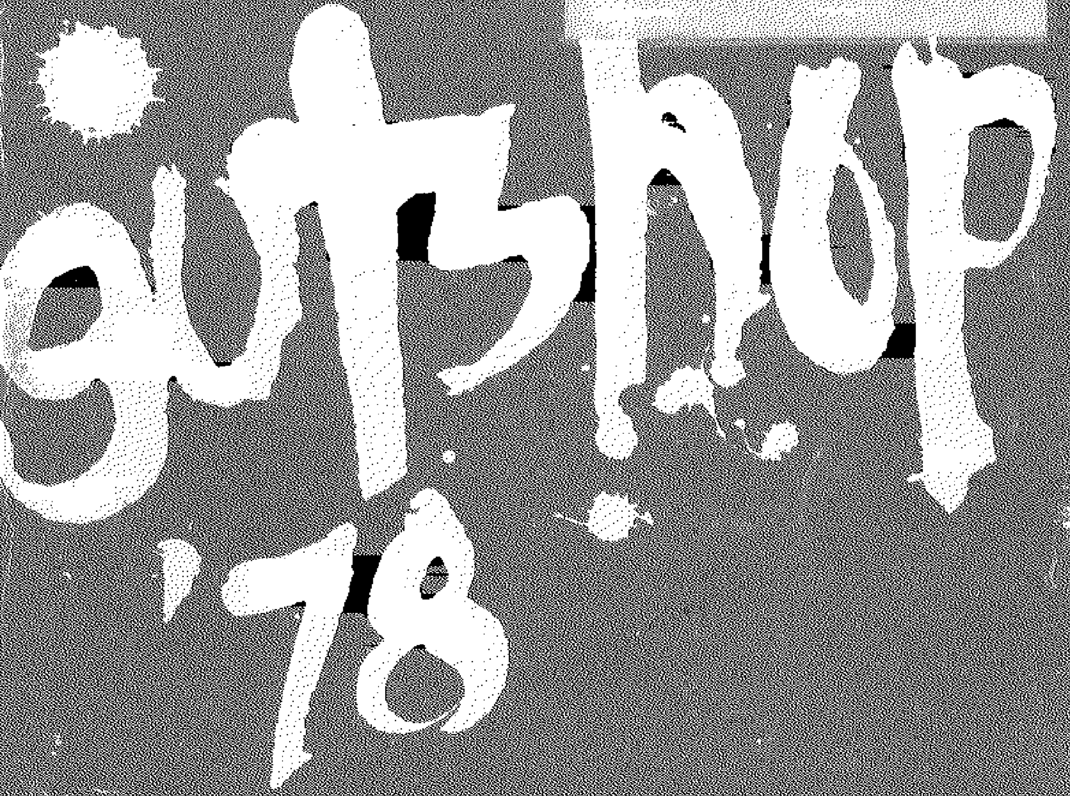
Fish Food Habits Studies Proceedings of the Second Pacific Northwest Technical Workshop



October 10-13, 1978
Lake Wilderness Conference Center
Maple Valley, Washington

Workshop Cosponsors

Fisheries Research Institute
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gutshop '78

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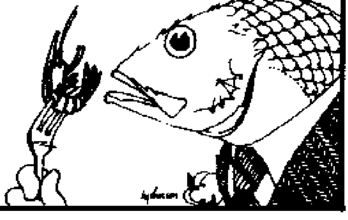
Editors

Sandy J. Lipovsky
Charles A. Simenstad

A Washington Sea Grant Publication
University of Washington
Seattle



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1st Pacific Northwest Technical Workshop
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Acknowledgments

We cannot pretend that we organized this entire workshop by ourselves. In fact, without the help and cooperation of the many people and institutions there would have been no GUTSHOP '78.

First, our thanks go to personnel of the Washington Sea Grant Communications Program at the University of Washington who prepared flyers, programs, nametags, and other informational material. The imaginative graphics were the creations of Kirk Johnson of Washington Sea Grant. The staff of the co-sponsor, the Fisheries Research Institute of the University of Washington, are to be thanked for assistance with the planning and programming. Two F.R.I. staff members, Bill Kinney and Jeff Cordell, were invaluable in their assistance with registration by seeing that some participants were picked up and delivered to and from Sea-Tac Airport.

Special thanks go to the staff of the University of Washington's Lake Wilderness Conference Center and especially to Director Peggy Ruthstrom, who worked closely with us for several months and who was responsible for the smooth organization during our stay at the Center. The meals and social hours were truly unforgettable and the friendliness deeply appreciated.

A special thank you goes to Dr. Robert Burgner, Director of the Fisheries Research Institute, who presented the opening address and who lent the support of the Institute. Mike Crow, of the UW Center for Quantitative Science is also to be thanked for his cooperation and energies in providing a truly impromptu presentation and subsequent manuscripts.

The biggest thank you goes to each participant for providing excellent presentations and dynamic discussions. We all look forward to GUTSHOP '80.

Introduction

GUTSHOP '76--the first Fish Food Habits Studies Workshop--was staged in Astoria, Oregon in October, 1976. Comments during the workshop and the results of a questionnaire distributed following the workshop indicated that, although the participants were quite satisfied with the achievements of that workshop, there was a need to continue such a gathering for scientists actively involved in studies of food habits, predation, feeding behavior, competition, and food web structure in fish communities. Since most of the participants voted to meet every other year, GUTSHOP '78 was scheduled to occur two years hence.

Site selection is an important aspect to our meetings and participants in 1976 unanimously voted to gather in "scenic and semi-remote" locations. As an alternative to Maui, the most often suggested site, we settled on the Lake Wilderness Conference Center, owned and operated by the University of Washington, and situated in the foothills of the Cascade Mountains. It was our intention from the beginning to maintain an informal atmosphere and to limit the number of participants so that everyone would have ample opportunity to see, listen, speak, and discuss.

The presentations were exceptional and the discussions following them dynamic and always animated. The advantages and disadvantages of field sampling procedures, laboratory techniques, statistical analyses, and interpretations of data were argued, embellished, explained, discounted, promoted, clarified, and tape recorded. It is from those tapes that the detailed discussion sessions were transcribed, condensed and included in these proceedings.

In addition to the regular sessions, conversations between as few as two and among as many as fifteen occurred day and night, indoors and outdoors, over coffee, along the lake, in canoes, across the volleyball net, and during the salmon barbecue.

We hoped to vary the program somewhat from GUTSHOP '76 and yet include a balance of material. The five session topics covered in GUTSHOP '78 were:

Methodology and Taxonomy
Statistical Analysis
Trophic Structure
Competition
Modeling and Summation (including Panel Discussion)

Several important themes emerged and it is important to emphasize them. Although some discussions verged on the comical at times and other times were very serious, one of the usual problems was always that of semantics. We tend to learn a concept and a definition but as time goes on we find it loosely applied and eventually without the distinction of being a definition at all. John Sibert became the honorary semanticist and rightly so, for it was he who demanded that we define terms before applying them to data. One scientist's idea of selectivity or competition, for examples, may differ widely from another's concept of the same two principles. Most of us have indeed become careless and it is important that we make sure to use clear definitions rather than ambiguous ecological jargon.

A second theme was that each study have specific questions to answer and that these be formulated into concise hypotheses which can be feasibly proven or disproven. Only then should a team go out to collect data based on a sample design specifically addressed to the question at hand. A good example is the use or non-use of empty stomachs. If the question is whether or not fish are feeding in a certain area or at a certain time, then empty stomachs become important information. Random data collection seldom yields good information. Correspondingly, one should have in mind a concept of the statistical analyses required prior to data collection so that it is gathered in a manner suitable to verify or nullify the hypothesis. It is at this point in the evolution of our specific discipline that mathematical models are becoming more important and useful for formulating hypotheses and focusing sampling designs and experiments.

And it was often brought out that we should know to what use the information will be put. What are our goals in generating this type of information? Are we going to influence management of a stock, improve the viability of a model, or assist those who are required to forecast and predict? One must have the goal in mind in order to derive the specific questions upon which to base a study.

Perhaps the underlying theme of this discussion was the ever present argument that research programs must be well-thought out far in advance of any field investigations and especially so if they involve typically expensive, involved food habits studies.

One of the most obvious advancements appeared in the statistical analysis session. In general, most procedures for testing or describing quantitative food habits data have originated from other sources, e.g. terrestrial plant or benthic invertebrate ecology. This year's session provided some of the newest, most original statistical approaches which have been developed specifically for the type of data we are collecting and the sorts of questions we are asking. This could not be better illustrated than by Mike Crow's lunchtime creation of a method to group predators and prey into guilds using a combination of cluster analysis and multivariate analysis of variance. This idea was so creative and important as a new statistical tool that we asked Mike to draft a short paper for inclusion with the proceedings, which he has gladly done. We can't help but look forward to this session at GUTSHOP'80, if not just for the results of some of the new techniques described at GUTSHOP '78.

We implied that one of the results of GUTSHOP '78 would be a handbook or a series of handbooks regarding methodology of fish stomach analysis including statistical analysis of data. It is still our desire to see this through but it will be a slow, involved process. On the other hand, perhaps the accumulating GUTSHOP proceedings are fulfilling the need. There is no doubt that there is a demand to stage a GUTSHOP '80 and we hope that someone from California or Canada will undertake the management. We have enjoyed producing GUTSHOPS '76 and '78 but feel it important to turn over the duties, enabling us to become active participants ourselves.

We hold the same opinion of GUTSHOP '78 as we did GUTSHOP '76 so please allow us to repeat: The success of this workshop resulted from the people who participated. They shared a special enthusiasm for their work and had a willingness to listen to new and different techniques. It was this ardent participation by each person that made this workshop so profitable.

Sandy J. Lipovsky

Charles A. Simenstad

19 March 1979

Welcome and Introductory Address

Robert L. Burgner, Director
Fisheries Research Institute
University of Washington

Welcome to GUTSHOP '78, sponsored by the Fisheries Research Institute and Washington Sea Grant Program. Particular welcome to our out of state participants from Alaska, British Columbia, Oregon, and California.

As you know, this is the second workshop--as the program flyer states--"for scientists actively involved in studies of food habits, predation, feeding behavior, competition, and food web structure in fish communities." Quite clearly, the succinct but inglorious title, "Gutshop," bestowed on this workshop by its co-chairmen, belies the importance and significance of the subject matter. Your first workshop, two years ago in Astoria, culminated in proceedings edited by Charles (Si) Simenstad and Sandy Lipovsky and published with help of Washington Sea Grant. Not only was the first workshop a success, but sufficient interest was generated to begin plans immediately for this second workshop, beginning here today.

The prime movers in this whole show are co-chairpersons Si and Sandy, who initiated the first workshop, carried through the proceedings, and maintained their enthusiasm to generate this second workshop. Our thanks go to them.

I hope you enjoy the setting here, and we're holding out for some continuing Indian summer for you. I have a personal liking for this place, having been here many times, and recall back to my first visit when this was Gaffney's Lake Wilderness Resort. Pacific Fisheries Biologists held annual meetings here in 1953, 1956, and 1960 before that organization grew beyond bounds, or perhaps the management had had all it could take. The last time I was here at a meeting, we were distracted by a rotenoning operating on Lake Wilderness being conducted by the Washington Department of Game to rid the lake of unwanted species so they could restock with trout. If we had time, I am sure this group could engage in an enlivened discussion of the pros and cons of the ecological consequences of lake poisoning. However, we'd better stick to the program.

Early in the game I was involved in food habits studies myself, but more recently have served as major professor for five M.S. students conducting fish food habits studies--three in freshwater, two in the marine environment. Two of these students are just now nearing completion of their studies, and one of them, Mark Hunter, will present a paper here. I have also participated in several other graduate committees or project reviews where primary or important emphasis was on fish food habits and species interactions. Each of these studies has been stimulating to me, and I have come away with a fair appreciation and some understanding of both the drudgery involved and the excitement of determining who eats whom in fish communities.

Our initial work in food habit studies in FRI started in Alaskan sockeye lakes, where we focused on density-dependent relationships between juvenile sockeye and zooplankton, on the competitive interaction between juvenile sockeye and other limnetic feeders, and on predator-prey interactions, particularly between Arctic char and juvenile sockeye. In the Chignik Lake system, information on growth and competition was an important component in our recommendations for radically modified escapement goals for the two lakes. These recommendations seem to have paid off handsomely in increased run magnitude. In the Wood River system, similar studies have led to present-day testing of lake fertilization as a means of enhancing growth and survival of juvenile sockeye, and to exploring means of minimizing char predation--a significant mortality factor to juvenile sockeye in the lake system. Although still largely unexplained, the strong cyclic nature of salmon runs in some Alaskan systems is believed to be closely linked to predator-prey interactions.

Working in Alaskan lakes posed difficulties in attempting year-round sampling of fish communities because the lakes were frozen over nearly half the year. Therefore, under IBP funding we welcomed the opportunity to focus on Lake Washington sockeye and fish community interactions here on a year-round basis. The results, summarized elsewhere by Dr. Eggers and co-authors, were somewhat surprising. It was found that (1) juvenile sockeye were highly elective in feeding, (2) the total zooplankton crop was only lightly touched by the juvenile sockeye and other pelagic feeding species, (3) when Daphnia appeared in the lake in abundance the juvenile sockeye readily switched to this large cladoceran, (4) predator avoidance is apparently at least an equally key component in juvenile sockeye behavior, and (5) the benthos-consuming species, particularly the lowly prickly sculpin, clearly predominated in the fish community of Lake Washington.

Our first significant efforts in the study of trophic dynamics of marine fish communities began in 1967 with our marine environmental monitoring at Amchitka prior to and following the AEC nuclear tests. While these studies were extremely interesting, Amchitka is an inhospitable work area under the best of circumstances, and long-term studies were a bit difficult to sell to our sponsor. We therefore welcomed the opportunity more recently to conduct year-round baseline studies in Puget Sound, of which you will hear more. Still more recently we have undertaken food habits studies in Kodiak estuaries.

Al Pruter, in his opening remarks two years ago, touched upon some experiences and valid precautions, but also emphasized some needs that bear re-emphasis. In particular, he brought out the responsibilities under our new U.S. Fisheries Management and Conservation Act to develop management plans (and, incidentally, environment impact statements) for the various specialized fisheries within our 200-mile zone. He noted that yield levels for each species had to be developed largely without consideration for community interaction, interspecific competition, and predation, simply because of a lack of understanding of these relationships. He appealed to the group as potentially extremely valuable contributors to the whole management area. Certainly, some efforts in this direction have been made in the two-year interim, and speakers at this workshop will address some of the results obtained. It is hard to conceive that major fisheries for target species such as Alaska pollock in the Bering Sea or Pacific Ocean perch and hake in the Gulf of Alaska do not have dramatic impacts on community interactions. I am sure you will find Dave Sommerton's scheduled discussion of hypothesized interactions between Pacific Ocean perch and Alaska pollock in the Gulf of Alaska of particular interest.

On another subject; we hear daily of plans for large-scale salmon enhancements, both private and public, and some private activities have progressed well beyond the planning stage. The prospect of doubling, tripling, or quadrupling juvenile salmon releases is raising the question among many as to whether there are indeed limitations to the carrying capacity of some environments, particularly those more restricted estuarine areas. The possibility of debilitating intra-and interspecific competition and of functional responses of predator populations to increases in concentrations of juvenile salmonids needs careful evaluation. Such possibilities need not preclude development of enhancement programs, but if planners are aware of these effects, they may be able to develop appropriate management strategies to circumvent serious food shortages and competition or predation interactions. I understand that discussions on this subject are part of your program.

Another area of importance is the potential effects of pollutants or enrichment on fish food chains and fish communities. Fortunately, a number of baseline studies have been undertaken that <u>begin</u> to address the potential vulnerability of these communities to perturbations such as the introduction of petroleum hydrocarbons. Baseline studies have been undertaken in Puget Sound, the Strait of Juan de Fuca, San Juan Islands, the Strait of Georgia, and in the Gulf of Alaska, including Cook Inlet, Valdez, and Kodiak areas. Baseline studies in themselves are not a cure, but help to bring an appreciation of community structure, and occasionally may provide sufficient population information against which future population changes can be measured. In the OCSEAP program, emphasis has shifted somewhat toward realizing the importance of physiological effects and of the greater vulnerability of estuarine communities to potential offshore oil spills. In our local estuaries the studies of Simenstad, Dr. Miller, and others in Washington and British Columbia have led to an appreciation of the greater vulnerability of nearshore fish assemblages because of their dependence on detritus energy sources and shallow sublittoral habitats. This situation tends to place the fish in more prolonged contact with a pollutant. Further, the prey resources upon which they feed are more sensitive to the toxic components of petroleum hydrocarbons, they are associated with the bottom sediments wherein the oil is typically entrained, and the trophic pathway from detritus to fish may be disrupted. It is important that concepts such as these be validated and set forth prominently so that the most efficacious guidelines can be implemented to protect our living aquatic resources.

It goes without saying that continual development and comparisons of methodology, statistical analyses and models are necessary components of food and fish community analyses. I see from your program that each has a niche on the agenda. Al Pruter, in his address, touched on the need to aim food studies to critical life stages (such as the larval stages), to understand the transfer of energy between trophic levels, and to determine environmental effects--all potentially requiring modeling and a multidisciplinary coordination among researchers. I fully agree.

So again, you have lots of ground to cover and some very important concepts to set forth. I am sure you will leave with new ideas, and hopefully with increased agreement on methodology and interpretation of results. Go to it!

SESSION I

Methodology and Taxonomy

SESSION LEADER
Jack Q. Word

PARTICIPANTS
Robert J. Feller
Colin D. Levings
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Jack Q. Word
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The Analysis of "GORP," Or How to Know the Guts Of Recalcitrant Predators

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Recalcitrant predators may be defined as those having partially or wholly indeterminate trophic connections when their stomachs are examined with conventional techniques. Few gut content analyses of fishes or invertebrates are truly quantitative and accurate for several reasons: (1) specimens may lose some fraction of their gut contents during capture or preservation; (2) digestion can proceed after incomplete preservation; (3) visually identifiable gut contents and pieces of prey are difficult to quantify in units of either mass or volume; and (4) there is usually a significant quantity of visually unidentifiable amorphous material ("gorp") present in the gut. Biases introduced by non-random collection and selection of specimens for analysis are beyond the scope of this discussion.

Other methods besides visual examination used to identify prey in the stomachs of predatory organisms include X-ray analysis for hard-bodied prey, use of various tracers or labels, chemical methods, direct observation in nature, caging or exclusion experiments, and serological methods (Kiritani and Dempster, 1973). None of these methods alone is ideal for any given predator-prey system, especially when several different prey types are potentially available. In situations entailing or necessitating analysis of predator stomachs containing large fractions of "gorp", serological methods are well suited. The basic serological, or immunological, method entails production of antibodies in rabbits or other small mammals via immunizations with an antigen solution (a soluble whole-organism extract or more specific proteins) from some organism of interest. Antibodies produced by the mammal's immune system in response to this stimulus will recognize and combine only with antigens similar to those used to induce the immune response. Once antibodies to all potential prey organisms are of sufficient specificity to distinguish unambiguously between antigens of different target prey organisms, they may be used to test for the presence of foreign soluble proteins (prey antigens) in the guts of suspected predators. One such test, the precipitin test, is performed by allowing the unknown gut content solution to diffuse through agar and come in contact with an array of prey-specific antibodies. A given prey organism's presence in the gut is indicated by the formation of antigen-antibody complexes, or precipitin lines, of the prey's antigens with their homologous antibodies. Several different prey may be detected simultaneously. We have been evaluating the utility of this methodology for routine use with benthic invertebrates, many of which ingest sediments and/or thoroughly chew their prey. Immunological methods have been used successfully in freshwater systems (Davies, 1969; Pickavance, 1970) and by entomologists (Dempster, 1960).

