predators do not significantly affect peracarid abundances in the eastern arm of Mugu Lagoon is unlikely to change.

The conclusion that vertical migration is not adaptive for avoiding fish predation, on the other hand, may be premature. It is based on hourly determinations of planktonic and benthic predation rates by the baited hook technique for only two periods, one period 54 hours spanning 9 days and one period of 38 hours spanning 3 days and the two outcomes did not agree. We have already discussed our reasons for having greater confidence in the April results when there was less possibility of confounding effects by crabs, which are a very different kind of predator. However, skepticism is called for until additional trials have been carried out under a variety of conditions (seasons, abundances of peracarids and fish) and with suitable controls for other kinds of predators, especially crabs. Furthermore, planktonic and benthic densities of peracarids must be monitored concurrently with the bait trials, rather than years apart as in this pilot investigation.

Most of the shortcomings above owe to the preliminary nature of this investigation and are easily remedied. However, two are not. The baited hook technique will never measure in true proportion the rates of predation of different kinds of predators (such as fish and crabs in this study). Perhaps observations in the laboratory will suffice to adjust this discrepancy.

Despite these drawbacks, we see major advantages of the baited hook technique over techniques used in other studies of fish-peracarid interactions. At least some of the time, the actual identity of a predator will be revealed by its capture on the hook. This is never exclosure experiments (Van Dolah, 1978; Nelson, 1979 a and b), although different types of cages can be set out in an area to separate the effects of different kinds of predators in some cases (Quammen, 1981). Also, the baited hooks to not alter the rest of the environment, as exclosures inevitably do. For organisms as mobile and responsive to new substrates as peracarids are, as evidenced by their role as earliest colonists of dredge spoil and defaunated substrates (McCall, 1978; Bowen et al., 1979, Yeo and Risk, 1979; Alldredge and King, 1980; Santos and Simon, 1980) this may be an important advantage.

Acknowledgements

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Food Consumption by Silver Hake (*Merluccius bilinearis*) on Georges Bank With Implications for Recruitment

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Introduction

The necessity of multispecies management has been a concern in the Northwest Atlantic especially since 1972 (cf. Brown et al., 1976; Edwards, 1976). A critical requirement for evaluation of biological (predator-prey) interactions within an assemblage of species is actual food consumption of the various species.

In this paper, we describe calculations of daily ration for silver hake, using quantitative data on stomach contents of field caught fish (Langton et al., 1980) and an exponential model of digestion in fish (Elliott and Persson, 1978; Eggers, 1977; Pennington, 1981). Ultimately, the data on daily ration will be used in a predator-prey based model of the interactions involving major fish species on Georges Bank. This model, named GEORGE, will be used to explore possible long-term effects of different management strategies on fish and invertebrates on Georges Bank.

Materials and Methods

Estimates of mean stomach contents are based on food habits data collected from 1972 to 1976 on spring and fall bottom trawl survey cruises from Cape Hatteras to the Gulf of Maine. Stomach contents were sampled and preserved in formalin for identification and weighing in the laboratory. Complete details of food habits data collection are available in Langton et al. (1980).

Food consumption is evaluated with the model proposed by Elliott and Persson (1978) and Eggers (1977):

$$\frac{dS(t)}{dt} = R(t) - \alpha S(t) \qquad (1)$$

where: $S(t)$ is weight of stomach contents
$R(t)$ is the rate of food consumption
α is the unit rate of evacuation and is a constant (for all fish in a given species).

This model assumes that gastric evacuation is proportional to the amount of food in the stomach (Elliott and Persson, 1978; Eggers, 1977). The exponential model of digestion is the most appropriate formulation to use (Cochran, 1979; Eggers, 1979; Elliott, 1979; Durbin and Durbin, 1980). The rectilinear model used by Daan (1973) gives similar results for the digestion of the first 90% of the stomach contents, but leads to an underestimate of daily ration by neglecting the last 10% of the stomach contents. Eggers (1979) has pointed out that if the amount of food in the stomach is periodic, then

$$\bar{C} = \alpha \bar{S} \tag{2}$$

where: $\bar{C}$ = average hourly consumption
$\bar{S}$ = average stomach contents.

Pennington (1981) has shown that even if feeding is not periodic, equation 2 still holds if samples are taken over a sufficiently long period of time. Pennington (1981) has also shown that equation 1 is more general than indicated by Eggers (1977, 1979) and Elliott and Persson (1978) and that given α, all that is necessary to estimate $\bar{C}$ is an estimate of $\bar{S}$. The procedure for estimating $\bar{S}$ from food habits data is explained in detail in Pennington (1981), and we have used his procedures in this paper.

Daily ration ($\bar{D}$) is then given by

$$\bar{D} = \alpha \bar{S}\, 24 \tag{3}$$

the variance of the $\bar{D}$ is given by

$$\mathrm{var}\ \bar{D} = 24\ \alpha \sqrt{\mathrm{var}\ \bar{S}} \tag{4}$$

$$\mathrm{var}\ \bar{S} = \sum_{i=1}^{24} \mathrm{var}(\bar{S}_i)/24^2 \tag{5}$$

$$\mathrm{var}\ (\bar{S}_i) = \sum_{j=1}^{k} (S_{i,j} - \bar{S}_i)^2/K(K-1) \tag{6}$$

where: $S_{i,j}$ = average stomach contents of fish in j^{th} tow during i^{th} hour
K = total number of tows during the i^{th} hour.