A full description of methods is outlined in Feller et al. (MS). Briefly, target prey organisms are starved after collection to clear their guts of foreign material and then ground whole in buffer solution. Protein concentration of the whole-organism extract is measured, and then the extract is injected into pairs of rabbits that were first bled to obtain samples of pre-immunization serum. The immunization schedule of Kenny (1971) was used. Immunization of single rabbits frequently results in death of the rabbit, but if pairs are injected, neither dies (Kenny's Law). After post-immunization serum is collected, it is tested by double diffusion precipitin tests (Ouchterlony, 1968) to see if antibodies to the target prey organism were produced, i.e., that precipitin lines form in agar between holes containing post-immunization serum and the target whole-organism extract. Finally, the entire array of potential prey organisms in the system of interest is tested against their homologous antisera, and each antiserum is tested against all other whole-organism extracts to check for cross-reactions. Presence of cross-reactions, or the formation of precipitin lines between an antiserum and heterologous whole-organism extracts, indicates that the antisera produced are non-specific. Various methods of specificity enhancement may be used to "clean up" such antisera, e.g., absorption, dilution, or suppression (Axleson and Bock, 1972). In making relatively unspecific antisera more specific, one must be careful that sensitivity (ability to detect small quantities of antigen) is not sacrificed disproportionately.

Our study area is an intertidal mudflat near the north fork of the Skagit River in northern Puget Sound. The benthic community there (Table 1) is extensively used as forage by juvenile pink and chum salmon, starry flounder, staghorn sculpin, three-spine stickleback, and other errant species (J. Congleton and J. Smith, pers. comm.). We have made "winter" and "summer" collections of animals by taking sediment cores at random from two different sites each season. The cores cover an area of 4.9 cm^2 to a depth of 2 cm and are preserved in 20% formalin for visual gut analyses or are frozen on dry ice upon collection for later immunological analysis. Larger potential predators like amphipods and shrimp can be examined individually, but smaller species must be lumped in the double diffusion precipitin analysis. Individual animals are examined for visual (microscopic) gut analysis.

Results to date are incomplete, as only a few species have been examined either visually or immunologically. Sample sizes are unequal and small, so these results should be regarded as preliminary only. The effects of space and time are confounded in the presentation given here, as we have combined results from the two seasons and sampling plots. In spite of these shortcomings, large differences exist between the direction and number of trophic connections determined visually and immunologically. Amorphous material dominates when predator stomachs are examined with the microscope, and most of the supposed deposit feeders contain sediments (Fig. 1). Bits and pieces of crustacean hard parts are found in the guts of fishes and the larger invertebrate predators. None can be identified to a lower taxon. The mudflat's benthic food web as revealed through immunological analysis (Fig. 2), however, contains many links that were not detected during microscopic analysis and were not expected for any *a priori* reasons. Most noticeable, the "gorp" and sediment components have disappeared. We did not prepare antisera to fresh or decomposed plant material (although it is possible), so that detrital components of the food web retain their usual status in benthic food web studies--that of heterogeneous and poorly characterized detritus. This material pervades the web and has not been diagrammed. Since our main focus has been towards analysis of benthic invertebrates, we did not analyze any fish stomachs immunologically. It is clear, though, that if antisera to the appropriate potential prey are available, community trophic connections, including those to fishes, can be identified much more completely with immunological methods than is possible with visual methods.

Immunological analyses may be performed on any desired fraction of a predator's stomach or hindgut contents whether they are fresh or quick-frozen. Formaldehyde causes the formation of strong cross-linkages in proteins, severely reducing their solubility. Specificity and sensitivity of immunological methods suffer immensely if preserved material is analyzed, and it is recommended that this tack be attempted only when all other methods have failed. Another problem is that antiserum specificity and sensitivity may be so high that secondarily ingested material (i.e., the gut contents of prey found in predator stomachs) may be detected. Finally, immunological methods are most useful in detecting presence or absence of those organisms for which specific antisera exist. Quantification is currently possible only in terms of protein concentration, a measure of little direct value in assessing the flux of energy in food webs. Despite these problems, we are encouraged by these few preliminary results and anticipate further application of immunological methods in the analysis of aquatic food webs.

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Table 1. Organisms of the Skagit River mud flat benthic community and a brief description of their feeding type.

ORGANISMS	FEEDING TYPE
Polychaeta	
Eteone longa	"pumping" carnivore
Nereis (Neanthes) limnicola	grasping-jawed omnivore
Pseudopolydora kempi japonica	tentaculate surface deposit feeder
Pygospio elegans	tentaculate surface deposit feeder
Hobsonia florida	tentaculate surface deposit feeder
Manayunkia aestuarina	ciliary tentaculate suspension feeder and facultative surface deposit feeder
Crustacea	
Corophium salmonis	antennal surface deposit feeder
Anisogammarus confervicolous	prehensile omnivore
Tanaid sp.	chelate particle browser
Bivalvia	
Macoma balthica	siphonate surface deposit feeder
Mya arenaria	siphonate, ciliary mucoid suspension feeder
Nemertea	
Paranemertes peregrina	proboscidial carnivore
Unknown sp.	proboscidial carnivore
Meiofaunal taxa	
Nematoda	epistrate detrital feeders
Harpacticoida	epistrate browsers
Huntemannia jadensis	algal and bacterial browser
Oligochaeta	epistrate browsers
Ostracoda	diatom and detritus feeders
Turbellaria	herbivores and carnivores

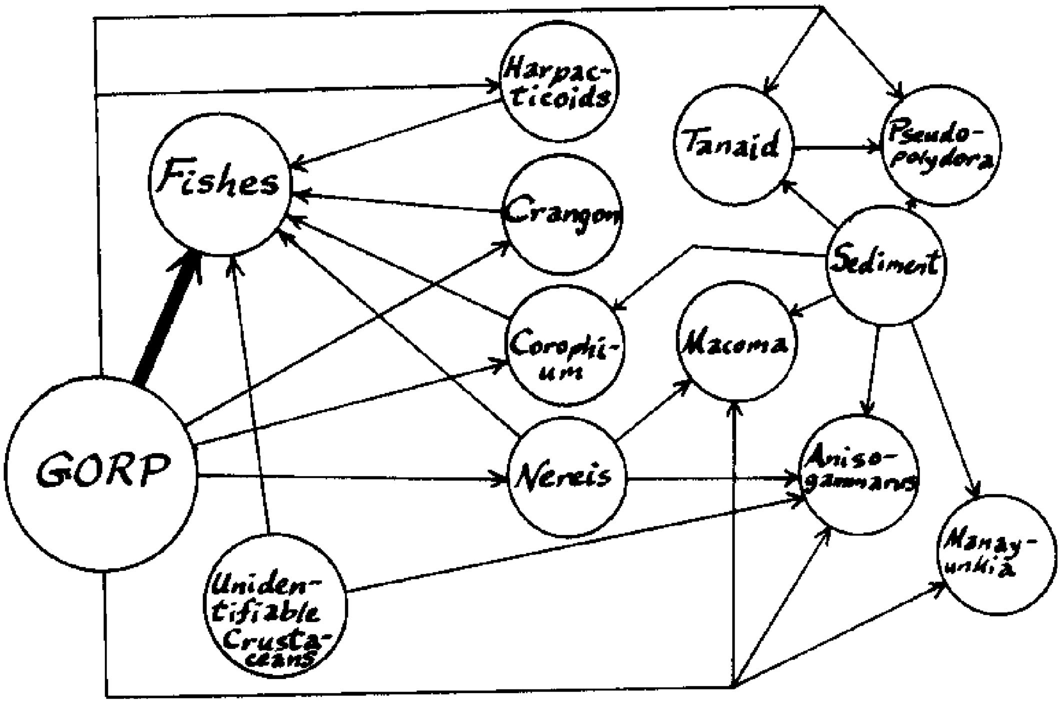

Figure 1. Preliminary and incomplete description (see text) of the Skagit River mud flat food web as evidenced by microscopical analysis of predator stomachs.

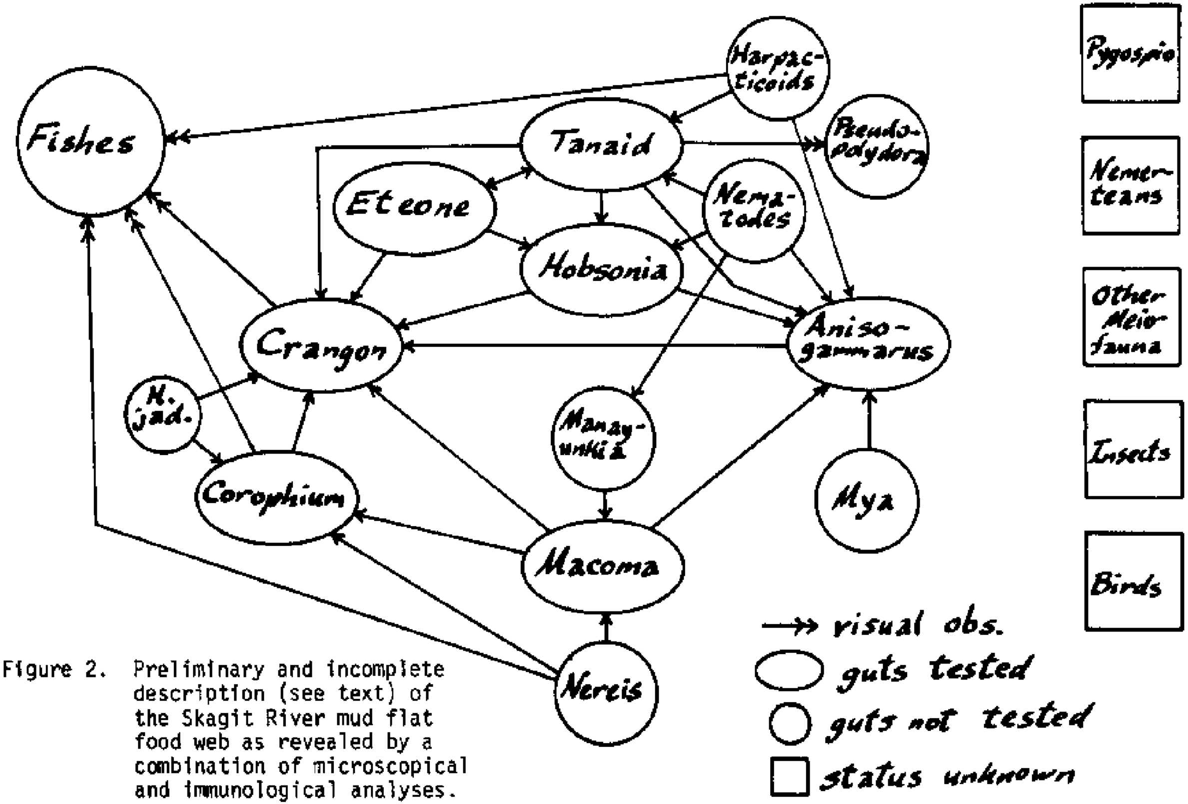

Figure 2. Preliminary and incomplete description (see text) of the Skagit River mud flat food web as revealed by a combination of microscopical and immunological analyses.

Sampling Techniques for Larger Epibenthos at Two B.C. Estuaries

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Introduction

Gut samples of juvenile salmonids from estuaries in B.C. show that the fish consume a wide variety of taxa (e.g. Sibert, 1977). The invertebrate taxa in the diets are mainly epibenthic, which can operationally be defined as "living in close association with the substrate". These organisms use diverse microhabitats and display different behaviours, so a variety of sampling techniques used to evaluate estuaries as suppliers of fish food have been developed.

This paper presents an overview of experience and results with these sampling devices, mainly at the Squamish and Fraser River estuaries in southwestern B.C. Emphasis will be on practical aspects of using the samplers, and data yielded are evaluated in relation to fish gut analyses, invertebrate behaviour, costs, and field logistics. No claim is made to the originality of the devices, but the estuarine applications of certain of the instruments may be unique.

Tidal Considerations

The estuaries we have studied are subject to tidal fluctuations of up to 5 m, and therefore biologists can directly observe or sample habitats of interest. However, data obtained at low tide can be misinterpreted if analyzed without complementary information from high tide work or information on the behaviour of organisms.

Low Tide Sampling

A. Direct observations

A visual inspection of estuarine habitats and associated animals can provide data on environmental heterogeneity and assist future survey strategies. Some organisms can be actually censused by direct observations of individuals (e.g. epifauna such as the mussel Mytilus edulis) or by traces and faecal material left by infauna (e.g. ghost shrimp Callianasa californiensis; Swinbanks and Murray, 1977).

B. Cores

We have used a simple cylindrical core with dimensions 25 cm x 20 cm length (9817 cm^3). Cores in mudflats on Roberts Bank, Fraser estuary were sectioned at 5 cm intervals and animals from each level examined. Organisms were most abundant in the upper 5 cm (Levings et al., 1978).

On mudflats where water is not available for sieving, the material taken by the core can be put into a large plastic bag for transport to a site where water is present. Sometimes the bags must be moved over large distances (up to 5 km at the Fraser estuary). Under these circumstances, it is far easier to recover the bags of sediment at high tide by boat. To locate the bags, a piece of light line with a float is attached. When tides flood the beaches, the bags can be identified by their floats and hence recovered.

C. Quadrats

Quadrats have been used to sample estuarine environments at a variety of locations and on several types of substrates. Depending on habitat type, usually 0.25 m^2, 0.06 m^2, or .01 m^2 have been used. Because organisms are most abundant in the upper part of the sediment column usually the top 2 cm has been scraped off with a trowel. Sampling the upper sediments only can be justified when "availability" for salmonids is considered, since many organisms living near the sediment surface can be "lifted" into the water column by currents or wave action. Some species (e.g. cumaceans), migrate out of the sediment during (flooded) hours of darkness (see below).

Quadrat sampling at low tide allows the investigator to sample standardized microhabitats, which can yield important data on how estuarine systems function. For example, at the Squamish estuary sedge rhizomes overhanging an embankment at low tide were found to harbour very large populations of a gammarid amphipod (Anisogammarus confervicolus) (Levings, 1973). Subsequent sampling on the embankment above the mat, about 3 m distance, showed that the amphipod population apparently changes its microhabitat preference on a seasonal basis (Fig. 1). The shift may be related to seasonal changes in food utilization by the amphipod - sedge debris and algae is more abundant on the embankment in winter months compared to summer when sedge growth "shades out" algal productivity (Pomeroy, 1977).

Quadrat sampling has also been used on rocky shores to evaluate the contribution of the barnacle nauplii to nearshore food webs (Wu and Levings, 1978). Nauplii can be dissected from adult barnacles and enumerated by count or biomass.

D. Debris sampling

Data on the distribution of some species of invertebrates, which are adapted to seek cover at low tide, can be obtained by qualitative sampling of debris (e.g. decaying vegetation, wood chips). This method has been used for examining the distribution of gammarids over the "unvegetated" sand and mudflats of the offshore Banks of the Fraser estuary (Levings and Pomeroy, in press). Usually the data are standardized by scaling counts of invertebrates by dry weight of debris.

High Tide Sampling

High tide sampling has been conducted with a variety of techniques, ranging from simple plankton nets to submersible pumps. The development of techniques has been highly influenced by physical conditions at the estuaries we have worked at. For example, excessive turbidity and high current speeds have prevented frequent use of SCUBA techniques. At other B.C. estuaries, where water clarity permits regular diving, diver-operated epibenthic sleds have been developed for meiofauna sampling (Sibert, 1977).

The timing of sampling for planktonic and epibenthic organisms is a major issue. Even though estuarine habitats are flooded, organisms may not swim into the water column unless activity rhythms permit. In some circumstances, river currents apparently override activity effects. For example at the mouth of the highly turbulent Squamish River (current speeds up to 300 cm s^{-1}), plankton tow catches of estuarine amphipods showed no patterns of temporal change in abundance (Levings, 1973) whereas in tidal creeks at the estuary the organisms demonstrated a clearly crepuscular activity pattern (Levy, 1977).

A. Plankton nets

Unsually a SCOR/UNESCO plankton net (50 cm diameter, 350 μ mesh size) has been employed, towed with a small (5 m) outboard-powered (40 hp) boat. Towing such a net in small tidal channels (some about 3 m wide) presents difficulties in manoeuvring, and if water is extremely shallow, propeller wash can lead to bottom "contamination" of the samples with sediments. Northcote et al.(1976) used a sled-mounted net in the Fraser.

B. A "drift" sampler

To document the vertical and temporal distribution of epibenthic organisms in the river channels of the lower Fraser, a "drift sampling" technique has been devised. The device is passive, and depends on currents to bring organisms into the net. Channels at the Fraser are relatively large (about 10 m depth; width up to 2 km), are not within the intertidal zone, and are characterized by brisk current speeds (over 300 cm s^{-1} at freshet) which can slow or reverse with tidal fluctuations.

A SCOR/UNESCO plankton net was mounted, with a swivel, on a line weighted by heavy concrete blocks (up to 200 kg). The net, which was fitted with a flowmeter, is able to orient to the direction of prevailing currents. The device therefore filters out organisms drifting up or down river, depending on depth of sampling, river currents, and tidal

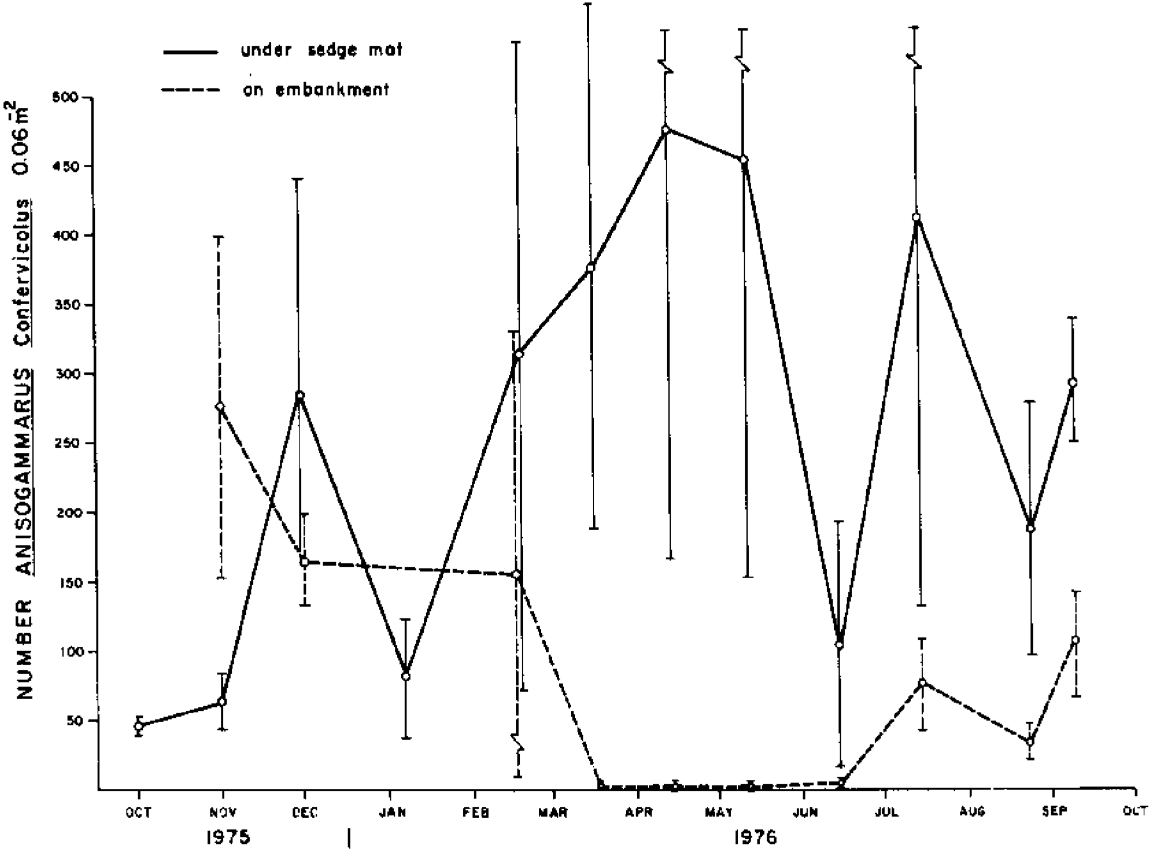

Figure 1. Seasonal change in abundance of *Anisogammarus confervicolus* at the Squamish River estuary, sampled with quadrats at low tide. The microhabitats are separated by about 3 m, and the rhizome mat is at the base of the embankment.

stage. The device was deployed from an anchored research vessel (14 m in length), and raised/lowered with hydraulic winches. Sampling occurred between 1800 and 2400 hrs to account of crepuscular activity of many species.

The sampler has proven to be a useful device for sampling in the lower Fraser. Dramatic differences in fauna and abundance have been documented, especially when samples are taken within and above the salt wedge (Fig. 2).

Data obtained before, during and after the 1978 freshet are being analyzed at present, and are expected to be of value when a proposal for river training works is scrutinized.

c. The DPV sampler

A diver-operated sampler has been developed for use at the Squamish estuary, although its use has been limited by turbidity conditions at this particular estuary.

A diver-propulsion vehicle (DPV) (Farallon Model MK II) was fitted with pieces of PVC piping (diameter 16 cm; area opening 0.02 m^2) mounted on either side of the DPV. A TSK Model 313 flowmeter was fitted between them. The DPV "hoops" were fitted with plankton net mesh (500 μ).

Results showed the device captured many of the common estuarine taxa (Table.1). As noted above, turbidity conditions limited its use at the estuary, and the device has not been routinely used.

TAXA	STN 1 PROX.	STN 2 DISTAL
MEDUSEA	**	-
CALANOID COPEPODS	***	**
OSTRACODS	*	**
NAUPLII	***	***
ZOEA LARVAE	-	-
ANISOGAMMARUS	*	*
NEOMYSIS	***	**
CRANGON	-	-
TOMOPTERIS	*	+
CLIONE LIMACINA	-	+
LARVAL FISH	*	-
FISH EGGS	*	*
Volume m^3	6.2	6.2

Key: - none; + few; * some;
many; * very abundant

Table 1. Use of DPV-mounted nets (22/IV/76) at a tidal creek in Squamish River estuary.
D: >1 m from bank; P: ≤1 m.

D. Plankton pumping

Because of the relatively weak tidal currents (usually less than 50 cm s^{-1}) over Sturgeon and Roberts Bank at the Fraser estuary, the "drift" sampler described above could not be used to sample these habitats. A plankton pump was therefore developed from a "stock" model sump pump. This device is described below.

A submersible sump pump (Paramount 3 SVWS) with intake diameter of 17 cm was deployed from our small research vessel. The pump has a simple 2-bladed vane design which minimizes damage to organisms. The 1 hp electric motor powering the pump requires minimum power of 3.5 kw, which was supplied by a generator on the vessel.

Discharge rate of the pump is approximately 0.56 m^3 min^{-1} at 5 m head. Water is discharged through a 7.6 cm diameter line fitted with a ball-type flowmeter (Fischer/Porter). To reduce damage to organisms when retained on sieves, the discharge line was connected with a header box. Water drained from this box through sieves (500 μ or 351 μ).

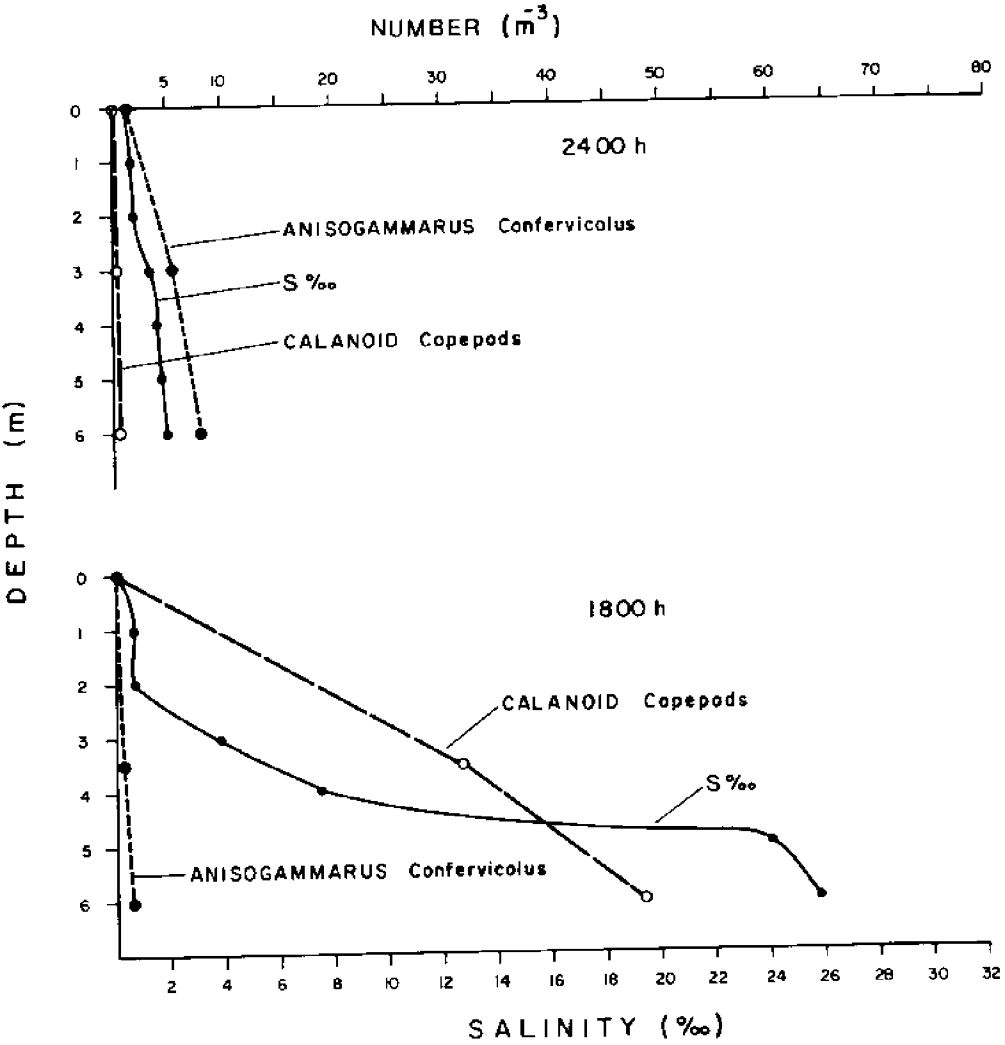

Figure 2. "Drift" samples from south arm of the Fraser River (Steveston Island). Upper: vertical distribution of calanoid copepods and *A. confervicolus* on an ebb tide. Lower: flood tide (April 4, 1978).

This pump system has proved to be very reliable and was operational in a relatively short time. Preliminary data show that more invertebrates, mainly calanoid copepods, drift in over Roberts Bank from the Strait of Georgia than drift out of eel grass beds on the foreshore.

E. Basket Trap Sampling

Basket traps similar to those used in freshwater have been successfully deployed at the Squamish, Cowichan, and Fraser River estuaries (Levings, 1975; Levings and Chang, 1977). Our prototype used wire baskets but subsequent experience has shown that mesh bags, which are cheaper, rust-proof, and lighter, can be used to hold the cover material (usually rockweed, Fucus vesiculosus). Baskets filled with vascular plant debris caught large numbers of Anisogammarus spp. in slough areas of the upper Fraser River Estuary (Nassichuk, pers. comm.).

One of the main advantages of basket traps is their "integrative" nature; that is organisms are sampled by the device over a period of several high tide cycles. Diel abundance patterns can be accounted for without the presence of the investigator.

F. Grab sampling

Two types of grab samplers have been used in sampling at the Fraser estuary, namely the Van Veen grab (Levings and Chang, 1977), and the Peterson (Northcote et al., 1976). Unless appropriate modifications are made to the grabs, these devices can "blow" epibenthos out of the path of the descending sampler.

Evaluation

Gut samples from salmonids have not been obrained at locations where all of the devices have been used. Gut content data are available from a number of studies conducted at the Squamish and Fraser River estuaries (e.g. Goodman, 1975; Danford, 1975; Levy and Levings, 1977) were used to construct Table 2.

For salmonid-related studies, an epibenthic sampler must adequately represent prey species' present in or near the top of the water column, at least at the estuaries considered here. For example, Dunford (1975) and Levy (1977) observed that juvenile chums fed near the water surface, and my analysis of data from offshore habitats (18 km from the mouth of the Fraser River) in the Strait of Georgia (e.g. Barraclough, 1967) showed that juvenile chum salmon fed on winged insects in almost equal proportions as calanoid copepods. Clearly any sampler which excludes pelagic or drift organisms will be biasing data. The samplers utilized to date do not adequately sample flying insects, and attention is required on this topic.

Low tide samplers "dilute" epibenthic fauna by including infauna which probably rarely become "available" to juvenile salmonids. On the mud/sand shores of estuaries, coring techniques might be less suitable than quadrats to sample the surface of sediments. However, some species of potential prey (e.g. Corophium salmonis) bury deeper in sediments than others (e.g. Anisogammarus spp.) and therefore the depth to which samples are taken may be dependent on enumerating specific taxa.

Results of an overall evaluation of the various samplers, using the criteria described above are shown in Table 2. Some factors are obviously subjective. Logistics and costs, in particular, can vary from one laboratory to another, depending on budgets and support facilities.

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LOW TIDE

GEAR	"EFFICIENCY" RE SALMONID GUT INTERPRETATION	LOGISTICS	COSTS	COMMENTS
CORES ON MUD/SAND	POOR	DIFFICULTY DEPENDS ON SIZE	LOW	POTENTIAL PREY "DILUTED" BY TRUE INFAUNA
QUADRATS ON MUD/SAND	MEDIUM	SIMPLE	LOW	SOME "DILUTION" BY TRUE INFAUNA.
QUADRATS	POOR	SIMPLE	LOW	LARVAE OR REPRODUCTIVE PRODUCTS MAINLY OF INTEREST
QUADRATS IN VEGETATION	MEDIUM	DIFFICULT	LOW	SUCCESS IS VERY SITE SPECIFIC
DIRECT OBSERVATION	POOR	SIMPLE	?	UTILITY IS SPECIES SPECIFIC

HIGH TIDE

GEAR	"EFFICIENCY" RE SALMONID GUT INTERPRETATION	LOGISTICS	COSTS	COMMENTS
PLANKTON NET OR SLED	MEDIUM	SIMPLE	LOW	DIFFICULT TOWING IN SHALLOW ZONES
DRIFT SAMPLER	GOOD	SIMPLE	LOW	REQUIRES RELATIVELY SWIFT TIDAL OR RIVER CURRENTS
DPV	GOOD(?)	MEDIUM DIFFICULTY	HIGH	REQUIRES GOOD VISIBILITY
PLANKTON PUMP	GOOD(?)	DIFFICULT	HIGH	POWER SOURCE REQUIRED
BASKET TRAP	MEDIUM	SIMPLE	LOW	SELECTIVE FOR CERTAIN ORGANISMS
BOTTOM GRAB	POOR	SIMPLE	MEDIUM	SOME "DILUTION" BY TRUE INFAUNA

Table 2. A comparison of some sampling methodology used for sampling epibenthic invertebrates at the Squamish and Fraser River estuaries.

Chum Salmon in a Tidal Creek Of the Squamish River Estuary, B.C.

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A frequent observation by investigators concerned with fish stomach analysis is the presence of "runs" of one or a small number of prey types in the gut. This phenomenon suggests that fish are capable of improving their feeding ability on particular prey types, and as a result, aquire specific prey disproportionately compared with their abundance in the environment. One mechanism that might account for the changes in feeding ability when there are repeated experiences with a particular prey is the formation of a "specific search image" (Tinbergen, 1960). Search image formation requires that the predator learns to recognize morphological characteristics of the prey and consequently increases its searching efficiency for that prey. Several laboratory studies (e.g. Ivlev, 1961; Beukema, 1968; Ware, 1971) show that fish possess a learning ability, and can alter their searching efficiency as a result of previous experiences with a given prey. Ivlev (1961) reported that in carp, the number of prior training periods has an influence on the electivity value, E (the proportion of food in the diet relative to the environment), and that "the habit of feeding on certain food continues even with the option of a much wider choice".

Chum salmon, *Oncorhynchus keta*, in the Pacific Northwest hatch out of the gravel in rivers and streams and migrate down to an estuary where some proportion of the population resides and grows before moving into marine littoral areas, and eventually into offshore marine areas. Stomach content analysis shows that epibenthic crustaceans are frequently important as a food source during the early phases of juvenile existence. Because of the low species diversity in estuaries (Odum, 1971) estuarine predators, such as juvenile chum salmon, are likely to have repeated encounters with a single, or only a few prey types.

To assess the role of experience in juvenile chum salmon, experimental animals were conditioned to feed on one of several prey types, then marked and released into a tidal creek in the Squamish estuary at the head of Howe Sound, British Columbia. Conditioning in the present study refers to the process of associative learning in an animal which is manifested by a change in some aspect of its behaviour. Thus a "fish conditioned to feed on a specific prey item" refers to an animal which has learned, through experience, to search for, approach, handle, and ingest that prey item.

After a period of time, experimentally introduced animals were recaptured and their stomach contents analysed. The primary aim of the experiment was to test whether experimental animals, in the field, would over-exploit prey animals of the type they had experienced previously, relative to animals lacking such experience. The technique also provided a means for assessing the relative availability of different prey types on subsequent introduction dates, as well as a means for determining the effect of prey behaviour on the vulnerability of the prey to the fish.

Methods

The animals used in the experiments were obtained from the Squamish estuary in early June and transported to the aquarium facilities at the Pacific Environment Institute, West Vancouver, B.C. The fish were maintained in circulating freshwater in 125 liter fiberglass tanks at densities of about 3 individuals per liter. Two species of estuarine crustaceans formed three of the prey types used in the conditioning experiments: the mysid, Neomysis mercedis (Holmes) and the amphipod, Anisogammarus confervicolus (Stimpson). Two different size classes of the latter were obtained with a series of 3 submerged sieves. After depositing about one thousand amphipods on the uppermost (coarsest) sieve, water was siphoned away from around the sieves and the hydrophilic amphipods would then crawl through the sieve screens until their body diameter was too great to allow further downward penetration. The amphipods remaining on two of the screens, 0.5 mm and 1.19 mm, were then used as food in the small and large amphipod treatment groups respectively. In addition, two groups of fish were fed with different sizes of Oregon Moist Pellets. A summary of the sizes of the various food types are shown in Table 1.

In addition to Oregon Moist Pellets, the fish were given a 10-minute meal of the live prey every day. After 30 days the fish were finclipped and transported back to the Squamish estuary in garbage pails. Introductions were made into a tidal creek (75 metres in length and 20 metres wide at the mouth) on two consecutive dates - July 15 and 16, 1976. After stretching a beach seine across the mouth of the tidal creek, the fish were introduced behind it on an ebbing tide. Following a 12-hour introduction period some of the experimental animals were recaptured (Ave. recapture rate = 18%) by working a small beach seine within the enclosure near low tide, and preserved in a 10% formaldehyde solution for subsequent stomach analysis. The stomach contents were analysed by three independent methods-percent frequency, percent occurrence (by summing the number of occurrences of all items and then scaling the values for the individual prey to a percentage basis), and percent volume (approximated by visually estimating the volumetric displacement of each prey type under a binocular microscope). A more detailed description of the methodology followed can be found in Levy (1977).

	PELLET TYPE A	PELLET TYPE B	SMALL AMPHIPOD	LARGE AMPHIPOD	MYSID
Number Measured	50	50	50	50	50
Mean Length mm	1.9	1.6	5.1	7.9	11.9
Standard Deviation	0.73	0.40	0.87	1.00	1.91
Mean Diameter mm	0.8	1.3	-	-	-
Standard Deviation	0.04	0.07	-	-	-

Table I. Sizes of different food types used in conditioning experiments.

Results and Discussion

Stomach analysis of the experimentally conditioned fish (Figs. 1 and 2) showed that:

1. The proportion of *N. mercedis* in the diet of the mysid-conditioned fish was higher than the proportion of *N. mercedis* in the other groups. When the occurrence of mysids in the diet was compared, a significant G-statistic resulted (Table 2).

2. The proportion of *A. confervicolus* in the diet was no higher for amphipod-conditioned fish and the G-statistic for the amphipod occurrence comparison was not significant (Table 2).

3. The proportion of *N. mercedis* was higher in the diet of all groups on the second introduction date (Fig. 2). The occurrence of mysids was compared in a 3-way G-test of independence (Table 3), and the significant IxO lack of independence indicated an effect of the introduction date on the occurrence of mysids in the diet.

Interpretation of the results from the experiment was complicated by the contrasting behaviour of the mysid- and amphipod- conditioned fish in the tidal creek. The aquisition of a higher proportion of *N. mercedis* by the mysid-conditioned fish was a result consistent with previous laboratory studies. Ware (1971) showed that the reactive distance of rainbow trout to unfamiliar prey doubled as the number of feeding experiences increased and suggested that the change was related to search image formation. The mechanism through which the mysid-conditioned fish acquired a higher proportion of *N. mercedis* probably involved a modification of searching behaviour, either through searching image formation or a change in the amount of searching effort expended in a particular microhabitat. Additionally, the juvenile salmon were observed in the laboratory to improve their handling efficiency of the mysids which are fairly large prey items relative to the size of the juvenile salmon predators. With experience, the predators learned to manipulate mysids in their mouths so that they were ingested either head-first or tail-first. Alternatively, mysids were grasped in the mid-dorsal region in such a way that the suction created by expansion of the buccal cavity caused the mysid to fold down onto the thorax thus reducing its size and creating a more easily ingestible particle.

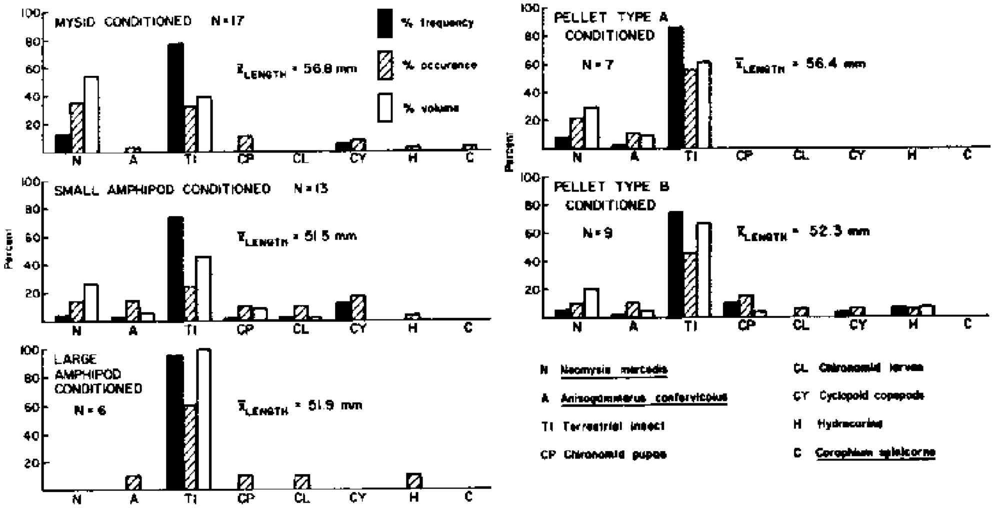

Figure 1. Diet of juvenile chum salmon introduced into the tidal creek on July 15, 1976.