All stomach contents and daily ration estimates are normalized to percent body weight.

The daily ration (% body weight) was expanded to yearly consumption by multiplying by 365 times the appropriate biomass for each age category of silver hake. The age categories are 0, 1, 2, 3, 4+. The biomass estimates were calculated utilizing a Northeast Fisheries Center (NEFC) assessment document (Almeida and Anderson, 1979), the length/weight equations in Wilk et al. (1978), and the von Bertalanffy growth equation of Almeida (1978). The estimates of abundance of 0-group fish were made by applying a simple exponential model to the number of age 1, using the estimate of natural mortality (M) from the cohort or virtual population analysis (VPA) (Ricker, 1975) with no fishing mortality (M = .4). The estimates of biomass are mean values for the period 1963-1972. Using the mean for 1963-1972 facilitates comparison with two recent papers dealing with fish production, consumption and biomass on Georges Bank (Grosslein et al., 1980; Cohen et al., 1981).

The digestion rate, α, was estimated from Fänge and Grove's Figure 4 (1979) based on the feeding type of different fish species. Silver hake is a macrophagus species based on the natural logarithm of the ratio (predator weight/prey weight) from Hahm and Langton (1980). The digestion rate was then considered to be a constant (at a given temperature) for all types and sizes of prey for all age classes of silver hake.

Results

Silver hake have a daily ration of between 0.6 and 2.2% body weight when all prey are included. The daily ration of fish prey alone ranges from about .1 to 1.9% body weight (Table 1). Excluding the 0-group fish, daily ration increases with age for silver hake, for all prey combined and for fish prey alone. The 0-group silver hake have a higher daily ration than the older fish for all prey except for the oldest fish (4+), but young-of-the-year silver hake do not feed heavily on fish. The total food consumption by silver hake is approximately 2 million metric tons of which 1.5 million tons is fish (Table 2).

Discussion

The daily rations we obtained using the modified Bajkov equation (Eggers, 1979) agree reasonably well with the published values for silver hake. Our values range from about .6-2.5% body weight/day (Table 1) in the lower end of the range of 1.3-5.7% body weight/day reported for the Northwest Atlantic by Edwards and Bowman (1979), Grosslein et al. (1980) and Durbin et al. (1980). Vinogradov (1977) calculated daily rations of silver hake in July 1971, 1972 and August 1972, 1973 for the same region and his values were 14.17%, 3.5%, 12.2% and 3.6% of body weight, respectively. Vinogradov (1977) determined digestion rate by calculating the maximum decrease in stomach contents from one trawl sample of fish to the next. He calculated daily ration by multiplying the digestion rate per hour (%/hour) by the number of hours digestion was occurring (for July 1971 it was 11 hrs.) and adding the amount by which the stomach contents increased over the rest of the day. The sample size was about 40 fish per trawl haul. It is possible that the fish caught at one time were under a different feeding regime than those at the next sampling time. Either or both of their factors may contribute to the differences in Vinogradov's data compared with our results.

Edwards and Bowman (1979) postulated that silver hake is a keystone predator controlling its own biomass through cannibalism as well as the biomass of other species by predation. There is some evidence that silver hake is controlling its own stock size through cannibalism.

Table 1. Mean stomach contents ($\bar{S}$) and daily ration (D.R.) as % body weight for different age silver hake. The digestion rate a = .055. Data for both seasons and all years combined. N is the number of fish caught in a particular age category.

Size (cm)	Age	N	Prey Type	$\bar{S}$	var $\bar{S}$	D.R.	Var D.R.
0-16	0	1223	All	1.219	0.020	1.609	0.035
17-24	1	245	All	0.475	0.015	0.627	0.025
24-29	2	426	All	0.517	0.020	0.682	0.035
30-34	3	503	All	0.684	0.028	0.903	0.048
$\geq$35	4+	318	All	1.693	0.088	2.235	0.153
0-16	0	1223	Fish	0.225	0.019	0.297	0.033
17-24	1	245	Fish	0.060	0.001	0.079	0.001
25-29	2	426	Fish	0.305	0.019	0.403	0.033
30-34	3	503	Fish	0.454	0.025	0.599	0.045
$\geq$35	4+	318	Fish	1.464	0.073	1.932	0.128

Table 2. Biomass and annual consumption by silver hake on Georges Bank.

SPECIES	AGE	BIOMASS (10^3TONS)	CONSUMPTION (TONS/YR)	
			ALL PREY	FISH
SILVER HAKE	0	3.61	21,201	3,913
	1	70.82	162,075	20,421
	2	120.92	301,006	177,867
	3	86.88	286,352	189,950
	4+	166.13	1,355,257	1,171,516
TOTAL			2,125,881	1,563,667

Bowman (NMFS, NEFC, unpublished data) has evidence that adult silver hake feed mostly on silver hake. About 75% of the diet of adult silver hake is fish and the remaining 25% is primarily euphausids. Based on the consumption estimates and using the predator to prey weight ratios in Hahm and Langton (1980), the range in numbers of 0-group fish consumed by silver hake can be estimated. The mean prey size of fish for the different age categories of silver hake are 0.54 g, 7.51 g, and 27.25 g for 2, 3, and 4+ fish, respectively. These weights correspond to silver hake in their first year of life. If we assume that the mean prey size is actually 10 times this to account for digestion of prey resulting in very small pieces identifiable only as fish, we will have a very conservative lower limit on the number of prey consumed (approximately 5 x 10^{10}), as well as an upper limit (approximately 10 x 10^{10}) based directly on food habits data. This range agrees well with the actual numbers of post-larval fish found on Georges Bank.