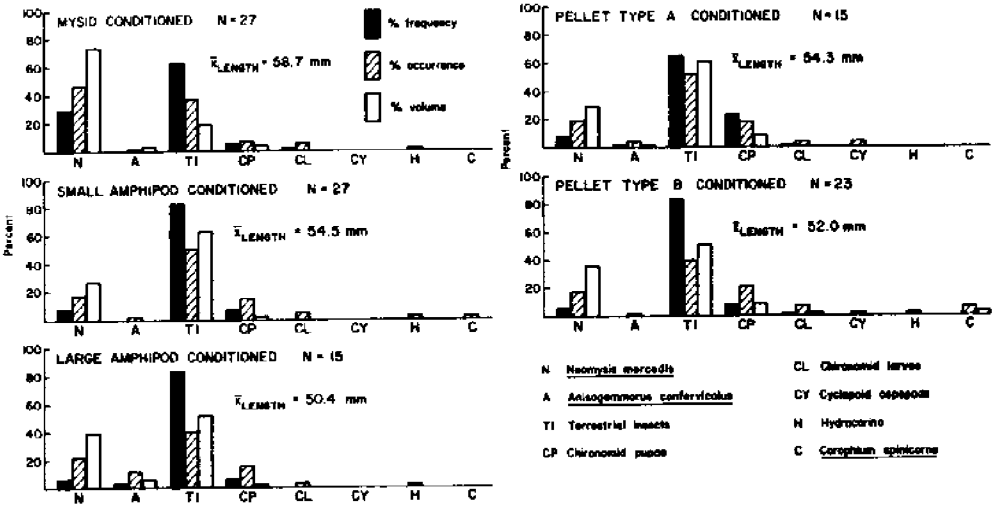

Figure 2. Diet of juvenile chum salmon introduced into the tidal creek on July 16, 1976.

Occurrence Of Mysids

	Mysid Conditioned	Other
Occurrence	31	38
Absence	13	77

G= 16.756 w/1d.f.
P<0.001

Occurrence Of Amphipods

	Amphipod Conditioned	Other
Occurrence	10	7
Absence	51	91

G= 2.396 w/1d.f.
N.S.

Table 2. Occurrence of mysids and amphipods in mysid- and amphipod-conditioned fish (combined results from July 15 and 16, 1976).

HYPOTHESIS TESTED	DF	G
CxO independence	4	18.692 **
IxO independence	1	6.002 *
IxC independence	4	7.836
CxIxO interaction	4	8.264
CxIxO independence	13	40.794 **

*=.01 < P < .05
**=P< .01

Table 3. Results from 3-way G-test of independence for conditioning history (C) x introduction date (I) x occurrence of mysids (O) for introduced juvenile chum salmon.

The absence of overexploitation of A. confervicolus by amphipod-conditioned fish contrasts the results from the mysid-conditioned animals. A. confervicolus is known to form a major constituent of the diet of juvenile chum salmon in the Squamish estuary (Levy and Levings, 1978) and is thus a palatable prey item. The apparent absence of this amphipod in the diet of the experimental animals most likely reflects a low amphipod abundance in the tidal creek at the time of the experiments. Plankton tows made along the margin of the tidal creek prior to and after the experiment (Table 4) show that A. confervicolus has a marked diel vertical migration behaviour. Davis and Holton (1976) showed that *Anisogammarus* in the Columbia River estuary were most vulnerable to their sampling device, an epibenthic sled, on a low slack tide between 1600 and 2400 hours. Since the experimental animals were introduced into the tidal creek between 0300 and 1300 hours, the diel behaviour of *A. confervicolus* could account for its low utilization as food by the juvenile salmon. An alternative mechanism which would cause a low amphipod abundance in the tidal creek at the time of the experiment is related to the animals seasonal pattern of abundance. Levings and Levy (1976) present data which shows that the abundance of *A. confervicolus* in the Squamish estuary during July is one order of magnitude lower than the peak period of abundance which occurs in May. Also, the proportion of juvenile amphipods (the size class utilized by juvenile chum salmon as food) present in the amphipod population in July is very low, as a large proportion of the population goes through reproductive stages at this time of the year.

	MORNING				EVENING	
	JULY 13/76		JULY 14/76		JULY 19/76	
SAMPLING TIME(HRS)	0740	0750	0710	0720	2155	2210
Anisogammarus confervicolus	6	10	3	1	866	1012
Neomysis mercedis	904	890	984	768	1044	844
Gnorimosphaeroma oregonensis	34	27	5	7	82	62
Insect Larvae	4	1	5	4	43	49
Corophium spinicorne	1	1	1	0	0	0
Hydracarina	1	1	0	0	0	0

Table 4. Numbers of epibenthic invertebrates caught in plankton tows in early morning and late evening prior to and after tidal creek introductions.

The higher utilization of *N. mercedis* as food by the experimental fish on the second introduction date likely reflects a difference in the abundance of mysids in the tidal creek on the two introduction dates. In contrast to *A. confervicolus* which remain exposed near the sedge rhizomes when the tide is low, *N. mercedis* moves in and out of the tidal creek with each flowing and ebbing tide. Consequently this behaviour is suspected to cause a variable mysid density in the tidal creek from day to day.

The results of these experiments show that the feeding behaviour of juvenile chum salmon can be modified in a manner which is consistent with search image formation. The manipulation of predators in tidal creeks holds potential as a method for increasing the understanding of trophic relationships in estuaries.

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Some Procedures for Assessing Organisms Associated with Rocky Substrata

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Studies of food habits in fishes are more meaningful if they determine not only what the fishes eat but also measure the prey that are potentially available to them. This is particularly important in studies that consider competition and feeding selectivity among predators. To measure potentially available food, or to determine if a resource becomes limiting, one must take consistent and quantitative samples of the biota within the feeding area. Furthermore, to evaluate the selectivity of a predator, one must consider organisms that are not preyed upon along with those that are.

An investigation of prey availability must also consider both temporal and spatial variations in density and distribution. Temporal variations, including seasonal changes and differences in distributions between day and night, can be profound, and understanding their patterns is important in determining how resources are utilized (Hobson and Chess, 1976).

It is a major task to monitor potentially available prey owing to the tremendous numbers and variety of organisms involved. Taxonomic problems are especially frustrating since many invertebrate groups, including the gammaridean amphipods and ostracods, are either difficult to work with, or poorly known, or both. Furthermore, to fully understand the interspecific relationships, taxa must be distinguished to species, and this is complicated by the fact that our knowledge of the systematics of many groups remains incomplete.

It is important to remember, however, that the availability of a given prey is not determined simply by its abundance. Availability is also determined by the predator's feeding strategy as well as the behavior and morphology of the prey. Thus studies of prey behavior should be an integral part of a comprehensive evaluation of food habits in fishes.

Background

The techniques described here, among others, were developed to monitor a variety of marine communities during comprehensive studies of feeding activities in fishes at Catalina Island, California (Hobson and Chess, 1976; Hobson and Chess, in prep.) Some of the same techniques are now being used in studies on the coast of northern California. This report considers methods developed to assess the organisms associated with rocky substrata accessible to divers using compressed air.

Selecting and Marking Study Sites

Preliminary surveys are important in selecting specific locations that characterize the general study area. Although it may be self-evident that data must be collected from a site that typifies the habitat under study, some investigators fail to meet this basic requirement. Study sites are usually selected on the basis of dominant or persistent floral components or type of substrata. Once the site is selected, spikes or stakes driven into the bottom permanently mark the places to be periodically monitored. For each assessment, a measuring tape (usually 25 m long) is laid out between the markers, and the macroorganisms within 2 m of the line are quantified.

Visual Assessments

Quantitative observations. Larger organisms within the transect area can be enumerated by simple visual count while swimming along the line. Macroalgae are assessed as to percent cover and relative species abundance.

Supplemental observations. It is important to include the many general, non-quantitative observations that are made during the course of a study--both inside and outside of the study site. General impressions gained from casual observations frequently provide meaningful insight into behavior and distribution of both invertebrates and fishes. Often such insight is needed for meaningful analysis of the quantitative data.

Collecting Procedures

Fishes. For gut content analysis, most fishes are collected by spear, but quinaldine is used to sample the most cryptic forms. The spears are multipronged and vary in length from 2 to 8 feet to meet the differing needs in collecting various sizes and species of fishes.

Algae associates. The organisms associated with the 3 or 4 most dominant species of macroalgae are collected by placing bags (fine mesh or plastic) over the algae and cutting it free. To evaluate substrata preference of the associated organisms an attempt is always made to collect a single species of algae in each bag. Other arborescent forms such as certain hydroids and ectoprocts are collected in the same manner when analyses of their associates are warranted.

Plankton. Organisms occurring in midwater are collected by pushing a meter net through the water column at a specific depth for a specific length of time. This method permits precise measurements of the organisms occurring at specific depths above particular substrata or habitats (see Hobson and Chess, 1976, 1978).

Epifauna. An airlift device, as described earlier (Chess, 1978), is used to quantitatively collect the epifauna from rock bottoms. The procedure described in this report is basically the same but employs a more versatile device (Fig. 1). Organisms are collected from within a .25 m^2 quadrat, using the airlift like a vacuum cleaner. The organisms are drawn up the tube, through a one-way valve and into a mesh collecting bag.

Figure 1. Flexible airlift device.

The modified device is made of flexible plastic corrugated swimming pool cleaner hose (38 mm I.D., 3 m long) rather than rigid PVC pipe. Two advantages of the flexible airlift is portability and ease of use in rough water. It can be easily coiled and stowed in a small boat. In strong wave surge the tube's flexibility allows it to sway back and forth, enabling the operator to maintain position and direct the nozzle of the airlift much easier than with the rigid tube.

As with the earlier device, this airlift is powered by low pressure air from a scuba regulator, either the diver's or a separate unit. Both devices are held vertical in the water by a donut buoy attached to the top and lead weights to the bottom. It is convenient to have the air supply (scuba tank) suspended in the water so that the valve and regulator are not damaged by striking the bottom and to increase mobility of the whole apparatus. Certain small steel or aluminum air tanks are buoyant when only partially filled (about 1500 psi). The manifold used to introduce air into the tube is a 12 cm length of PVC pipe glued top and bottom around a perforated portion of the tube. An even flow of small bubbles from the perforations causes less turbulence and is more efficient than if large bubbles from a single air inlet were employed. The one-way valve at the top of the tube prevents escapement of organisms back down the tube. It can be easily fabricated of wet-suit neoprene by first gluing a piece about 15 cm long into a cylinder of sufficient diameter to slip over the tip of the tube, then cutting two opposite sides from the top about 1/3 down and gluing the margins of the inside edges of the cut together, thereby forming a closed slit at the top. It allows easy flow of air and material into the bag and prevents its return. The collecting bags are fabricated of .333 mm plankton net material.

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Prey Availability and the Diets Of Two Co-occurring Flatfish

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This paper was presented by Gregor M. Cailliet.

Various approaches have been used to compare the diets of marine fishes. Their prey are generally divided into several higher taxonomic categories which form the basis of most comparative feeding studies. In this paper, we contrast this standard taxonomic classification of the invertebrate prey of two demersal flatfish to a simple ecological classification based on prey habitat requirements and activity patterns. The taxonomic grouping provides little insight into the relationships between the two predators or between predator and prey. On the other hand, the ecological classification suggests important behavioral differences between the predators, while helping to illuminate predator-prey interactions.

Methods

Individuals of two species of flatfish, Citharichthys sordidus, the Pacific sanddab (85 specimens), and Parophrys vetulus, the English sole (45 specimens), were collected by hand spear and otter trawl from sand flats in central Monterey Bay, California during June and July, 1975 and October, 1976. A sampling station was located on each side of the Monterey Submarine Canyon. The northern station was in 30 m and the southern station was in 24 m of water. The diets of these fish were examined as part of a larger experimental study of the effects of fish predation on a community of benthic invertebrates.

All fish were weighed and standard length was measured. Fish stomachs were removed and preserved in 4% formaldehyde. Stomach contents were identified to the lowest possible taxa and the proportion that each prey item contributed to the total volume of the stomach contents was estimated. Polychaete and mollusc fragments could easily be identified to species by setal and shell characteristics. Fragments were counted as single individuals unless two fragments obviously came from different animals.

The index of relative importance (IRI) was used to estimate the contribution of major taxonomic groups to the diet (Pinkas, Oliphant, and Iverson, 1971). The index was calculated as IRI = (N + V) x FO where N is the numerical percentage a food type contributes to the total diet, V is its volumetric percentage and FO is its percent frequency of occurrence (that proportion of stomachs containing the food item). To avoid the bias inherent in averaging nearly empty or overly full guts all calculations were based on the summation of all the specimens of a species at each station.

Prey species were also grouped by their habitat requirements and activity patterns. The first group included deep burrowers that were not active at the sediment surface (e.g., capitellid polychaetes such as *Mediomastus* and *Heteromastus*). The second group contained deep burrowers that were primarily active at the sediment surface. It included the polychaetes *Nothria elegans*, *Amaeana occidentalis*, and *Magelona sacculata* that fed at the sediment surface, but were also capable of retracting deep into the sediment. Most of the infaunal biomass was in these two groups. The third group contained shallow burrowing species that were active at the sediment-water interface. It had the largest number of species and individuals and the numerical dominants were amphipods, ostracods, and small polychaetes. The last group included active swimmers such as mysids, euphausiids, and fish that were rarely found in bottom core samples. This classification is based on the observations made during a more extensive field study of the natural history of the local benthic invertebrates (Oliver, et al., in preparation).

Results

Citharichthys sordidus, the Pacific sanddab, ranged from 85 to 211 mm in standard length ($\bar{x}$ = 137 mm), while *Parophrys vetulus*, the English sole, was considerably larger with a range of 140 to 352 mm ($\bar{x}$ = 228 mm). Both fish consumed a wide range of prey species and their diets showed considerable overlap in species composition. Nevertheless, there were marked differences that were consistent in the samples taken from the northern and southern sandflats. In general, crustaceans were the major prey of *C. sordidus* (Figure 1), while polychaetes were more important to the diet of *P. vetulus* (Figure 2).

Euphausiid and mysid crustaceans accounted for most of the number and volume of crustaceans consumed by *C. sordidus* at both stations. They are mobile members of the plankton. The polychaete prey were almost exclusively the species that feed at the sediment surface, especially *Nothria elegans*, *Amaeana occidentalis* and *Magelona sacculata*. The tentacles of the terebellid, *A. occidentalis*, were consumed far more frequently than the animal itself. Juvenile rockfish, *Sebastes* spp., and their scales were also found in several *C. sordidus* stomachs. The relatively high volume of molluscs (Figure 1) was due to a few large razor clams, *Siliqua* sp., whose siphons protrude just above the sediment surface.

Parophrys vetulus consumed large numbers of surface dwelling crustaceans including the amphipods *Paraphoxus epistomus* and *P. daboius* and the cumaceans *Mesolamprops dillonensis* and *Hemilamprops californica* at the northern area, but not at the southern site. The principal crustacean species consumed at the southern station was the crab,

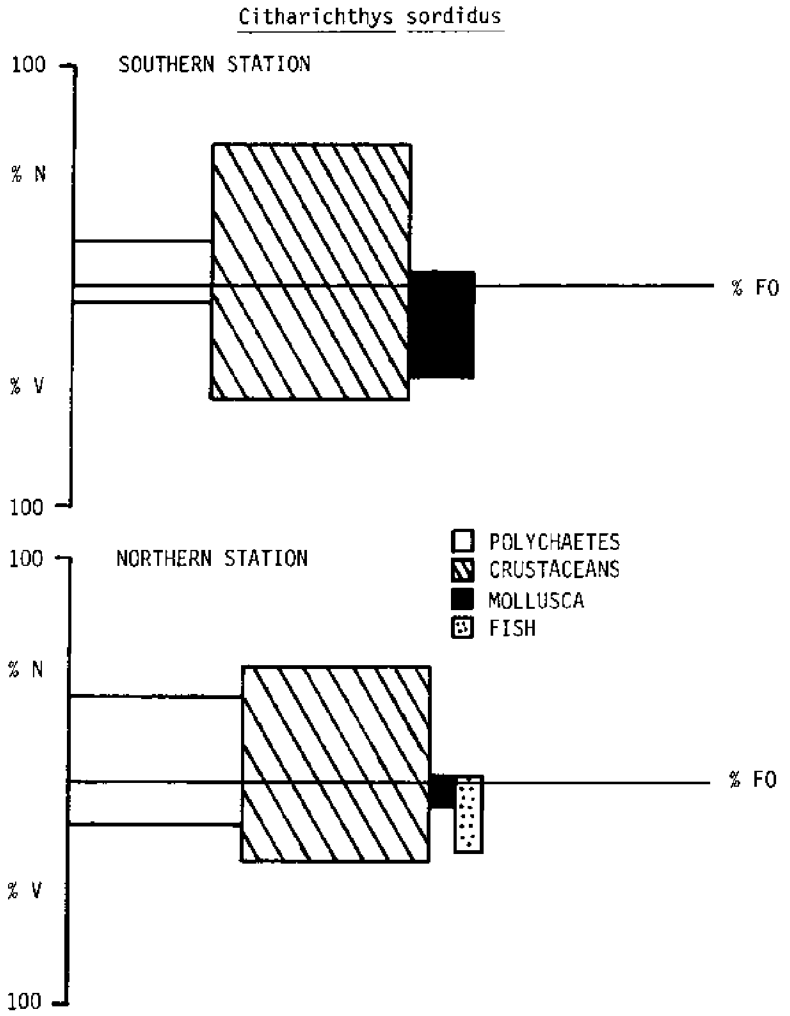

Figure 1: Relative importance of prey items in <u>Citharichthys sordidus</u>. Major prey taxa were ranked by the Index of Relative Importance (IRI's) which is a combination of percent by number (% N), percent by volume (%V), and percent frequency of occurrence (%FO).

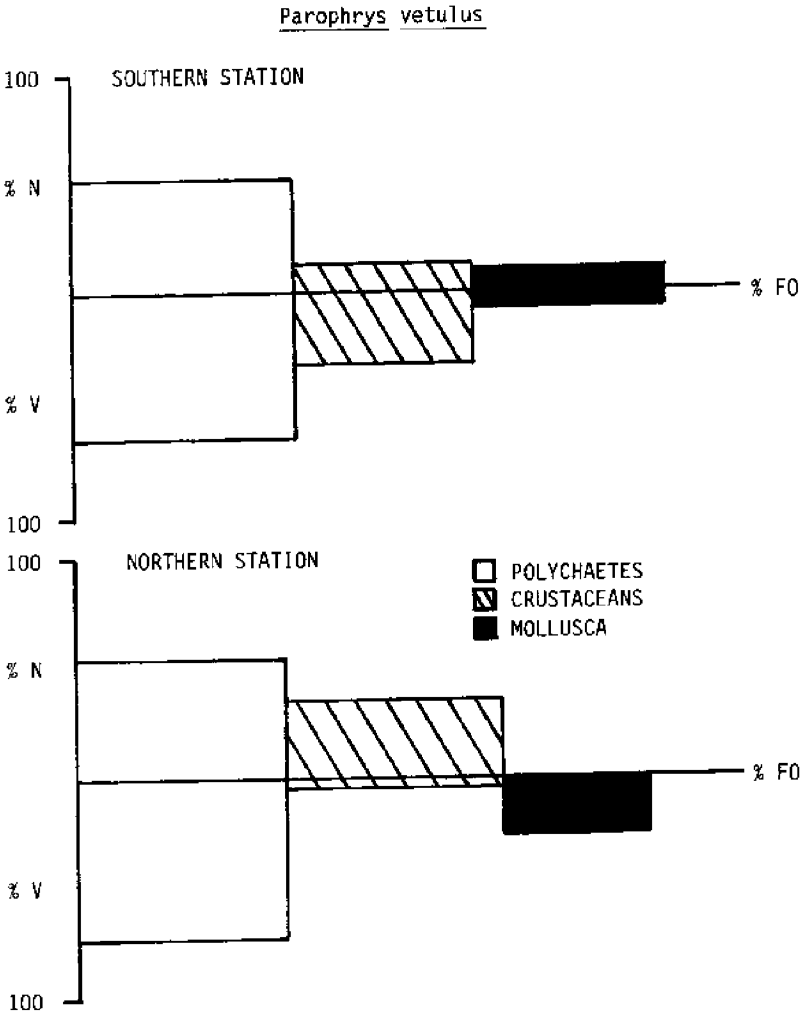

Figure 2: Relative importance of prey items in *Parophrys vetulus*. Major prey taxa were ranked by the Index of Relative Importance (IRI's) which is a combination of percent by number (%N), percent by volume (%V), and percent by frequency of occurrence (%FO).

Pinnixa franciscana. A large number of juvenile Eumida tubiformis (polychaete) were also eaten at the northern area. This and several other species periodically occur in dense but ephemeral patches along the sand flat, rarely surviving periods of strong wave surge (Oliver, et al., in preparation). The polychaetes, N. elegans, A. occidentalis and M. sacculata, were taken frequently at both stations. Unlike C. sordidus, a wide variety of other polychaetes were also consumed in varying quantities.

When the invertebrate prey are classified by their natural history, other differences between the feeding habits of the two predators emerge. Deep burrowing species that were not active at the sediment surface were never captured by C. sordidus, but were commonly taken by P. vetulus (Figure 3). For example, the abundant and deep burrowing polychaete, Mediomastus californiensis, as well as Heteromastus filobranchus and Prionospio cirrifera were not consumed by C. sordidus; yet they were commonly eaten by P. vetulus. Other deep living species were also only found in the stomachs of P. vetulus. Species that burrowed deeply, but were active at the sediment surface, were common in C. sordidus stomachs (Figure 3); often, however, only the most anterior portion of the body was present. Parophrys vetulus also preyed heavily on this group (Figure 3), which included the surface-active polychaetes, Magelona sacculata, Nothria elegans, and Amaeana occidentalis. These species were abundant members of the infaunal community in both areas (Oliver, et al., in preparation). Shallow burrowing, surface-active forms were the most important prey for P. vetulus at both stations and for C. sordidus at the northern area (Figure 3). This group accounted for most of the dietary overlap between the two fish. Hyperbenthic animals were frequently taken by C. sordidus, but were rarely captured by P. vetulus. The hyperbenthic prey group, including active swimmers such as euphausiids and the mysid, Neomysis kadiakensis, was the most important prey group for C. sordidus at the southern station. The shallow-burrowing, surface-active species were most important at the northern area (Figure 3).

Discussion

Parophrys vetulus digs into the sediment to extract burrowing species that are not active at the substrate surface. We have observed this digging behavior in the field for P. vetulus, but never for Citharichthys sordidus. Parophrys vetulus consumed a large number of benthic invertebrates that live on or in the sediment. Some of these are quite mobile and frequently swim off the bottom (e.g., oedicerotid amphipods and cumaceans). Most of the prey, however, are primarily infaunal creatures that burrow into surface sediments. Parophrys vetulus rarely consumed active hyperbenthic or pelagic animals that come close to the bottom (Figure 3). Presumably these species are too mobile to catch. On the other hand, Citharichthys sordidus does not dig into the sediment nearly as extensively as P. vetulus. It caught active swimmers and all the shallow-surface fauna, but did not feed on species that are only active deep in the sediment (Figure 3). Moreover, the tentacles and extreme anterior ends of many deep-burrowing, surface-active worms were much more common in C. sordidus. Thus, a consideration of the habits of the prey suggests that P. vetulus is much better at digging and sifting for prey, whereas C. sordidus is a poor digger and is more adept at a hunt and peck or sit and wait feeding strategy.

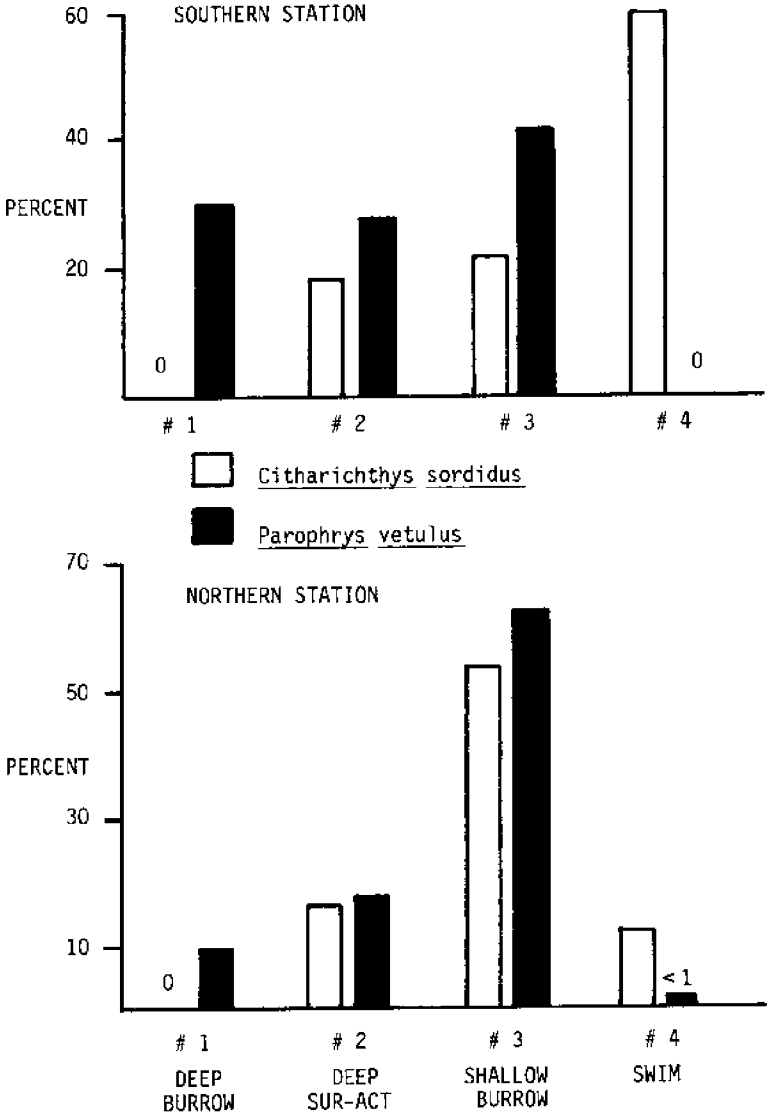

Figure 3: The numerical percentage of the various prey groups in the flatfish diets. Prey species were grouped according to habitat requirements and activity patterns: #1) deep burrowers not active at the sediment surface, #2) deep burrowers active at the sediment surface, #3) shallow burrowers active at the sediment surface, #4) hyperbenthic or planktonic forms.

These hypothetical feeding behaviors correspond to morphological differences between the two fish. Citharichthys sordidus has larger eyes and a larger mouth. Parophrys vetulus has slightly smaller eyes, a smaller mouth, a narrower gape, and a broadly pointed snout. These traits only suggest that P. vetulus is a better groveler than C. sordidus.

The zonation of the benthos along the northern and southern sand flats is highly dependent upon wave induced substrate movement (Oliver, et al., in preparation). Polychaetes that burrow deep into the sediment or maintain permanent burrows are more abundant in deeper water. Crustaceans are most abundant in shallower areas where sediment movement is more intense. This shallow crustacean zone is shifted into deeper water along the northern study area because of a local increase in wave energy there. Wave-energy is less intense along the southern sand flat. Therefore, the northern site is characterized by many shallow-burrowing amphipod and ostracod crustaceans and relatively few polychaetes. In contrast, the southern station is characterized by species found in deeper water and includes more relatively large, deep-burrowing polychaetes and few crustaceans (Oliver, et al., in preparation).

This difference in bottom community composition was reflected in the diets of the two fish. The dietary contribution of shallow-burrowing, surface-active forms was higher for both fishes at the northern station (Figure 3), where these prey were also the most abundant members of the benthic invertebrate community (Oliver, et al., in preparation). Owing to the increase in polychaetes and the decrease in these surface forms at the southern station (Oliver, et al., in preparation), P. vetulus captured many more deep burrowers there (Figure 3). Hence, the postulated behaviors of the predatory fish are consistent with the dietary patterns and changes in prey abundance found at the two study areas.

Parophrys vetulus consumed many more species of benthic prey than C. sordidus. This might be expected for an animal that also digs and sifts the sediment for its food as opposed to one that feeds almost exclusively on prey that emerge from the bottom. Nevertheless, both species consumed many species of prey within their hypothesized behavioral constraints. Furthermore, they are opportunistic feeders that readily consumed periodic and patchy concentrations of available food. This opportunistic behavior is exemplified by the large number of newly settled Eumida tubiformis eaten by P. vetulus at the northern station.

The Index of Relative Importance (IRI) values, based on the major taxonomic groups that are commonly used as prey categories, give little insight into the behavioral differences between the two fish (Figures 1 and 2). The index can be easily adapted to a more ecologically meaningful grouping of the prey. The problem, of course, is that a more realistic classification requires an understanding of the natural history of prey.

Indices of selectivity or electivity (Ivlev, 1961) and similarity (Horn, 1966) are sometimes used to estimate the difference between the composition of a pool of potential prey and a predator's diet. These estimates of apparent selectivity are highly dependent upon the species comprising the potential prey pool. An index based on all the benthic and hyperbenthic animals would indicate more selectivity for the fish in this study than one based on only the functionally available prey.

We hope these results will serve to caution investigators that the usefulness of a given index can be considerably enhanced by greater attention to natural history, in this case of the fish prey species.

Acknowledgments

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The Infaunal Index
A Relative Abundance Measure of the Benthic Infauna and How it May Be Applied to Fish Food Habits Studies

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Detailed knowledge of the types of food acceptable to fish, and the manner in which such information is obtained, is generally required prior to the efficient management of fish stocks. However, the identification of all prey species found in fish stomachs and the comparison with the abundances of those prey items in the environment is very expensive and time consuming. Because of these constraints, research efforts are limited in the number of fish species that can be studied at a time. Moreover, effective management of any fish stock must also incorporate studies on the feeding interactions of all the species likely to influence the target stock of fish. Techniques are therefore required that rapidly determine the degree and manner by which each species selects its prey without exponentially increasing the cost of the investigation.

A method is proposed in this paper which may provide a rapid, cost-effective technique for assessing the feeding habits of soft-bottom benthic fish species as well as providing some means of estimating dietary overlap in multispecies fisheries. It is a corollary to a new method (Infaunal Trophic Index) of analysis and interpretation of the benthic infaunal communities which has been developed for assesssing the southern California coastal shelf. A brief description of the Infaunal Trophic Index in its present form will precede the discussion of its application to fish feeding habits.

The Infaunal Trophic Index

The Infaunal Trophic Index determines the relative importance of different invertebrate feeding strategies for soft-bottom communities. It measures the relative abundance of 47 invertebrate species which have been divided into four feeding categories (Table I). These categories range from suspension to subsurface deposit feeders and are related to the amount of organic material in the sediments (Word, 1979).

The total abundances of these species contained in each of the Infaunal Trophic Index feeding categories are used to calculate the index. The formula used for this calculation is:

$$\text{Infaunal Trophic Index} = 100 - 33\text{-}1/3 \left[\frac{0n_1 + 1n_2 + 2n_3 + 3n_4}{n_1 + n_2 + n_3 + n_4} \right]$$

where n is equal to the number of individuals in subgroups 1 through 4.

The sampling variations obtained with this index are less than five percent for replicate 0.1 sq m Van Veen grab samples, less than five percent for samples taken during different seasons at the same station, and approximately ten percent at stations sampled over twenty years apart (Word, 1979). Thus, the index value is very consistent and single samples can often provide characteristic values for each station. (As a result of inconsistent recruitment sizes of the various species in the four groups, a single-seive mesh diameter (e.g., 1.0 or 0.7 mm) should be selected and standardized upon for each study.)

Application of Index to Fish Food Studies

The useful application of this index to feeding studies is dependent upon two criteria. First, the fish predator must actively seek its prey items in a fashion that is consistent with other individuals of its species and that will result in a collection of food items that are indicative of certain prey exposure types. Second, that the categories defined by the Infaunal Trophic Index correctly portray the exposure types identified by the various fish species being studied.

The degree and type of exposure of the four Infaunal Trophic Index groups were investigated by determining the vertical distribution within the sediments. Table 2 shows that each of these groups are distributed differently within the sediments. If this vertical separation of the groups correctly portrays the way a particular species of fish views its environment then comparison of stomach and Infaunal Sediment Indices at a minimum of two stations can provide excellent information on the selectivity or generalization of this fish's feeding habits. Two examples will be presented in this paper that seem to support the view that the vertical separation of these groups within the sediment actually does represent the way these species view their environment.

The Dover sole, Microstomus pacificus, was collected at one station with a high Infaunal Trophic Index (>90) and at another location with a low index score (<10). The stomachs of the fish from both location had index values that were very similar to the values in the sediments where they were collected. This indicated that the fish was a generalized feeder seeing all categories I - IV in the same manner and feeding on them roughly in proportion to their presence.

On the other hand the yellow chin sculpin, Icelinus quadreseriatus, normally feeds upon small epifaunal crustacea (e.g., Euphilomedes and Photis, ostracods, amphipods). This fish is not abundant in areas of low crustacean abundance (Palos Verdes) while it is extremely abundant in areas where they abound. Establishing the Infaunal Trophic Index values at each of these stations will provide values of less than 20 and around 60. The stomach index values would be roughly the same at both locations (~ 60) and thus indicate a preferance for species at this index level. Small epifaunal microcrustacea (e.g. Euphilomedes and Photis) are most abundant at these values. Therefore this species would be considered a selective feeder if the above results were obtained.

Implications

Applying the Infaunal Trophic Index to study fish feeding habits over soft-bottom marine communities could provide useful insight into predator/prey interactions. It was not designed for application to rocky habitats or to open ocean pelagic communities and would not be useful when applied to these environments. However, the idea of defining and separating the prey into various exposure types and comparing stomach and habitat indices should provide similar information.

The implications resulting from investigations of this type and the discovery of specialized and generalized fish feeding types are many. The brief comparison of two species of fish inhabiting relatively similar habitats showed that one was a generalized feeder (*M. pacificus*) and suggested that the other was a specialized feeder (*I. quadreseriatus*). It showed that competition for food supplies between these two species would only be possible at an index level in the sediments of about 60, and that enhanced invertebrate abundances at this index level could result in enhanced populations of the yellow chin sculpin (*I. quadreseriatus*).

Certain studies (Mearns, A.J. and L. Harris. 1975) have shown that Dover sole grow faster in regions that seem to have low Infaunal Trophic Index scores. These areas generally have only slightly higher standing crops than areas with high Infaunal Trophic Index scores. This suggests that enhancements of populations of the Dover sole would occur in regions that can be maintained at these lower index levels.

The rapid accumulation of this type of cost effective data appears to provide the information on multispecies models that will not only allow the comparison of predator feeding relationships, but also the potentials for enhancing fish populations of different feeding strategies, and the potential for increasing growth rates of a particular species by selectively enhancing food sources which the fish will eat and are more easily convertible to energy as was demonstrated in the case with the Dover sole.

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Contribution No. 135, So. Calif. Coastal Water Research Project, 1500 E. Imperial Hwy., El Segundo, CA 90245

Table I. Groupings of Infaunal Index Species, their generalized feeding strategies and the groups overall response pattern to outfall discharge sites.

GROUP I - Suspension Feeding

This group contains species common and relatively abundant in control regions. They become less dominant upon approaching outfalls or accumulations of organic materials in sediments. (19 species, 7 Taxa)

Suspension	Suspension & Surface Detritus	Carnivore
Ophiuroidea - *Amphiodia* (*Amphispina*) *urtica*, *Amphiodia* (*Amphispina*) *digitata*, *Amphiodia psara*, *Amphiodia occidentalis*, *Amphiodia* spp.	Amphiopoda - *Ampelisca pacifica*, *Ampelisca hancocki*, *Ampelisca brevisimulata*, *Ampelisca macrocephala*, *Ampelisca cristata*, *Paraphoxus bicuspidatus*, *Metaphoxus frequens*, *Heterophoxus oculatus*, *Ampelisca* sp., *Paraphoxus* sp., *Metaphoxus* sp., *Heterophoxus* sp.	Polychaeta - *Sthenelenella uniformis*
Phoronida - *Phoronis* sp.		

GROUP II - Combination of Suspension and Surface Detritus feeding

This group of species can become abundant in areas dominated by species in Group I but they do not become dominant in samples until approaching the fringes of areas influenced by the deposition of particulate organic material. Increases in concentrations of these deposits correlated with a decline in the abundance of these species and an increase in the abundance of Group III species. (14+ species, 7 Taxa)

Suspension & Surface Detritus	Subsurface & Surface Detritus	?Carnivore	Surface Detritus
Amphipod - *Photis brevipes*, *Photis californica*, *Photis* spp.	Polychaeta - *Medionastus* spp. (several species)	Polychaeta - *Myriochele gracilis*, *Myriochele* *sp*.	Pelecypoda - *Mysella pedroana*, *Mysella tumida*, *Mysella* sp. (several species)
Ostracoda - *Euphilomedes producta*, *Euphilomedes carcharodonta*, *Euphilomedes longiseta*			
Polychaeta - *Tharyx* spp. (several species)			
Pelecypoda - *Axinopsida serricata*			

GROUP III - Dominated by Surface Detritus feeding

This group of species although often present were never abundant at control stations. Their abundance increased upon closer proximity to outfalls and became dominant in areas of increased particulate organic loadings of sediment. As the levels of these organic loadings increased this group of species were replaced by Group IV species. (4 species, 4 Taxa)

Surface Detritus	Suspension & Surface Detritus	?Suspension & Surface Detritus
Pelecypoda - *Parvilucina tenuisculpta*, *Bittium* sp. (UI)	Pelecypoda - *Macoma carlottensis*	Pelecypoda - *Spiochaetopterus costarum*

GROUP IV - Dominated by Subsurface Detritus feeding

These species are rarely encountered in undisturbed control or natural conditions. They thrive and increase in abundance especially at those stations where the fallout of particulate organic material creates a superabundance of food. There are often very noticeable odors of hydrogen sulfide produced in these sediments. (10 species, 8 Taxa)

Subsurface Detritus	Unknown Feeding Type
Polychaeta - *Armandia bioculata*, *Shistomeringos longicornis*, *Shistomeringos* sp., *Ophryothrocha* sp., Dorvelleidae, UI, *Capitella capitata*, Oligochaeta (Tubeficidae, UI)	Amphipoda - Stenothoidae UI (2 species)
Pelecypoda - *Solemya panamensis*, *Solemya* sp.	

Table 2. Vertical distribution of the four Infaunal Trophic Index categories (percentage of each group at depths within the sediment).

STATION I 12.5 m depth Infaunal Trophic Index Score = 69.9

	0 - 2 cm	2 - 5 cm	5 - 10 cm	10 cm +
Group I	100%	--	--	--
Group II	47%	47%	5%	--
Group III	--	--	--	--
Group IV	--	--	--	--

STATION II 13 m depth Infaunal Trophic Index Score = 67.7

	0 - 2 cm	2 - 5 cm	5 - 10 cm	10 cm +
Group I	100%	--	--	--
Group II	23%	42%	35%	--
Group III	--	--	--	--
Group IV	--	--	--	--

STATION III 60 m depth Infaunal Trophic Index Score = 36.0

	0 - 2 cm	2 - 5 cm	5 - 10 cm	10 cm +
Group I	--	--	--	--
Group II	56%	32%	12%	--
Group III	38%	57%	5%	--
Group IV	2%	19%	78%	--

SESSION 1 Methodology and Taxonomy

Discussion

Immunological techniques applied to questions of predator-prey interactions, an imaginative approach described by Bob Feller, understandably raised some questions. Word was interested in knowing how sensitive the test was, to which Feller replied that he and his colleagues could detect things on the order of micrograms. How did Feller handle "mixed gorp," or a digested mass of several food items, Cailliet queried. The technique described was to place the "mixed gorp" in the center of the reaction plate surrounded by an array of standards; where a positive reaction occurred they recorded the known prey item.

Mearns wanted to know if any organisms with toxic properties had been identified. Feller replied that one rabbit injected with *Paranemertes sp.* died. Feller went on to say that if a person holds a live *Paranemertes sp.* in his hand and allows the worm to penetrate the skin with its proboscis that there is a definite painful sensation. The rabbit died of anyphalactic shock soon after the injection was administered.