The number of 0-group silver hake at age 4 months (Bolz and Lough, 1981) (about the time that the larvae become juvenile fish) compared to the number of 1 year olds on 1 January of the next year is shown in Table 3. The instantaneous mortality expressed as Mt (t = 3 months) is between about 4.5-7, yielding annual M's between 18-27 yr^{-1}. This natural mortality is extraordinarily high and indicates that mortality after the larval stage can regulate year-class strength. Zero group silver hake are in the preferred prey size range (Hahm and Langton, 1980) of adult silver hake and therefore presumably the high mortality is due to cannibalism.

Recent trends in silver hake recruitment and spawning stock size are shown in Figure 1 and suggest that at high levels of spawning stock, cannibalism may be a significant factor in regulatory recruitment. In the period before intense foreign fishing on Georges Bank (prior to 1968), recruitment continued to increase with stock size until possibly some critical value was reached and then declined precipitously followed

Table 3. Calculation of mortality estimates for 0 group silver hake. Larval data from ICNAF larval herring survey (Bolz and Lough, 1981). One year olds from Almeida and Anderson (1980).

YEAR	NUMBER OF 0 GROUP	NUMBER OF 1 YEAR OLDS	Mt
1972	1.3×10^{11}	1.05×10^{9}	4.82
1973	2.2×10^{11}	9.79×10^{8}	5.41
1974	4.7×10^{11}	5.12×10^{8}	6.82
1975	6.8×10^{10}	6.50×10^{8}	4.65
1976	2.0×10^{11}	6.00×10^{8}	5.81

$$\frac{\text{number of 1 year olds}}{\text{number of 0-group}} = e^{-Mt} \qquad t = 2\text{-}4 \text{ months}$$

by a decline in adult biomass. A similar pattern appeared to begin after 1968 but high fishing mortality presented a build-up in abundance of adults, and recruitment declined presumably due to factors other than cannibalism.

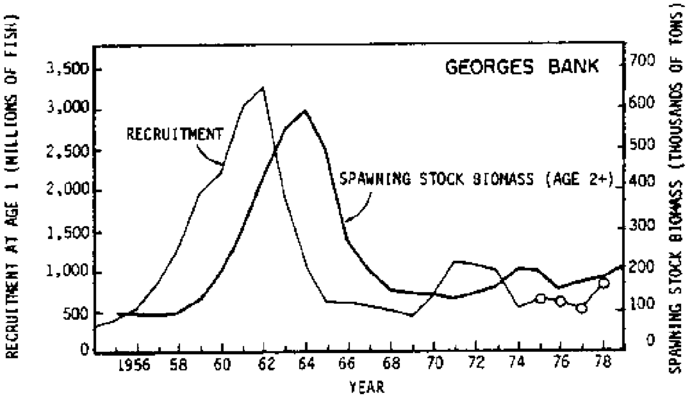

Figure 1. Georges Bank silver hake spawning stock biomass (age 2+) in 1955-79 and abundance at age 1 of the 1954-78 year-classes. (Open circles indicate estimated year-class sizes.)

Using haddock data based on Smith et al. (1979) (Table 4), the mortality in the juvenile stage (0-group, post-larvae) is in the same range as for silver hake, i.e. Mt = 5.5-8.7 (t = 3 months) at a time when haddock, based on their weight, are vulnerable to silver hake predation. Haddock also have a very high mortality earlier in their larval period, but the high mortalities after the larval period do indicate that predation could have a significant effect on year-class strength.

Table 4. Calculation of mortality estimates of 0-group haddock on Georges Bank based on numbers estimated on 1 October from April-May larvae data (Smith et al., 1979), t=3 months. M was calculated for early May to late May and late May to June. M=.1757 day^{-1} and .0134 day^{-1}, respectively. The lower value was chosen since a mean of the two values of M leads to less 0-group fish in October than 1 year-old fish on 1 January.

YEAR	LARVAE	CALCULATED 0-GROUP ON OCTOBER 1	1 YR OLDS	Mt
1974	6.8×10^{10} (Apr-May)	1.71×10^{10}	2.10×10^{6}	10.8
1975	1.7×10^{11} (Apr-May)	4.38×10^{10}	2.01×10^{8}	6.77
1976	9.6×10^{10} (Apr-May)	2.42×10^{10}	13.3×10^{6}	8.88
1977	5.24×10^{11} (Early May) 4.45×10^{10} (Late May) 3.06×10^{10} (June)	7.69×10^{9}	1.2×10^{6}	10.15

There are a number of possible sources of error in our estimates. The daily ration determination is critically dependent on the digestion rate (α) that is used. Fänge and Grove (1979) point out that digestion rate varies with temperature, meal size, prey type, predator, size of the fish and previous feeding history. Durbin et al. (1980) assumed that all species had the same α varying with temperature and prey type (fish vs. all other prey). We have chosen α to vary with temperature and prey size, keeping it constant for all sizes of a given predator. Insofar as large fish of a species have the same prey as the smaller ones, no error will be introduced. In some species, notably silver hake, cod and pollock, the larger fish feed more heavily on fish than do the smaller ones. They can be considered functionally different species and perhaps should have a different digestion rate such as used by Daan (1973).