Sometimes we encounter bits and pieces of organisms in the guts and if we are experienced we can often idenfity to what the fragment belonged. What if fish consume fragments of something and digest it beyond recognition? Feller responded that the immunologic technique can be sensitive down to tissue parts of a known species, i.e. palps from a polychaete or siphons from a bivalve. Entomologists have been able to differentiate among eggs, larvae, pupae, and adults of insects with this technique. In cases such as chironomids, digestion can mask the characteristics which distinguish a pupae from an adult and this technique lends itself to answering this type of question.

Levy's paper raised a question regarding gear efficiency. He replied that the results he had presented were unscaled; that is, he and his colleagues did not sample with 100 percent gear efficiency. "We only catch some fraction of the fish which are upstream of the nets," Levy expalined, "The way we measured that proportion is through the use of what I call the 'gear efficiency factor'. And on many occasions when we set nets, what we do is to take a known number of marked individuals upstream of the net and look at the recovery rate of the marked individuals in the gear. So, on any one day, say if we capture 40 percent of the marked chum fry that were released at the time the nets were set, we know that we would have to scale up the numbers of chum by a factor of two and one-half." Jaenicke asked if Levy had a mark retention problem when using colored grits; none was documented.

Sometimes data is grouped by category for purposes of statistical analysis. Chess asked Cailliet if putting amphipods into a general group causes a problem. He cited the example that not all amphipods are shallow burrowers neither are they all active at night. Might their behavior differences indicate that they should not be so generally categorized? Cailliet replied that more specific categorizations were indeed made for the slough. Chess cited an example of <u>Citharichthys stigmaeus</u> consuming aorid amphipods during the night but never during <u>the day</u> because of the activity patterns of the aorids. One must be careful when defining feeding guilds. Mearns added that Cailliet's study seems to confirm what Jim Allen (formerly of SCCWRP and now completing doctoral studies) predicted several years ago.

Cailliet asked Word how many core samples were required to indicate a reliable infaunal index. Word briefly described the problem of taking replicate samples and finding widely differing infaunal indices. For example, windrows of debris exist in their study area so that, even when sampling on the same LORAN-C coordinates, one might take a scoop off the top of the pile the first time and a core off the bottom of the pile the next time. The depth differences would also be important to invertebrate distribution. However, assuming a fairly even bottom distribution, Word recalled a standard of about 2 when analyzing 10 replicates. Cailliet supposed that the tenth-meter grab sampled a large enough physical area to incorporate patchiness; Word agreed. Cailliet then surmised that the same kind of index might be applied to fish stomachs.

Feller asked why, if depth distribution of organisms was important, take grab samples which ruins the spatial distribution of organisms. Word clarified that it isn't the sampling that destroys the distribution but rather what one does with it after bringing it up. Feller said why not use a box core? A box core, Word explained, is fine if one desires to sample a small area, 0.06 square meters for example. They are extremely heavy and one needs a 120-foot boat to handle it, whereas a grab sample will penetrate the minimum requirement of 10 centimeters and is much easier to handle.

Word took the opportunity to interject some comments regarding Feller's immunological work. Word would like to get to the point where he could definitively say whether a mollusc was a filter feeder or a shallow deposit feeder. Word hypothesizes that molluscs are shallow deposit feeders but how can one verify organic material in that way. He suggested that perhaps immunology is the answer. He expressed interest in using the technique to answer some of these questions.

A brief discussion ensued after Sibert's slides on epibenthic methodology regarding how many species a person ought to be able to identify. Again, the replies indicated that one must have a specific question in mind before deciding what data will sufficiently answer that question. In some cases it might be important to know broad taxonomic groups of invertebrates only whereas someone else may judge it necessary to identify everything to species. An important thought is that one can always group data after the sorting process but if it is recorded in a general way then it can never be separated into specific components. Funding restrictions often hamper detailed identifications but it is for each research team to decide.

Perhaps clustering and looking for recurring patterns is the answer for some people. Word detailed his infaunal index briefly and summarized that he felt that looking at 47 species was sufficient to answer his questions. Observations are also useful. Along the southern California shelf it is pretty much current swept and wave swept and one can go down and pick up suspension feeders because that is the only way they can feed and survive down there. It is an interesting environment because of the tricks and techniques developed by the fish to catch organisms out of the water column.

Feller returned the discussion to statistics and asked if Word's infaunal index was amenable to statistical tests such as estimates of variability to see if areas really are different according to the index. Furthermore, he wanted to know, if this index was any different than a bunch of separate Ivlev electivity indices? Each test is for a specific application, Word explained, and the infaunal index is designed for a specific reason. Recruitment patterns play an important role in the study areas. If one species is recruiting with a certain abundance and another species is doing the same thing, or relatively the same thing, they we might be able to predict one from the other. There is something in there with recruitment that would be interesting to follow and to reason how one continues to obtain similar numbers. A five percent change in the index usually indicates a significant change. Feller wondered if diversity indices had been calculated on the same data as the infaunal indices (yes) and did they show the same trends (no). Word said that diversity works on how everybody fits together rather than on the community as a whole.

Word went on to mention the importance of looking at the total dynamics of a system; instead of looking at numbers of individuals one should look at the total amount of production created during one year's period of time in each individual area. Valuable information might be generated in this way. Of course, this would be a challenging project. A first attempt might be to rear dominant benthic organisms in a laboratory setting to determine life cycle, etc. One could extract information on 30 species of polychaetes for example and determine if they have a one or two-year life cycle or perhaps a two month or three day cycle. Corresponding field sampling would be time consuming and expensive but extremely interesting.

Levings asked Word about looking for trends when comparing benthic and fish data. Are there differences in fish communities in terms of spatial distribution with the benthic communities? Word replied that, yes, they have seen enhanced populations of a particular fish species in areas where enhanced numbers of individuals in the sediments were recorded.

When Jim Allen analyzes his fish stomach content data and collection data together it can then be combined with the benthic data and he (Word) expects to find some interesting results.

Sibert questioned Chess' theory of ignoring anomolous food items. The same thing occurs in Canada; say a fish will attack a zoea or some kind of larva, yet Sibert believes it to be an important event in the life of the fish and one that should not be ignored. Chess rephrased his idea to say that one should pay attention to anomolous food items but not to overemphasize it. For example, if a fish preyed upon three species of benthic invertebrates most of the year but during an annual migration of anchovies the fish switched to feed on anchovies for a period of two weeks the importance of anchovies in the diet might be overemphasized in terms of the total array of prey important to the predator fish. Sibert again questioned that it would be overemphasized. Chess reflected a moment then explained that he would recommend frequent small samples to occasional large samples. A five fish sample of each species taken weekly would yield more reliable information than taking a large sample of each species quarterly. If that quarterly sample was taken during a time of feeding upon a "just passing through" prey item the data would be distorted. Word brought up the example of squid schools in southern California. Chess agreed that nearly everything switches to feeding on squid at some point. They undergo a big spawning every two or three years and if one went in and took a big sample it would appear in everything but could be considered an anomolous food supply. It is natural but it misrepresents the general feeding pattern of that particular species. Sibert rephrased it to being a part of the general pattern. Chess then reconsidered his choice of the word anomolous after which Sibert (the philosopher) succinctly stated that if one has limited resources one should allocate one's sampling effort in such a way that one's understanding is optimized. Cailliet took advantage of this opportunity to enter the discussion with the reminder of a paper prepared 15 years ago in which the author examined communities of organisms in the sea then detailed a list of characteristics that one would have if one were a good member of the community, an atypical member, or a stray that comes in once in awhile. He suggested that there are several criteria by which one can judge the importance of a prey item such as how numerically abundant they are, how frequent they are, how often does it occur in the diet, how numerous is it when it does occur, how volumetrically important is it, etc.

Chess remarked that what it all boils down to is what is available at the time which relates to selectivity. Sibert (the etymologist) challenged the liberal use of the word availability. Chess quickly reworded his comment to "potential" availability within a given habitat or substrate. When an animal is truly available, that means the dentition of the predator has to meet with its visual acuity and the structure of its gill rakers has to meet with the behavior patterns and size of the prey. Everything must fit, then it becomes true availability. Koski commented that perhaps true availability is reflected in the stomach contents.

Word then brought up an interesting point of differences in feeding between territorial and non-territorial fish. For example, a territorialist such as a bass feeds within his defined space while a species such as a salmon travels among many habitats. Fish must have an idea of what it wants to eat but what factors are important in the formulation or menu-planning as it were? Another idea that presents an interesting challenge is the idea that fish may "practice" their capturing techniques on small or relatively unimportant items so that when the choice food is presented they are prepared to capture the requisite quantity.

Koski brought up the idea of caloric content again as an important method of prey evaluation. Perhaps eggs are preyed upon for a week or two days very intensively but those eggs may give the predator a boost that will last for a month or so because of the nutritive value of the protein content. It seems, and it has been shown, that coho juveniles who will feed on salmon eggs in the fall will have an enhanced growth rate. That is a very important food source but may occur only for a couple of days or a week or a very short period of time compared to other sources of food. Mearns suggested that there is a way to measure that. Eggs typically contain more DDT than other organisms animals might consume, depending on the lipid content. He tantalized the group with this idea then proceeded to explain that he would elaborate the next day, about trophic transfer of pollutants. He further suggested that being able to forecast the transfer of pollutants is one of the important reasons for conducting studies around outfalls.

The next period of discussion centered on the nutritional requirements of a fish. It was suggested that John Halver might be able to address the group in 1980 regarding nutrition and nutritional requirements. Sibert suggested that instead of measuring food why not do some experiments and look at the growth rate, growth efficiency and the ingestion efficiency of different foods. Feller suggested it as a good topic for a Ph.D. thesis.

Simenstad suggested that we look at what the cues are that fish are behaviorally responding to. What notifies a fish that food is nearby? An olfactory response or visual perception of contrast, shading, apparent size, etc.

SESSION 2

Statistical Analysis

SESSION LEADER

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Statistical Analysis of Diet Differences Related to Body Size

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Technical Paper No. 4996, Oregon Agricultural Experiment Station

Abstract: A method applicable to stomach content data is reviewed. The method tests for significant differences in presence/absence of prey through a size-range of a predator species. The technique also provides information on how to classify the predators into size strata that best display size-related heterogeneity; and shows whether the dietary tendencies change abruptly about a threshold, or continuously over the size range.

Introduction

Change in natural diet with increase in fish size is a common observation. Sometimes the change occurs over a narrow range of sizes, and the "threshold length" concept (Parker and Larkin, 1959) is applicable. Size-groups of a fish species with different food-energy sources may be called "feeding stanzas", after terminology by Paloheimo and Dickie (1965). Alternatively, size related changes in diet may occur evenly across the predator's size range, and any equal-interval stratification of sizes would be adequate for discription of dietary changes.

Statistical testing should be carried out to distinguish apparent size-related relationships from random variation. The iterative chi-square technique used here provides information on how to combine the stomach content data into predator size strata to best demonstrate size-related heterogeneity. It also shows whether the dietary changes occur abruptly about a threshold, or continuously over the size range.

Since the method was previously printed only in manuscript form (Tyler 1969), it seems useful to review it in the content of this predation workshop.

Analytical Method

The measurement of dietary change is based on the presence or absence of the prey species in the predator's stomach, not on volumetric occurrence, or the number of occurrences, within the predator's stomach. It is considered here that if most of the predator individuals contain the prey species there is strong affinity between predator and prey. There is often a direct relationship between percentage of fish stomachs holding a prey species and the quantity of that prey species in the stomach (Tyler, 1971). This relationship is sometimes difficult to prove with parametric statistics because of large variances associated with mean quantities of food in stomachs. It is the large variance problem that prompts the use of frequency data in the heterogeneity testing presented here.

As an aid in describing the method, examples were drawn from data on the white hake, *Urophycis tenuous* - a commercially exploited species off New England and eastern Canada. The fish individuals were 17 to 46 cm long. The prey species was the shrimp, *Pandalus montagui*. The data were taken during September, October, and November, 1965, as part of a study in Passamaquoddy Bay, New Brunswick (Tyler, 1972).

The method uses the chi-square statistic to distinguish heterogeneity at the 1 or 5% significance levels (Snedecor and Cochran, 1967). Contingency tables (2 x n) relate presence or absence of prey in stomachs and predator size. The predator size range is initially divided into 3 centimeter strata so that the size of the first contingency table is 2 x (size range)/3. Tests are made on sub-table of this general contingency table. Starting at the small end of the size range, the first test is calculated on the first 2 cells of the general contingency table, i.e., the first two 3 cm strata.

$$\begin{array}{ccc} A & C & A + C \\ B & D & B + D \\ A + B & C + D & N = A + B + C + D \end{array}$$

A is the number of stomachs in the first stratum containing the prey taxon, B is the number of stomachs in the first stratum without the prey taxon, C is the number in the second stratum with the prey taxon, and D is the number in the second stratum without the prey taxon.

The second test compares the first 3 cells of the general contingency table.

$$\begin{array}{cccc} A & C & E & A + C + E \\ B & D & F & B + D + F \\ A + B & C + D & E + F & N = A + B + C + D + E + F \end{array}$$

The next test compares the first 4 cells, and so on, until the final test compares all strata simulataneously. The number of tests in the series equals the number of strata minus one.

Following the generation of chi-square values for this series, the length range is restratified into groups of 4 cm and another series of tests is performed; then groups of 5 cm, etc., until the stratum becomes so large that one stratum includes the entire size range of the predator. At this point, testing is completed.

For interpretation, a series of chi-square values should be graphed against number of strata in the test (Fig. 1). The chi-square values calculated on one stratum size constitute a series. The trend of the

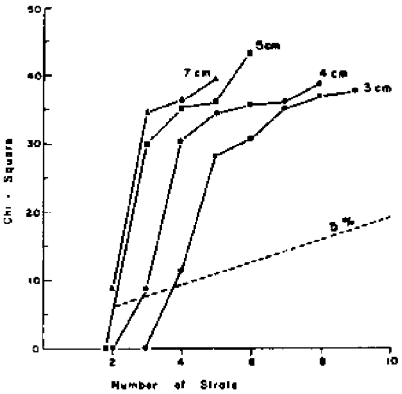

Figure 1. Chi-square values in tests of homogeneity on 2 x n contingency tables of fish length and presence of prey. The stratum width is indicated at the end of the line connecting chi-square values in each series of tests.

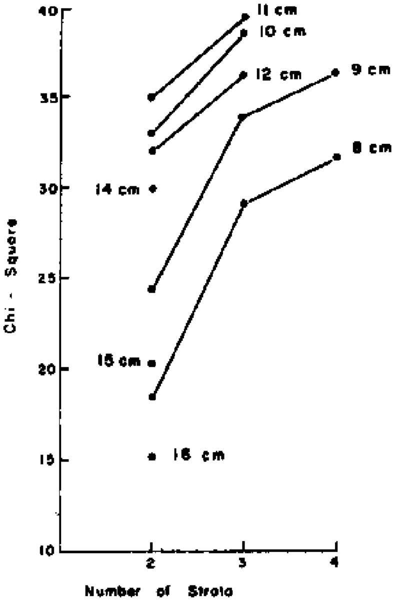

Figure 2. Chi-square values as described in Figure 1.

chi-square values from each series of tests is shown by the lines joining them. The 6 cm line is omitted because it follows the 5 cm line closely.

When the lengths are stratified into 3 cm groups, heterogeneity increases significantly when the fourth stratum is added to the contingency table. The fourth stratum is the group of fish 26 to 28 cm in length (inclusive). In the 4 cm stratification, heterogeneity occurs when the 25 to 28 cm fish are added; in the 5 cm stratification, when the 27 to 31 cm fish are added; in the 6 cm stratification, when the 29 to 34 cm fish are added; and in the 7 cm stratification, when the 24 to 30 cm fish are added. A change in feeding tendency occurs somewhere among the 24 to 34 cm fish. The chi-square values tend to reach a plateau after heterogeneity from this size range is added. This means that the addition of fish between lengths 34 and 46 cm does not continue to increase heterogeneity. Forty-four fish were tested in the 34 to 46 cm size range. One may conclude that there is only one center of heterogeneity (threshold length) along the length range of the sample. If heterogeneity changed continuously there would be no plateau in Fig. 1. If a predator had a third feeding stanza (second threshold length) the chi-square values would resume a rapid rise following the plateau. Whether or not there is a plateau is left as a subjective decision. Border line cases should probably be categorized as continuous change so that the establishment of feeding stanzas is more eventful.

Large stratifications are used to estimate the threshold length. Chi-square values are significant when the first 2 strata are compared for stratum widths of 8 to 16 cm (Fig. 2). Heterogeneity increases as the size of the stratum increases until the 11 cm strata are tested, at which point heterogeneity progressively decreases. That is heterogeneity is maximized with 11 cm groupings and progressively decreases with further increases in stratum size. The first contingency table at the 11 cm stratification compares fish 17 to 27 cm long with fish 28 to 38 cm long. The sample range of 17 to 46 cm should apparently be divided in two at 28 cm.

The threshold length concept is only an abstraction of reality. There is no implication that a fish actually crosses a knife-edge into another life-history stanza. Also, the threshold length is not precisely determined in a statistical sense. Inspection of Fig. 1, particularly the 4 and 5 cm stratum series, indicates that if the process of dividing the length range in two were begun at the 46 cm end instead of at the 17 cm end, heterogeneity would not maximize while the division was within the first 20 cm (46 to 26 cm), since that range is fairly homogeneous. Stratification from the 46 cm end toward the 17 cm end would be to estimate the threshold length as 25 or 26 cm, rather than 28 cm as in the forward solution. To further illustrate this point a perfectly symmetrical contingency table is constructed as follows:

cm. group	1	2	3	4	5	6	7	8	9
no. with prey	8	8	8	6	5	4	2	2	2
no. without prey	2	2	2	4	5	6	8	8	8

By inspection, the threshold length is the fifth cm group. Chi-square values are calculated by dividing the table into a series of two-strata, contingency sub-tables. The first value is calculated for the first cm group versus the pooled groups 2 to 9. The second value is calculated for the pooled 1 to 2 cm groups versus the pooled 3 to 9. The series is continued until the pooled 1 to 8 is compared against the 9 cm group. The resulting chi-square values are:

Split between	1&2	2&3	3 & 4	4 & 5	5 & 6	6 & 7	7&8	8&9
Chi-square	4.05	9.26	16.20	18.00	18.00	16.20	9.26	4.05

The chi-square value of 18.00 is first obtained when the 5 cm group is pooled with groups 6 to 9, and is obtained again when it is pooled with with groups 1 to 4. Thus there are two equally good stratifications that maximize heterogeneity.

Graphical Summaries of Findings

A few additional plots are useful for understanding size-related differences. Percentage of fish that ate Pandalus is plotted in Fig. 3 for 4 cm strata. The 4 cm stratification provides a group split at 28 cm, the threshold size found in the analytical process described above. The rapid change in feeding tendency in the 25 to 28 cm fish is evident. Within this group, 20% of the fish contained Pandalus. No fish smaller than 25 cm contained Pandalus. In length strata which include fish larger than 28 cm, 60 to 65% had eaten Pandalus.

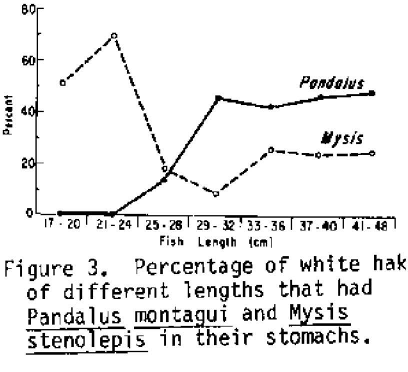

Figure 3. Percentage of white hake of different lengths that had Pandalus montagui and Mysis stenolepis in their stomachs.

Pandalus was not the only prey that occurred with variable frequency over the predator size range. Percentage of stomachs containing an oppossum shrimp (Mysis stenolepis) decreased with increase in predator size (Fig. 3). The threshold length with respect ot this prey was 26 cm. In addition, the fish Lumpenus maculatus and the shrimp Crangon septemspinosa showed significant heterogeneity over the predator size-range. These two prey taxa could not be statistically tested in finely divided, predator, length-strata because each taxon occurred in fewer than 16 stomachs, and generally there were only 0 to 5 observations in each contingency cell (Snedecor and Cochran, 1976). Frequencies were tested with a 27 cm threshold length (taken as the mean of 28 and 26 from Pandalus and Mysis tests). Significant chi-square values were found. The results are summarized in a radial plot (Fig. 4) where values on the spokes are percentages of stomachs containing the prey. The circular arrangement tends to give a better resolution of stanza differences than the usual histogram plot.