Perhaps the most serious source of variability is the spatial and temporal variability of the fish and their prey on scales finer than we can resolve. Pennington et al. (1980) have shown that the variability within a tow is greater than the variability between tows for the same or different cruises.

Another major source of error is that the abundance estimates of 0-group fish are very poor; there is no VPA data on young-of-the-year fish and our survey trawl does not sample them adequately. This makes it very difficult to assess the contribution of 0-group fish to the diets of their predators. Along with errors associated with estimating α, this is the major stumbling block in analyzing multispecies interactions. The mortalities associated with 0-group fish are large enough to affect recruitment. Errors in estimates of 0-group abundance can therefore contribute serious errors to estimates of the number of recruits.

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Session V Discussion
Fish Feeding as a Structuring Force on Prey Communities

Glenn VanBlaricom, Discussion Leader

Questions Following Irvine Presentation:

Feller asked what proportion of the reef is covered by territories and how important is the fish feeding activity on the structure of the reef as a whole. Irvine said that since this particular species is the behavioral and numerical dominant, its territories cover most of that portion of the reef which have territories. Some areas of the reef are apparently not suitable for territories and most areas of the reef have other territorial species occupying them. Crow asked how long an individual damselfish would remain on a given territory. Irvine replied that these fish and their territories are relatively long-lived, spanning in her experience at least several years occupying the same site. Turnover appears to be low.

Questions Following Hixon Presentation:

Breitburg inquired if similar patterns resulted for the sessile invertebrates that settled on the plates as for the algae. Hixon said they still had not completed working up these data. He did think, however, that the diversity outside the territories would be low, but that the differences would not be as significant as with the algae. There is a strong relationship between the kinds of algae that grow and the invertebrates that associate with these algal turfs. Rowley asked if there was a difference in the effect of damselfish grazing in the middle of a territory versus on the edge, considering that they might have different motivations and different species to chase in these two zones. Hixon responded that he did not think so, but that he really could not say because his settling blocks were stuck right in the middle of an individual's territory. Irvine mentioned that in the Caribbean both live coral and algae occurred within the territories, whereas in Hixon's Hawaiian system, no live coral was there.

Questions Following Crow Presentation of Bohnsack Paper:

Cailliet asked whether these predators actually eat the things that they are being considered to influence. Crow said that he did not think that their stomachs were examined, but that the literature indicated they did. Cailliet wondered if it would be possible to distinguish the effect of divers taking both small and large fish from those of the removed predators, since they would presumably have similar effects. Roberts inquired about the distance between the control and fished area, which was large, and whether it could be certain the effects were related only to spearfishing. Crow mentioned that it was his impression that similar assemblages of fishes occupied both general regions in these waters off Florida. Larson asked whether the reef open to spearfishing did not result in those fish being more wary of divers. Crow said that it is suspected that they may avoid that reef entirely. Feller asked how long Crow thought it would take for the reefs now being fished to reach the same state of succession as the reef which has been unfished for years. Crow felt that changes would occur quite rapidly since artificial reefs in the area have attracted similar fishes within months. Broad migration patterns appear to occur going north in the summer time and south in the winter and this may help colonization some. Herbold asked whether there had been records of predator abundance on the reef prior to fishing and Crow indicated that no records had been kept. McAllister and Crow discussed, in some detail, the methods used by Bohnsack to estimate species composition and relative abundance of fishes on these reefs.

Questions Following Cowen Presentation:

Roberts inquired what the response of the sheephead might be if sea otters were transplanted to San Nicholas Island. Cowen thought that since the sheephead have such flexible diets and did not appear to require urchins, sea otters would not influence them very much. Field asked if the size of the sea urchins was a problem for the sheephead to eat. Cowen said that he had observed sheephead eating all sizes of urchin, but the largest sheephead do tend to eat the largest sizes of sea urchin. Herbold asked if Cowen thought the sheephead were actually controlling the size of the urchin population. Cowen said most of the areas where large densities of sea urchins occurred were also areas where few sheephead occurred or appeared to feed much. Rowley asked if Cowen had any information on the importance of urchins in the diet of sheephead from barren grounds. Cowen did not have any stomachs analyzed from these areas yet, but from dives there he has not seen very many broken urchin tests. Carpenter asked why it seems to be taking so long for the urchins to come out in his experimental plots, and is there a difference in the sizes of those that do versus those that do not? Cowen is not sure why or where these urchins are coming from, and he is not seeing a trend in size frequencies. For now, he is still not ruling out recruitment. Another possibility he mentioned is that they can react to remains from other urchins which have been eaten or broken, a phenomenon which has also been shown for tropical urchins, and this could keep them away for at least awhile.