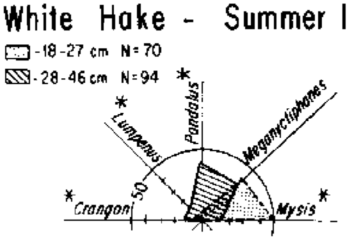

Figure 4. Percentages of fish in two feeding stanzas that contained various prey. Lines between axes connect the percentage points. The asterisk indicates a significant difference (P=0.05) between feeding stanzas.

Acknowledgements

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The Use of Pielou's Method to Determine Sample Size in Food Studies

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Introduction

It is usually difficult to determine the sample size required to adequately describe the diet of a fish population. Because of patchy prey distribution and selective feeding by individual fish, the prey are not normally distributed among the fish and contents of individual stomachs do not represent the diet for the population. Usual statistics, therefore, cannot be used to estimate sample size. An alternative may be to use a method for estimating population diversity suggested by Pielou (1966a, 1975). In this paper I review Pielou's method and discuss its application in food studies.

Review of Pielou's Method for Calculating Diversity

Pielou (1966a) argued that neither Brillouin's index (Brillouin, 1962) nor the Shannon index (Shannon and Weaver, 1959) accurately calculates the diversity per individual (H) of a population which cannot be sampled either totally or randomly. Brillouin's index:

$$H = (1/N) \log (N!/\Pi N_i!) \qquad (1)$$

where N is the total number of individuals and N_i the number in the i^{th} species, measures the actual diversity per individual of a population or collection in which all the members have been identified and counted (Pielou, 1966a, 1966b). The Shannon index:

$$H' = -\sum_{i=1}^{S} p_i \log p_i \qquad (2)$$

where p_i is the proportion of the i^{th} species in the population and S is the number of species, approximates H when the number of individuals in each species is large (Pielou, 1966b). An estimate of H', the unknown diversity per individual in the population, is obtained by substituting values from a representative sample for population values (Pielou, 1966b, 1975).

The diversity of large, patchily-distributed populations is more accurately measured by Pielou's method based on the random pooling of subunits within the sample than by calculating (1) or (2) for the total sample. Although Pielou's method was originally proposed for use with plant and animal communities sampled by quadrat, Hurtubia (1973) has shown that it is also appropriate for measuring dietary diversity. Dietary diversity, which always refers to diversity per individual prey unless otherwise stated, can be calculated in the following manner: Given a sample of n fish, randomly order the fish from 1 to n. Calculate diversities of successive stomachs according to a general form of Brillouin's index:

$$H_k = (1/N_k) \log (N_k!/\Pi N_{ki}!) \qquad (3)$$

where H_k is the diversity in K pooled stomachs (K = 1 to n), N_k is the number of individuals in these stomachs, and N_{ki} is the number of individuals of the i^{th} species in K pooled stomachs.

Plot H_k versus K, the number of pooled stomachs (figure 1). As the stomachs are pooled, H_k initially tends to increase (although sometimes quite erratically). If K is large enough, H_k should eventually level off at a point t.

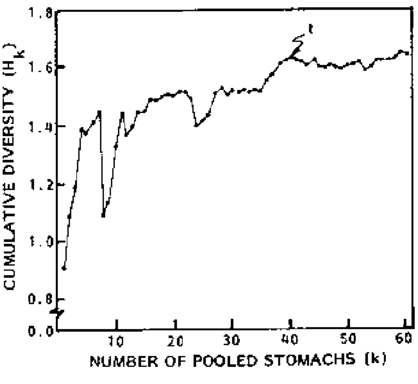

Figure 1. Cumulative diversity, H_k, versus number of pooled stomachs, k, for threespine stickleback (Gasterosteus aculeatus), age I, from Lake Nunavaugaluk, Alaska. Point t indicates where the diversity stabilizes.

To understand why H_k behaves this way, we need to examine how the index responds to dietary changes. It is most sensitive to changes in species (S). Adding new species to the pooled stomach contents increases diversity, particularly when the total number of individual prey (N) is low. Increasing N also increases diversity, especially when N is low, although the effect is much less than adding new species. Changes in the apportionment of N among the prey species affects diversity: for a given N and S, diversity is greatest when N is evenly divided among S. Uneven proportions result in lower diversity.

As stomach contents are pooled, N is usually low at first, and additional species and numbers of individual prey cause H_k to rise sharply. As N increases and most species are included in the sample, the increase in diversity caused by additional stomachs will not be as great. At the same time, the number of prey in the common species will be increasing disproportionately to the less common species, tending to decrease diversity (Pielou, 1966a). If these effects balance, the diversity stabilizes, and point t can be visually determined from the graph of H_k versus K.

When the plot of H_k versus K levels off, the diversity in the diet of the population (H') can be estimated from H_k values for K>t. Although H_k is dependent on sample size (Pielou, 1966a), the increment in diversity per individual prey (h_k) after t can be considered an independent estimate of H' (Pielou, 1975). To calculate h_k, multiply H_k by N_k to obtain the total diversity of the K^{th} sample. Values of h_k between consecutive samples are then given by:

$$h_k = (N_k H_k - N_{k-1} H_{k-1})/(N_k - N_{k-1}). \qquad (4)$$

The mean of the h_k's may be used to estimate H' (Pielou, 1975) as follows:

$$H' = \bar{h} = \frac{1}{n-t} \sum_{k=t+1}^{n} h_k \qquad (5)$$

where n equals the number of stomachs in the sample. The variance of H' is calculated by:

$$\widetilde{\mathrm{var}}\ (H') = \widetilde{\mathrm{var}}\ \bar{h} = \frac{1}{n(n-1)}\ (\Sigma\, h_k^{\,2} - n\bar{h}^2) \qquad (6)$$

where n equals the number of h_k values for H_k>t. If the stomachs are pooled several times, using a different random order each time, the median result has been used (Pielou, 1975; Heyer and Berven, 1973).

Use of Diversity to Estimate Sample Size

Definition and interpretation of diversity

Pielou (1966a) states that "any number of quadrats in excess of t suffices to 'represent' the population in the sense that enlargement of the sample would cause no further increase in diversity". Does any number of stomachs in excess of t also suffice to represent the diet of the population?

To answer this question we need to define diversity as measured by the Brillouin index. Both the Shannon index and the Brillouin index are based on the information theory and measure the amount of information gained per symbol when a message composed of known symbols is received (Pielou, 1966c).

Several authors have disputed the use of the information theory in ecological studies, stating that it has no direct biological interpretation and the traditional diversity-stability concept is unfounded (Goodman, 1975); it is not necessarily based on a species importance in the community (Hurlbert, 1971); and attempts to relativize diversity indices give unsatisfactory results (Peet, 1975). Other authors feel that the measure of uncertainty given by the information theory is a reasonable measure of diversity in a population regardless of whatever false analogies have been built around it (Pielou, 1969), and have found it useful in interpreting empirical data (Haedrich, 1975; Heyer and Berven, 1973; and Hurtubia, 1973).

Dietary diversity, as given by the information theory, could be considered simply as the uncertainty associated with an individual prey picked at random from the diet of the fish population. The more prey species and the more even their representation in the diet, the greater the diversity of the diet and the greater the uncertainty of picking an individual of a particular species.

The point where the cumulative diversity of the pooled stomachs stabilizes, then, is the point where additional stomachs will change neither the number of species nor the proportions of the accumulated prey enough to alter the uncertainty associated with picking each individual prey. Therefore, it seems reasonable to assume that the cumulative diet at this point can be considered approximately that of the population, and that t indicates the sample size sufficient to represent the population.

Evaluation of the cumulative diversity method

To evaluate this method of determining sample size, I compared two groups of 40 sockeye salmon (*Oncorhynchus nerka*) fry each to one group of 80 threespine stickleback (*Gasterosteus aculeatus*) from Lake Nunavaugaluk, Alaska. Fish for each group were taken from the same habitat during two-week periods. In the first sockeye group, group A, a sufficient sample size of 30 fish was estimated by the cumulative diversity method. In the second sockeye group, group B, the cumulative diversity did not stabilize, indicating 40 fish was an insufficient sample of that population. Various-sized samples from groups A and B were compared to the same 80 threespine stickleback, group C, using percent weight data in Kendall's tau coefficient of rank correlation (Sokal and Rohlf, 1969; Tate and Clelland, 1957) and nonparametric multivariate analysis (Mantel and Valand, 1970). Kendall's tau coefficient of rank correlation measures association between groups based on pooled data for each sample. The multivariate analysis measures whether "closeness" of prey in the diet is related to group of fish and is based on individual fish rather than pooled data. The objective of this experiment, however, was not to determine whether differences existed in the diets of the groups being tested, but rather to determine whether the magnitude of each test statistic was less variable when a sample was judged sufficient than when it was not.

The results of these tests were consistent with expected results based on the estimated sample sizes for the two groups (Table 1). For group A, samples of 30 and 40 fish gave similar values; samples of only 10 or 20 fish gave singular values. This indicates 30 fish was a sufficient sample. For group B, values from all sample sizes differed indicating an insufficient sample.

Obviously, this one example is very limited in scope; however, it does support the use of cumulative diversity indices in estimating sample size and perhaps will stimulate further investigation.

Table 1.--Diet comparisons between 80 threespine stickleback (group C) and two groups of sockeye fry (A and B) using Kendall's tau coefficient of rank correlation and nonparametric multivariate analysis. Comparisons were based on the percent weight of prey in the diets. (W = Student's t.)

	A versus C		B versus C	
No. fish (A&B)	Rank Correlation τ	Multivariate Analysis W	Rank Correlation τ	Multivariate Analysis W
10	1.41^{ns}	-10.46†	0.85^{ns}	-7.82†
20	1.57^{ns}	-1.54^{ns}	0.00	-5.44†
30	1.10^{ns}	-3.11*	0.35^{ns}	-8.39†
40	1.10^{ns}	-4.95†	0.28^{ns}	-13.26†

^{ns} nonsignificant at $\alpha = 0.05$; * significant at $\alpha = 0.01$;
† significant at $\alpha = 0.001$

Considerations for using the cumulative diversity method

In conclusion I would like to mention some practical considerations for using this method. A notable disadvantage is the extensive time required if many calculations are done manually. In addition each estimate of sample size should be based on several random poolings of the same stomachs. If the diet contains various-sized prey, the diversity index for a group of fish feeding mainly on a few large prey can be greatly influenced by a single fish feeding on many small prey. An approach suggested by Wilhm (1968) of using biomass to estimate diversity might be preferable to numbers. Another difficulty is the subjective method of selecting t on the graph. Pielou (1975) suggests checking for serial correlation in the h_k's past t to determine whether a sufficiently large t has been chosen. Also, confidence intervals on each estimate of H' should overlap considerably if enough points beyond t have been calculated.

The advantages of using this method are clear. In addition to providing a means of estimating H', it also provides a method of estimating sample size based on both the number of species and their proportions in the diet. Its real value, however, will be established by how accurately it describes adequate sample size in future investigations.

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Statistics of Selectivity

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Abstract

No statistical significance can be attached to values of most traditional indices of selectivity (e.g. forage ratio, (p_1/p_2); Ivlev index of electivity, $(P_1-p_2)/(p_1+p_2)$; where p_1 = proportion of prey taxon in diet of fish and p_2 = proportion of prey taxon in environment). The natural log, L, of the odds ratio $(O = p_1(1-p_2)/p_2(1-p_1))$ has several desirable properties as an index of selectivity. A standard error can be calculated for L, enabling tests of statistical significance to be applied (e.g. is the degree of selection significantly different from zero). L varies symmetrically from $-\infty$ to 0 in the case of negative selection and from 0 to $+\infty$ in the case of positive selection. The calculation of the statistic is simple and easily understood, and no information is lost as in rank correlation methods.

Introduction

Feeding selectivity is an important component in studies of community trophic structure. Comparison of food of fish with the fauna present in the same time and place is often required in studies of optimal foraging (Pyke et al, 1977). A quantitative approach is often desirable for comparisons of feeding selectivity between size groups or species of animals. Indices of selectivity can be used to provide a basis for quantitative description and comparison of food habits.

In this paper I have explored the desirable properties of an index of selectivity and have briefly reviewed the properties of two traditional indices of selectivity; the forage ratio (Allen, 1941; Hess and Schwartz, 1940), and the Ivlev index of electivity (Ivlev, 1961). Finally, the log of the odds ratio is proposed as a preferable statistical index.

Desirable Properties of An Index of Selectivity

The index of selectivity reflects the degree of difference between composition of fish diet and composition of the surrounding fauna. A prey taxon can be defined as positively selected when its relative abundance among items consumed is greater than its relative abundance in the environment. Conversely, a taxon can be defined as negatively selected when its relative abundance in the environment is greater than its relative abundance in the diet. The assumption is made that all taxa in the environment have been accurately sampled and are equally available to the fish; and that all prey items can be identified and are digested at the same rate. Otherwise, it would be necessary to make appropriate modifications in the counts of prey and available animals.

An index of selectivity should be easy to interpret. The distribution of potential values of an index should be symmetrical and consistent. If relative proportions of prey within the stomach and the environment are reversed, the index should take on the same value, but with the sign of the value reversed. It is difficult to interpret an index which takes on values from 0 to 1, in the case of negative selection and values from 1 to +∞, in the case of positive selection. An index which ranges from -1 to 0 for negative selection and 0 to +1 for positive selection is preferable.

Observed differences between the compositions of fish diet and the compositions of co-occurring fauna should be capable of being tested for statistical significance. The questions may be asked: are relative proportions of a prey taxon in the diet and the environment statistically equal given the size of the samples; i.e. is a prey taxon consumed selectively or non-selectively? Furthermore, is the level of selection encountered by one prey taxon statistically equivalent to that encountered by another and is random variation alone the source of the difference? It would appear that the index of selectivity should be compatible with statistical hypothesis testing procedures.

It is important that the appropriate index be used with respect to the questions addressed by a study. Inadequate data may restrict the use of some indices. Non-parametric tests of association, such as the Spearman coefficient of rank correlation, may be applied to determine if the degree of relationship between prey taxon rank in diet and environment is significant. Broad questions of feeding selectivity, such as whether selective feeding is a seasonal phenomenon for a species (Neill, 1938), can be answered by using rank correlation tests. Non-parametric tests are statistically more robust; assumptions underlying these tests are generally simple. This approach may be valuable when samples are nonrandom. However, when sampling schemes are believed adequate and data are detailed, the loss of information inherent in the use of a non-parametric test makes the latter undesirable.

The Forage Ratio

The forage ratio developed by Allen (1941) and by Hess and Schwartz (1940) relates percentage of the diet contributed by a prey taxon to its percentage of the co-occurring fauna:

$$FR = \frac{p_1}{p_2}$$

where p_1 = percentage of diet comprised by a given prey taxon

p_2 = percentage of food complex in the environment comprised by the given taxon

An example is shown in Table 1. The statistic ranges from 0 to 1 for negative selection (lines a,b, and d) and from 1 to $+\infty$ for positive selection (line c). No tests of statistical significance are available to insure that differences from 1 are not due to random variation.

Table 1. A comparison of the forage ratio (FR), Ivlev index of electivity (E) and log of the odds ratio (L) using as an example varying levels of a prey taxon in the diet (p_1) and in environment (p_2).

	p_1	p_2	FR	E	L
a)	.45	.60	.75	-.14	-.61
b)	.30	.40	.75	-.14	-.44
c)	.45	.30	1.50	.20	.65
d)	.30	.45	.66	-.20	-.65

where p_1 = percentage of diet comprised by a given prey taxon

p_2 = percentage of food complex in the environment comprised by the given taxon

The Ivlev Index of Electivity

The index of electivity, developed by Ivlev (1961) is as follows:

$$E = \frac{p_1 - p_2}{p_1 + p_2}$$

where p_1 = percentage of diet comprised by a given prey taxon

p_2 = percentage of food complex in environment comprised by the given taxon

The index was designed to replace forage ratio-type indices. E has a symmetrical distribution around a mean of 0, ranging from 0 to -1, in the case of negative selection; and from 0 to +1, in the case of positive selection, which makes values easy to interpret and compare (Table 1, lines c and d). No tests of statistical significance of differences are available.

The Odds Ratio and its Log

Jacobs (1974) described a modification of the forage ratio which is identical to the odds ratio advanced by Fleiss (1973), which is:

$$O = \frac{p_1 q_2}{p_2 q_1}$$

where p_1 = percentage of diet comprised by a given prey taxon

q_1 = percentage of diet comprised by all other prey taxa

p_2 = percentage of food complex in environment comprised by the given taxon

q_2 = percentage of food complex in environment comprised by all other taxa

Jacobs apparently overlooked several important properties of this index and its natural log, L. L is symmetrically distributed about a mean of 0 and ranges from 0 to $+\infty$, in the case of positive selection and 0 to $-\infty$

in the case of negative selection. According to Fleiss (1973), a standard error of L can be computed:

$$S.\ E.\ (L) = \sqrt{\frac{1}{n_1 p_1 q_1} + \frac{1}{n_2 p_2 q_2}}$$

where n_1 = total number of prey in diet sample

n_2 = total number of food organisms in environmental sample

p_1, q_1, p_2 and q_2 as previously defined.

Since L has a lognormal distribution, the null hypothesis that an observed L is not significantly different from 0 (prey is consumed nonselectively) can be tested as follows: The difference is expressed in terms of standard normal deviates:

$$z = \frac{L_{observed} - L_{expected}}{S.\ E.\ (L)}$$

where $L_{expected}$ = 0 in this case. The value can then be compared to values found in a table of areas of the normal curve (z distribution) to determine the probability of obtaining such a difference. The log of the odds ratio has another property not found in the forage ratio or the Ivlev index. Where ratios of p_1 to p_2 are the same, the larger the absolute difference between p_1 and p_2, the greater the absolute value of L. Compare lines a and b of Table 1.

Summary

The log of the odds ratio meets all the criteria for a desirable index of selectivity. It is superior to traditional indices of selectivity not only because of its ease of interpretation and comparison but also because it is easy to derive and calculate. The odds ratio also reflects the absolute differences between percentage composition in diet and environment for prey where the ratios of these percentages are equal. The significance of results can be tested statistically if accurate unbiased samples can be obtained. This is often difficult in the case of typical benthic prey organisms which are patchily distributed. Thus, assumptions and qualifications should be clearly stated before the index is applied.

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Comparison of Food Array Overlap Measures Useful in Fish Feeding Habit Analysis

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Introduction

In many studies involving the feeding habits of fishes, data are gathered which lead the investigator to ask whether the diets of two species differ, how much they may differ and whether the apparent differences are statistically significant. Similar questions are also asked for locations, times, sexes, sizes or ages of fish. A variety of overlap or similarity measures have been developed and applied to fish feeding habit studies. The simplest overlap measures rely upon the presence or absence of species (Southwood, 1966) and were originally used to compare morphological characters for taxonomic purposes (Sokal and Sneath, 1963). Although this kind of measure has been applied to ecological studies (Odum, 1971), relative abundances of species are not considered and inaccurate and often misleading values can result. Other measures consider the relative values of paired variables and are thus more responsive to differences in species abundances or proportions (Horn, 1966; Odum, 1971; Pielou, 1972; Goodall, 1973; Boesch, 1977; and Hurlbert, 1978). One disadvantage of this kind of measure is that there are no universally accepted significance levels for the similarity values. An additional approach has been to use correlation coefficients to measure overlap (Goodall, 1973; Hurlbert, 1978), and in fact, rank correlation coefficients have been specifically applied to fish feeding habit studies (Fritz, 1974). This approach does allow tests of significance of correlation coefficients between two arrays of species. None of the measures mentioned take into account the variability in species composition among individual samples. As Horn (1966) noted: "Indices...are only appropriate in situations in which there is implicit confidence that the proportions of items in each category are adequately characterized." It is assumed here that this requirement is satisfied.