Ebeling asked if Cowen had noticed any variation in the size of males at his study site since Ebeling has noticed that individuals of both sexes at a site off San Onofre are smaller, and individuals off San Miguel Island are huge. Cowen has noted very large females off San Nicholas Island, some over 15 pounds. Ebeling then asked if Cowen thought this might be due to exploitation and whether the fish might be induced under heavy fishing pressure to reach maturity at an earlier age or smaller size. Cowen thought that this might be possible, but that he could not rule out environmental factors influencing different subpopulations occurring along the coast. Ebeling then asked if, in the areas where smaller individual sheephead occurred, the urchins are escaping predation by being too large for even the large sheephead to batter, ram or handle. Cowen thought there might be a refuge in size, but often where one sees urchins out in the open, it is not due to reduced sheephead predation entirely, but also may relate to such factors as spine length. Cailliet asked if there were any other potential competitors that eat similar arrays of prey as the sheephead and, if so, have any of these moved into the experimental plot. Cowen replied that plenty of different predators eat the small crabs, and the fish fauna off these islands is both abundant and diverse, but that most of them do not feed on the same items as the sheephead. Maule noted that there was a commercial urchin fishery off Santa Barbara and wondered if similar exploitation efforts occurred anywhere near the island study sites. Cowen replied that urchins are exploited by divers at San Nicholas Island, but that the reef he is studying is small enough that they do not bother to work there. But on one occasion, Cowen had noted a large dive boat in the area, but fortunately found that these numerous sport divers were actually diving on an adjacent reef, not the area where his experimental plots were located.

Questions Following Chapman Presentation:

Simenstad asked about potential tidal effects and wondered if resuspension of sediment was a factor in the distribution of peracarids. Chapman noted that fewer peracarids were collected during higher tidal currents, but that they also responded to temperature and moonlight. Chapman felt that the role of tides on predation was minor, especially since, in the Mugu Lagoon system, tidal currents were usually slight. Also, since much of the area was relatively coarse sand, resuspension was not common.

Questions Following Cohen Presentations

Larson was curious that Cohen felt that they would not be able to detect recruitment cycles when fishing started, since, if the adults actually exerted this tremendous predatory effect on the juvenile recruits, you would expect to see a jillion recruits when adults were fished, unless these now abundant recruits start competing with each other and limiting themselves in some other way. Cohen replied that they do not know that they are cannibalistic all the time or just when conditions may be bad, but they still wonder why the number of recruits has not increased, since they certainly have the fecundity to do so. Karpov asked what time of day the samples were taken and Cohen said that they were taken just about every hour of the day over the sampling period. A general discussion followed discussing Bajkov's equation and the role that temperature may have played in their calculations. La Bolle questioned Cohen's contention that mortality occurring at the postlarval stages (mostly cannibalism) was more important than mortality in the larval stages since no information on larval abundance was available. Cohen rephrased his point to state that mortality by cannibalism, since it appeared to be so prevalent, was an extremely important factor to consider when evaluating what influences recruitment.

Eggers mentioned that he had heard of similar postlarval mortalities being influential on several Bering Sea fish populations, so that this influence on recruitment may not be so unusual.

General Discussion of Fish Feeding as a Structuring Force

Van Blaricom posed a question: "Tropical reef systems appear to be dominated by herbivores, whereas in temperate systems, there are mechanisms available that have very tight control over herbivore densities and this obviously has major consequences on the macrophyte assemblages and associated structures in the habitat. Why do you suppose tropical herbivores are out of control?"

Hixon stated that this was a good question, but that he was not sure that the tropical herbivores were out of control. Rather, he felt that the densities of sea urchins are not that dissimilar between tropical and temperate reef systems, especially in temperate systems without sea otters. He mentioned another difference which should have been considered, that coral reef systems have a good deal of algae housed within the corals themselves. In considering the fishes, Hixon thought that it was strongly related to phylogeny and zoogeography, where the temperate region is missing whole groups, usually families, of herbivorous fishes. He feels that this may have been the result of some major evolutionary constraint such as the effect of colder waters on digestion processes.

Irvine mentioned that juveniles of herbivorous fishes often were more carnivorous than the adults. Grossman contended that herbivorous fishes weren't that rare in temperate systems. In the rocky intertidal on the Pacific coast, for example, there are three or four species which are herbivores. Many fishes tend to have algae in their guts, but most do not feel that these fishes can utilize it, so they discount herbivory. Hixon commented on Californian subtidal reef fishes and pointed out that the only herbivorous species were the opaleye and half moon. With these fishes also, it has commonly been suggested that they ingest algae to obtain energy from invertebrates which live epiphytically. Simenstad pointed out that, in the Pacific Northwest, once you go outside the littoral zone, there are virtually no herbivorous fishes which therefore make no impact on the algal communities living there. Chapman asked why there appear to be so many predatory fishes in higher latitudes and why there appear to be such high densities of invertebrates there as well. He felt that this was especially true for crustaceans and that these organisms exhibited tremendous turnover rates. Simenstad pointed out that a more relevant question might be to relate algal production and biomass, herbivory, and the detritus-based food webs, which in the northern latitudes is a much more tightly interacting system than in the tropics. Therefore, since most of these invertebrates, especially the crustaceans, are detritivores, the answer to Chapman's query may be indeed related to the large standing stocks of macro- and microphytes. Sorden pointed out that there were as many or more species of crustaceans in the tropics, but conceded that their standing stocks might be less than those in temperate regions. Also, the behavior of invertebrates might differ considerably between these regions. Cross mentioned that some isopods he has studied come out only once every five days to two weeks to feed and that this would seriously influence which fish feed on them and how influential this feeding pressure is. Rowley suggested that it would be interesting to study members of tropically-derived families in both temperate and tropical areas to see how they differ from each other, since there may be some kind of subtle enzyme shift or behavioral shift in colder waters. Ebeling mentioned that a researcher at U.C.L.A. is studying this kind of thing with girellids. He then asked whether it was still thought that the rate of metabolism is temperature-dependent where other metabolic processes could be acclimated. If so, herbivores in temperate areas might suffer from an inability to digest algae in these colder waters.

Grossman mentioned that one herbivorous cottid, Clinocottus globiceps, apparently did not have the typical herbivorous alimentary morphology, yet tended to consume algae. He guessed that perhaps it is the way their guts utilize plant cells, perhaps using low pH or something, thus allowing the food value to be assimilated rather than passed. Larson then asked whether it might be a mistake to view this from the fish's point of view. Maybe these apparent differences are related to differences in standing stock and production of algae in temperate versus tropical reefs. That is, production of algae may actually be as high or higher on tropical reefs but utilized more efficiently by more consumers. Still, this does not explain why so little of the algal standing stock or production is consumed on temperate reefs. Cowen suggested that perhaps it is the quality or biochemistry of the algae in the two regions that influence the ability of the fish and invertebrate consumers to utilize them. Or, perhaps temperate algae have more defense mechanisms. Cailliet mentioned that Lyn Montgomery at Northern Arizona University is presently studying the food value and digestibility of different kinds of algae by fishes in order to shed some light on this interesting question.

Summary and Recommendations

GUTSHOP '81 presentations and discussions involved an even broader scope of topics, habitats, and fish taxa than either of the two previous workshops. Topics included: 1) statistics and presentation of results; 2) benefits and constraints upon laboratory and microcosm feeding experiments; 3) sampling problems; 4) mathematical and conceptual models of predator-prey interactions; 5) bioenergetic experiments and models; 6) competition and partitioning of prey resources; 7) feeding behavior; and, 8) predation effects upon the structure and abundance of prey assemblages. Almost all the major habitats of fishes were represented: 1) temperate and tropical marine waters, including rocky littoral, sublittoral, demersal, midwater, and deep-sea demersal habitats; 2) estuarine waters, including littoral and shallow sublittoral habitats; and, 3) lacustrine and riverine freshwater habitats. Fishes from at least 22 families were discussed, including: Clupeidae, Salmonidae, Myctophidae, Gobiesocidae, Gadidae, Syngnathidae, Mullidae, Kyphosidae, Embiotocidae, Pomacentridae, Labridae, Clinidae, Blenniidae, Stichaeidae, Pholidae, Gobiidae, Scorpaenidae, Anoplopomatidae, Hexagrammidae, Cottidae, Cyclopteridae, and Pleuronectidae.

Although considerable attention has been paid to statistics and graphical presentation of fish stomach analysis data in past GUTSHOPS, the results of Session I illustrated that these topics still present problems to many investigators. Therefore, we have continued to test and resolve alternative statistical approaches through the GUTSHOP discussions and Mike Crow's presentation illustrated the latest iteration in the continuing quest for straightforward, robust procedures for testing the significance of different diets. Ironically, his conclusion was that, in most cases, complicated multivariate methods are not justified and are often invalid, given the requisite assumptions. His recommendation was a feeding mode x predator group contingency table which could be tested by X^2-distributed statistics. While there was some question about the feasibility and subjective aspects of categorizing prey categories according to feeding modes, this method represents a very direct means to interpret the significance between food habits. Similarly, Dave Levy made a strong argument for portraying stomach analysis results in simple graphical format for descriptive purposes. Given the easily understandable trends evident in a trophic spectrum diagram, graphical representation may be more than sufficient to address management and other qualitative purposes of fish stomach content data. Many of the problems associated with fitting stomach contents data to existing parametric, non-parametric, and mutlivariate statistics lie in the inherent variability and inconsistency of the data, which was dramatically illustrated in the paper by Pennington, Bowman, and Langton. It was continuously pointed out, however, that variability can originate from the sampling design and sample treatment as well as a natural result of variability in individual fish foraging behavior; these factors must be separated if statistical tests and interpretations are to be valid.

A new topic to the GUTSHOP discussions of methodology was that of laboratory or microcosm experiments of fish feeding technology. Both Simenstad and La Bolle described the various constraints upon such controlled experiments, both in achieving and maintaining the desired experimental conditions as well as interpreting the results in the light of the biases introduced by the "bottle" effects of aquaria and cages. Although their presentations were basically descriptions of the methodological adaptations involved in reducing such biases, it was apparent that the insight into predator-prey behavioral interactions possible with such experiments is invaluable.

Another topic unique to GUTSHOP '81 was that of the bioenergetics of fish feeding, perhaps one of the most pertinent sessions of the workshop because of the recent conceptualization of fish food habits in terms of optimal foraging strategies based upon energy budgeting. Papers presented in this session fell into three general categories: 1) the bioenergetics of optimal foraging; 2) the trophic transfer of non-assimilated energy from fishes; and, 3) the bioenergetic effects of feeding activity upon growth and metabolism.

In the one paper discussing the theoretical approach to predicting the rate and composition of prey ingested, Doug Eggers illustrated that such models often suffer from inherent circularity due to forcing the model to predict observed patterns of prey selection in the absence of empirical data (i.e. fraction of reactive field searched per unit time). As pointed out by Doug, many of these problems could be resolved with the proper experimentation on feeding behavior as described in Session I by Simenstad and La Bolle. This reiterates the argument for parameterizing models such as optimal foraging with rigidly-controlled experiments, testing the models in microcosms, field manipulations, or natural experiments, and for formulating field experiments and sampling designs around conceptual or predictive models as exemplified by the approach of Cochran and Rice.

Considerable discussion was generated by Bruce Robison's presentation on nutrient transfer through midwater fishes, much of which reflected the problems with trying to balance nutrient or energy flow through consumer organisms by piecing together a series of independent measurements in an almost unmeasurable system such as the epi-/mesopelagic region. Despite the multitude of unanswered questions, Robison's measurements of digestion and assimilation efficiencies in midwater fishes suggests that the bioenergetics of fish assemblages may differ dramatically in different habitats and indicate divergent pathways and modes of trophic energy transfer and recycling.

The other papers in Session II (Yoklavich, Sullivan, Boehlert, Pandian) tended to portray a common purpose, that of relating energetics and growth of fishes to variations in their prey consumption, behavior, and habitats. Among diverse audiences such as that at the GUTSHOP, this has the effect of opening up a number of alternative, bioenergetically-based hypotheses to explain the periodicity, rate, and composition of prey consumption of fishes in their natural environment. Interactions with their more ecologically oriented colleagues, on the other hand, encouraged the physiologists to consider intra- and interspecific, predator-prey, and other ecological interactions as constraints to the bioenergetic aspects of fish feeding. This discourse suggests that, by trying to understand the synergistic effects of bioenergetic and ecological influences upon fish distribution, behavior, and growth, we may have a greater insight into the dynamics of their food habits. Perhaps one of the most important contributions of the GUTSHOPs is to promote the integration of these traditionally isolated disciplines in this manner.

Six epigrammatic presentations focused on the subject of Session III, competition and resource partitioning. An important point of discussion revolved around the role of scale in defining fish community structure in terms of deterministic processes; even the paper by Gary Grossman, which argued against the resource partitioning paradigm and determinism, could be viewed as an illustration of local stochasticity embedded in global determinism and persistence (see discussion following Moyle and Allen presentations). Equally germaine to the questions of coevolution, competition, and resource partitioning is the method of defining fish groups or guilds. As brought out by Ralph Larson, without actually measuring such interactions among species in the field, it is difficult to legitimately presume active division of prey resources or foraging space. The only nondescriptive alternative is the approach mentioned in Al Ebeling's presentation of comparing species' realized and fundamental niches through manipulative experimentation or comparative studies of species in areas with and without other guild members.

Subjects covered in Session IV, Feeding Behavior of Fishes and Prey, diverged from our original intent, which was to delve into the strictly mechanistic, behavioral interactions between fish predators and their prey. Specifically, we had hoped to hear papers and discuss the strategies by which fishes optimized their capture of preferred prey, identified and rejected undesirable prey, and altered their foraging behavior as a function of hunger, previous experience, and prey escape responses. Three papers, those by Adams, Pearcy et al., and Sorden, approached foraging behavior indirectly from the standpoint of the periodicity of prey in fish stomachs and the known behavior and microhabitat attributes of the dominant prey. The presentation by Laur and Ebeling was, in fact, the only one visually documenting modes of food handling and feeding periodicity. It is obvious that direct observation was the only method by which these investigators would have been able to differentiate the surfperches according to generalized, (e.g. "browser-picker", or specialized, e.g. "crunching" or "oral-winnowing") foraging modes and relate these behaviors to the fishes' functional morphology, in this case the surfperches' elaborate pharyngognathy. This is undoubtedly just one example of many behavioral approaches to fish feeding ecology which we would benefit learning about in future GUTSHOPS.

Accordingly, we hope that some of us will explore beyond our usual gastrointestinal fixation to in situ observations and experiments, enabling us to report back on how such information has altered earlier conclusions concerning the mechanisms of fish foraging inferred from stomach contents analyses.

Session V, Fish Feeding as a Structuring Force on Prey Communities, was another new topic to the GUTSHOP at the session level; Glenn VanBlaricom's presentation on the effect of bottom-feeding rays upon benthic community structure at GUTSHOP '76 was one of the few to address this question and it was logical that he should lead the session for GUTSHOP '81. From the diversity of the papers presented in this session, including effects of fish herbivory upon algae communities, effects of fish predation on herbivores as an indirect structuring force on algae communities, the influence of fish predation upon peracarid crustaceans, and the fisheries management implications of cannibalism upon prerecruits, this topic is apparently one which is approached from a variety of hypotheses and methods. One of the obvious conclusions of these studies was that important secondary and tertiary effects of fish predation pressure on the "realized niche" of prey populations and associated species, such as changes in competition between prey and nonprey species or a significant change in the magnitude of herbivore grazing, must be considered in addition to the direct predation effects. And, in most cases a reasonable knowledge of the population dynamics of the dominant prey species must be gained in order to determine the long-term effects of size-, age-, or life history stage-specific predation upon production. The simplest possible model might be that of cannibalism, as documented for silver hake on Georges Bank by Cohen and Grosslein. But even at this level of complexity, somewhat elaborate documentation of the important population parameters regulating recruitment (mortality rates, age at recruitment, stock assessment of larvae and juveniles) are required before fish (e.g. adult silver hake) foraging can be identified as the causal mechanism. Perhaps on the other end of the scale of complexity in food web interactions, the illustration of damselfish structuring coral reef algae communities and succession patterns described by Gail Irvine was facilitated by the use of manipulative experiments which permitted testing of hypotheses about causal mechanisms, something virtually impossible in the Georges Bank silver hake population. As was illustrated in Gail's paper, visual documentation of damselfish behavior was also a critical source of data on food selection and algae removal ("weeding") which produced the observed algae community within damselfish territories.

Reflection on the presentations and discussions of GUTSHOP '81 leaves us comparing our intentions and aspirations with the resulting scope and resolutions of the workshop. Despite the continued emphasis on methodology and statistics over the three GUTSHOPs, new questions and problems continue to arise; we no sooner resolve one conflict, such as the appropriate statistical tests for comparing fish diet composition, than we uncover another, such as the sources of high variability around consumption rate estimates. It would appear that sampling and experimental designs applicable to fish food habits studies are still in need of discussion. One of our most elusive topics, which we hoped to address in Session IV, is that of fish foraging behavior and predator-prey interactions. It is apparent that much of the ambiguity in interpreting the contents of fish stomach contents originates from our typically a posteriori view of the predation event. Although there were references to behavioral observations throughout the workshop, these were usually ancillary observations and the feeding behavior of the fish and the escape response of the prey were seldom related to the observed prey selection. We obviously need to delve more into the behavioral aspects of fish feeding. And, while GUTSHOP '81 did include productive sessions on the bioenergetics of fish feeding and fish feeding as a structuring force on prey communities, there was little time to cover these topics effectively. In the case of bioenergetics, the physiology of feeding and digestion was a topic raised frequently in discussion but one of which we were only poorly informed. Session V on the effects of fish predation on prey communities generated more presentations and discussion than we had anticipated and we still had not touched on the effects of zooplanktivorous or soft-bottom benthos fish predators upon their respective prey assemblages; there appears to be considerable scope for growth of these topics above and beyond GUTSHOP '81.

At the end of GUTSHOP '81 we circulated a questionnaire regarding the need and desire for a future GUTSHOP and the evaluation of this workshop. We received 67 responses, many of them with extensive suggestions and constructive criticisms. Virtually 100% of the respondees felt that there should be another GUTSHOP. The majority (72%) thought that it should occur in 1983, 18% in 1982, and 10% in 1984; most proposed the fall (Oct.-Dec.) (59%) or winter (Jan.-March) (21%) as an optimum time. The Asilomar Conference Center obviously made a good impression, as 23% considered it the optimum location for the next workshop; other common suggestions were anywhere along the central west coast (18%), Oregon (15%), Santa Barbara (13%), Seattle (8%), and British Columbia (7%). Among the preferred topics were: 1) methodology and sampling design (16%); 2) statistics (16%); 3) bioenergetics, physiology, and nutrition of feeding and digestion (15%); 4) behavioral interations between fish predators and their prey (13%); and, 5) competition, resource partitioning, and community structure (10%); other, less popular topics for consideration included modeling and simulation, use of food habits information in fisheries management, and structuring of prey communities by fish feeding. Approximately 72% thought that the number attending GUTSHOP '81 was the optimum group size (100); 17% suggested under 100; 7% recommended 100-200 participants; and 4% felt that there should be no limit to the number attending. The idea of associating GUTSHOP with another meeting (i.e. ESA, ASIH, WSN, etc.) was overwhelmingly (89%) rejected. More than 65% of the respondees suggested that there be no geographical restriction placed upon the participants; 20% thought that it should be restricted to the western U.S. and Canada; 8% recommended that only U.S. scientists participate; 6% wanted it left open to North America; and 2% suggested North America and Europe. Common recommendations for changes in the workshop format included: 1) more time for meal and recreational breaks; 2) more time for discussion and open microphone type of sessions; 3) shorter talks; 4) a poster discussion; and 5) divided working groups for further discussion. The respondees uniformly supported the existing format of consecutive sessions and the approximately three day duration of the workshop. Five responses (7%) recommended that proceedings not be published, while several others suggested that they be upgraded by being circulated through an established journal as a special issue. And, while there were many suggestions that we continue to organize the workshops, a number of the respondees volunteered their assistance or that of their organization in sponsoring the next GUTSHOP.

Considering these responses and the results of GUTSHOP '81, we make the following recommendations relative to the pursuit of a fourth GUTSHOP:

1) A GUTSHOP be scheduled for fall (late November-early December) 1983;
2) It occur at either Asilomar Conference Center or in Santa Barbara;
3) The duration be three to three and a half days, with sessions occurring both during the day and at night separated by recreational breaks;
4) Presentations be fewer or briefer, leaving more time for general discussion;
5) Session leaders are encouraged to be responsible for a stricter selection of papers, perhaps organizing the session with an introductory plenary paper of longer length than subsequent papers;
6) Preference be given to papers written specifically for the GUTSHOP objectives and topics, not to those shoehorned into the session topic merely by creative titling;
7) Session topics include methodology, sampling design, and statistics; the bioenergetics and physiology of feeding and digestion; behavioral aspects of fish foraging and prey escape; competition, resource partitioning, and community structure, including prey switching; ontogenetic changes in food habits, including feeding in fish larvae; and effects of fish predation in structuring prey assemblages; and,
8) Proceedings be published, perhaps in association with an established scientific journal.

We hope that you find these proceedings as informative and instructive as we have found the process of preparing them. It was our intent to portray all questions, answers, and discussions as exactly as they occurred and, where it was necessary to paraphrase, have attempted to retain and isolate the salient points; we hope that any misinterpretations are minor and assure the authors that it was unintentional!

As in previous GUTSHOPs, it is our sincere hope that these proceedings will provide the impetus for many of you to direct your investigations of fish feeding toward newer questions with different approaches such that, come GUTSHOP '83, we will have addressed and answered most of our existing riddles and will have a whole new generation of riddles to solve.

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