Even though many overlap measures have been proposed, few studies have empirically compared how the various indices behave with known arrays. In his recent review, Hurlbert (1978) evaluated several overlap measures by using various predetermined assemblages. However, the number of species used in each assemblage was only five, a number which to many investigators of fish feeding would seem very low. It is not uncommon in such studies to find individual fish containing as many as thirty different kinds of prey items. In additon, Hurlbert (1978) did not evaluate differing levels of species presence/absence overlap, nor assess how the various measures behaved when calculated for two assemblages with unequal numbers of species, a condition which is also very common in fish feeding studies.

The objective of this paper is to evaluate measures that compare two arrays of species, each with some sort of importance value, such as percent by number or volume, frequency of occurrence, or IRI value (see Pinkas, et al., 1971) or that measure the amount of correlation between two arrays. In all cases, the species will represent prey and the array will represent all the prey consumed by a predator population. Hypothetical prey arrays will be created so that the selected overlap measures can be calculated for various combinations of predators. These measures will be compared to determine how each behaves in relation to prey species richness (number of species) and evenness (distribution of species abundances within a prey array), amount of presence/absence overlap between prey arrays, and in comparing predators which feed on unequal numbers of prey species. It is hoped that these results will aid other investigators in deciding which overlap measures to use and in interpreting their values as they relate to various characteristics of a predator's prey array and levels of overlap.

Materials and Methods

Hypothetical prey arrays were chosen to represent three general kinds of fish predators: specialized (six prey types), intermediate (thirty prey types) and generalized (sixty prey types) (Figure 1). These values were chosen to reflect observed prey diversities in fishes (Cailliet, 1976). In addition, each kind of predator was made to exhibit both low and high evenness of relative abundances among prey types (Figure 1). In order to closely approximate and cover the range of observed patterns of distribution of prey frequency, prey arrays were arbitrarily categorized and arranged as (1) even (evenly distributed prey abundances) and (2) uneven (including normal distributions and those skewed to the right and to the left) (Figure 1). The actual prey abundance values were expressed as numerical proportions (P_i) and were arbitrarily chosen to fit the distributional patterns described in Figure 1 as accurately as possible (Table 1). With the exception of one array of normally distributed prey species, all prey were arranged by rank, with the more abundant species either at the right or left extreme (Figure 1).

Pairs of prey arrays were selected to represent the range of possible combinations and to evaluate the effect of prey species richness and evenness, the amount of overlap and the inequality of prey diversity on the overlap measures chosen. Prey comparisons have been divided into those which measure overlap between predators with equal numbers of prey species, and those which have unequal numbers of prey species (see Figures 2 and 3). In the equal prey comparisons, species overlaps were arbitrarily set at 100, 66 and 33 percent. For example, in

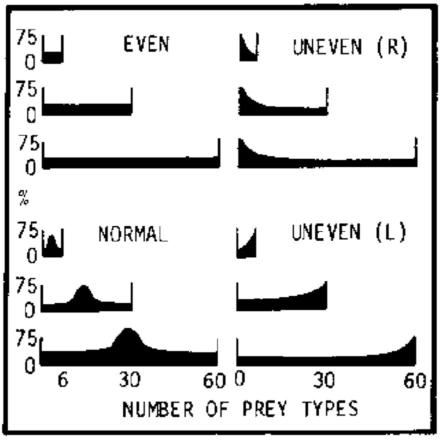

Figure 1: Diagrams of four patterns of prey frequency distributions for the three levels of diversity.

TABLE 1: PATTERN OF DISTRIBUTION OF PREY TYPE FREQUENCIES AMONG PREDATOR CATEGORIES

Prey (Pi) Values	High Diversity Even	High Diversity Uneven	Intermediate Even	Intermediate Uneven	Low Diversity Even	Low Diversity Uneven
0.70						1
0.50				1		
0.40		1				
0.18					1	
0.17					2	
0.16					3	
0.10		1				1
0.08						1
0.06						1
0.05		2	4	4		
0.04			10			1
0.03			10			
0.025	1					
0.023	4					
0.021	6		4			
0.020	6	3		6		1
0.019	4					
0.017	20					
0.016		9				
0.015	4			6		
0.014		4				
0.013	7					
0.012	4	6				
0.010	2	3	2	5		
0.005				8		
0.002		7				
0.001	2	24				
Total	60	60	30	30	6	6

Note: The normal distribution has the same prey pi values as the uneven, but they are arranged symmetrically.

the 33 percent overlap comparison between specialized predators, only two prey species are common to both predators. In addition, pairs of prey arrays were divided into those that compared even with even (A), uneven with uneven (B) and even with uneven distributions. In the latter category, the uneven distribution was skewed to the right (C) or to the left (D) (Figure 2). Uneven distributions can assume a variety of shapes. To test whether a non-skewed distribution with the same P_i value would affect the measures, we made three comparisons between normal distributions and those skewed to the right (see Figure 1 and Table 2). In the unequal prey comparisons, all prey species of the predator with the lowest diversity overlapped entirely with the prey array of the other. Thus, the presence/absence overlap varied only with the amount of difference between paired prey arrays. The same kinds of comparisons with differing skewness were made (Figure 3).

Five overlap measures were chosen for comparison, based on their frequency in the literature and their potential applicability to fish feeding habit studies. The first measure, presented and utilized by many investigators, including Sanders (1960), Odum (1971), Frame (1974) and McEachren, et al., (1976), is the percent similarity index (PSI), which is calculated by summing the smallest percent by number of each species pair between both predators. The second measure (R_0) was proposed by Horn (1966) and is based upon the Shannon-Wiener information function. It has been used by various authors, including Kohn (1968, 1971 and Kohn and Nybakken (1975). A third measure (C_λ), was proposed by Morisita (1959) and presented in detail by Horn (1966). It is based on Simpson's diversity index and has been applied to fish

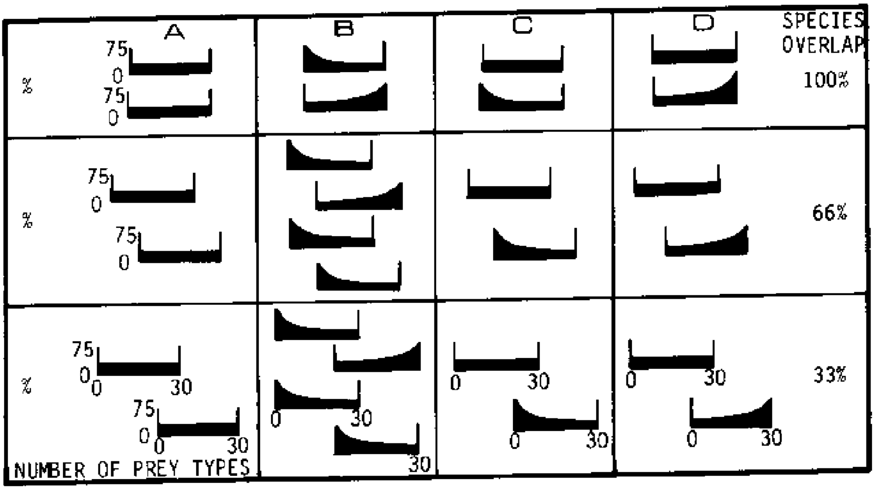

Figure 2: Diagrams of four categories of equal prey comparisons (A: even versus even; B: uneven versus uneven; C: even versus uneven, right skew; and D: even versus uneven, left skew) for three levels of presence/absence overlap (100%, 66% and 33%). See Table 2 for additional details.

feeding studies by Zaret and Rand (1971), Pearcy and Ambler (1974) and Bray and Ebeling (1975). The fourth overlap measure is the competition coefficient (O_{xy}), presented first by Levins (1968) and later discussed by Hurlbert (1978). The version used here is the combined equation presented by Hurlbert (1978). Finally, the fifth measure is a similarity index based on Euclidean distance ($S_{ij} = 1 - D_{ij}$), as presented by Boesch (1977), and was used by Sale and Dybdahl (1975) in their study of feeding in coral reef fishes.

Three correlation measures were also calculated. The first is the product-moment correlation coefficient (C_p), which is discussed by Goodall (1973) and Hurlbert (1978). The second one is Kendall's rank correlation coefficient (τ = tau), which is presented in Sokal and Rohlf (1969) and Siegel (1956) and has been used in feeding studies of birds (Baker and Baker, 1973) and fishes (Bray and Ebeling, 1975). Finally, the third measure is Spearman's rank correlation coefficient (r_s), which is also presented in Siegel (1956) and has been applied to fish feeding by Fritz (1974). In both rank correlation calculations, the equations used were those that corrected for ties.

The choice of these five overlap measures and three correlation coefficients does not imply that these are the best indices available. They have arbitrarily been chosen for this evaluation of overlap measures. Other measures may, indeed, perform better than any of these (see Hurlbert, 1978); however, one should evaluate the most commonly used measures before attempting a more comprehensive assessment.

Since these eight measures were calculated for each of the 66 comparisons of prey arrays and resulted in 528 values, it was decided to present the data in three forms, each useful to the reader in different ways. First, the actual values were presented in tabular form (Table 1). One can compare these values to particular prey array comparisons with similar richness, evenness, skewness and amount of overlap. Also, one can look for trends in these data in addition to those discussed here. Finally, using the standard levels of significance for the three correlation measures, (Siegel, [1956]; Sokal and Rohlf, [1969]), one can see which comparisons resulted in positively (* or **), negatively [(*) or (**)] or non-significant (ns) correlations (see Tables 2 and 3).

The second way that the results were presented was to calculate the mean values for each of the five overlap measures in each of the comparisons that had positively, negatively or non-significant product-moment correlation coefficients (see Table 4). Here, it is not implied that it is statistically correct to apply this test of significance to these data; rather, significance levels were merely used to organize comparisons so that the behavior of the overlap measures might be more easily understood.

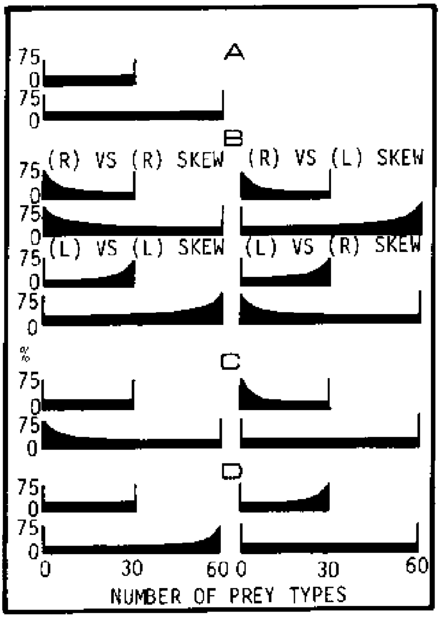

Figure 3: The four categories of unequal prey comparisons using the 30 and 60 prey arrays as examples. See Figure 2 and Table 3 for additional details.

Finally, the third way of presenting results was to plot values of three of the overlap measures against two variables which were thought to influence their behavior (see Figure 4). First, values for PSI, C_λ and S_{ij} were plotted, using the equal prey array comparisons only, against the number of prey species involved in a comparison. The decision to use only these three indices was based on space limitations and upon the observation that two pairs of indices appeared to behave similarly, and in some cases, identically. That is, PSI values were often similar to R_0 values, and C_λ values were similar or identical to O_{xy} (see Table 2). Second, values of these three indices were plotted against the percent overlap to determine whether they responded to this independent and arbitrarily set measure of similarity. The same reasoning regarding selection of those indices applies here.

Results and Discussion

Overlap Measures

Equal Prey. As the degree of overlap decreased from 100 to 33 percent, all five indices exhibited the same trend (Table 2, Figure 4). Four of the indices (PSI, R_o, C_λ and O_{xy}) dropped strongly with decreased overlap, while one (S_{ij}) decreased only slightly. This trend is expected, since the values should drop as overlap is lowered. In the even versus even comparisons, all measures were more responsive to, and had higher values with increased overlap, than in any of the other uneven comparisons (Figure 4).

Prey diversity influenced the overlap values as well, and as before, one index (S_{ij}) behaved differently than the others. As richness increased (more species per comparison), S_{ij} increased markedly, while the others decreased slightly (Table 2, Figure 4). This index (S_{ij}) therefore appears to be more sensitive to rare species and was consistently higher when many species were included than the other four indices. Also, for comparisons in which the diversity (richness and evenness) were identical regardless of overlap level, both C_λ and O_{xy} behaved identically. When diversities differed (i.e., even versus uneven distributions), these two indices differed slightly.

Prey distribution (skew) appeared to be an important factor, especially in comparisons with high overlap. As would be expected, uneven versus uneven comparisons (left versus right skew, Figure 2-B) yielded the lowest values for each of the indices in nearly all of the test cases when compared to the other categories of comparison (even versus even and even versus uneven, Figures 2-A, C, D, Table 2). PSI and R_o were less sensitive to skew than C_λ and O_{xy}. Uneven versus uneven comparisons showed PSI and R_o to have consistently higher values than C_λ and O_{xy}, while in even versus even comparisons, all four indices were similar. So, PSI and R_o appeared to respond to both rare and dominant species, while C_λ and O_{xy} tended to emphasize dominant species. Again, S_{ij} behaved differently than the others and was strongly influenced by the rarer species since, for similar overlaps and skew in comparisons it became larger as the number of species increased. However, the effect of skew was difficult to discern, due to the influences of percent overlap and prey richness. The normal distribution of prey behaved much in the same way as either the right or left skewed distributions (Table 2). For all indices, the normal versus right skew comparisons yielded roughly the same values as for the right versus left skew comparisons.

Unequal Prey. For each measure, the values tended to decrease moderately as overlap decreased, but not in all comparisons (Table 3). The variation in these values, however, cannot be attributed to overlap alone, since species richness varied with overlap. In unequal prey comparisons, species richness and percent overlap vary simultaneously. The low diversity prey is always overlapped entirely by the richer

TABLE 2: COMPARISON OF OVERLAP MEASURES AND CORRELATION COEFFICIENTS: EQUAL PREY

	---------Overlap Measures---------						--------Correlation Coefficients--------					
	n	PSI	R_o	C_λ	O_{xy}	S_{ij}	C_p		τ		r_s	
A. Even vs Even												
1. 66% overlap												
a. 6 vs 6	8	0.650	0.665	0.662	0.662	0.664	-0.343	ns	-0.043	ns	0.192	ns
b. 30 vs 30	40	0.560	0.653	0.625	0.625	0.834	-0.169	ns	0.051	ns	-2.754	(**)
c. 60 vs 60	80	0.580	0.651	0.631	0.631	0.885	-0.229	ns	0.112	ns	-6.957	(**)
2. 33% overlap												
a. 6 vs 6	10	0.320	0.334	0.335	0.335	0.529	-0.657	ns	-0.371	ns	-0.308	ns
b. 30 vs 30	50	0.220	0.299	0.272	0.272	0.768	-0.595	(**)	-0.288	(**)	-5.622	(**)
c. 60 vs 60	100	0.238	0.302	0.285	0.285	0.840	-0.624	(**)	-0.230	(**)	-12.369	(**)
B. Uneven vs Uneven												
1. 100% overlap												
a. 6R vs 6L	6	0.240	0.391	0.089	0.089	0.034	-0.351	ns	-1.000	(**)	0.000	ns
b. 30R vs 30L	30	0.240	0.382	0.039	0.039	0.287	-0.100	ns	-1.000	(**)	-3.866	(**)
c. 60R vs 60L	60	0.072	0.185	0.011	0.011	0.403	-0.089	ns	-1.000	(**)	-8.633	(**)
d. 6N vs 6R	6	0.280	0.466	0.145	0.145	0.064	-0.268	ns	-0.200	ns	0.371	ns
e. 30N vs 30R	30	0.305	0.463	0.067	0.067	0.297	-0.068	ns	0.163	ns	-1.424	(**)
f. 60N vs 60R	60	0.214	0.321	0.028	0.028	0.407	-0.071	ns	0.053	ns	-4.548	(**)
2. 66% overlap												
a. 6R vs 6L	8	0.120	0.169	0.016	0.016	-0.004	-0.302	ns	-1.000	(**)	-0.325	ns
b. 30R vs 30L	40	0.120	0.169	0.006	0.006	0.276	-0.098	ns	-1.000	(**)	-5.570	(**)
c. 60R vs 60L	80	0.040	0.072	-0.001	0.001	0.400	-0.073	ns	-1.000	(**)	-11.978	(**)
d. 6R vs 6R	8	0.200	0.350	0.130	0.130	0.056	-0.151	ns	0.111	ns	0.221	ns
e. 30R vs 30R	40	0.200	0.325	0.057	0.057	0.294	-0.041	ns	0.092	ns	-2.905	(**)
f. 60R vs 60R	80	0.140	0.258	0.048	0.048	0.414	-0.023	ns	0.080	ns	-7.105	(**)
3. 33% overlap												
a. 6R vs 6L	10	0.040	0.055	0.003	0.003	-0.010	-0.239	ns	-1.000	(**)	-0.613	(*)
b. 30R vs 30L	50	0.050	0.058	0.001	0.001	0.273	-0.080	ns	-1.000	(**)	-7.019	(**)
c. 60R vs 60L	100	0.020	0.020	0.000	0.000	0.399	-0.059	ns	-1.000	(**)	-14.884	(**)
d. 6R vs 6R	10	0.060	0.151	0.059	0.059	0.018	-0.170	ns	-0.231	ns	-0.344	ns
e. 30R vs 30R	50	0.060	0.136	0.026	0.026	0.282	-0.054	ns	-0.249	(*)	-5.707	(**)
f. 60R vs 60R	100	0.020	0.060	0.005	0.005	0.401	-0.054	ns	-0.260	(**)	-12.242	(**)
C. Even vs Uneven: Right Skew												
1. 100% overlap												
a. 6E vs 6U	6	0.480	0.774	0.518	0.601	0.428	0.851	*	0.856	ns	0.964	*
b. 30E vs 30U	30	0.540	0.764	0.297	0.454	0.540	0.403	ns	0.959	**	0.814	**
c. 60E vs 60U	60	0.494	0.683	0.224	0.391	0.608	0.395	**	1.033	**	0.617	**
2. 66% overlap												
a. 6E vs 6UR	8	0.410	0.638	0.464	0.538	0.379	0.254	ns	0.040	ns	0.238	ns
b. 30E vs 30UR	40	0.430	0.568	0.224	0.342	0.517	0.165	ns	0.124	ns	-2.726	(**)
c. 60E vs 60UR	80	0.441	0.561	0.172	0.301	0.505	0.153	ns	0.166	ns	-6.940	(**)
3. 33% overlap												
a. 6E vs 6UR	10	0.260	0.423	0.377	0.483	0.350	0.169	ns	-0.244	ns	-0.281	ns
b. 30E vs 30UR	50	0.220	0.315	0.147	0.224	0.493	0.033	ns	-0.232	(*)	-5.561	(**)
c. 60E vs 60UR	100	0.238	0.239	0.128	0.224	0.584	0.095	ns	-0.223	(**)	-12.306	(**)
D. Even vs Uneven: Left Skew												
1. 66% overlap												
a. 6E vs 6UL	8	0.200	0.321	0.095	0.110	0.216	-0.728	(*)	-0.843	(*)	-0.300	ns
b. 30E vs 30UL	40	0.185	0.283	0.023	0.050	0.460	-0.378	(*)	-0.811	(**)	-5.507	(**)
c. 60E vs 60UL	80	0.114	0.181	0.015	0.027	0.558	-0.366	(**)	-0.827	(**)	-12.181	(**)
2. 33% overlap												
a. 6E vs 6UL	10	0.060	0.117	0.028	0.033	0.188	-0.544	ns	-0.677	(*)	-0.588	ns
b. 30E vs 30UL	50	0.060	0.098	0.008	0.012	0.453	-0.293	ns	-0.676	(**)	-6.998	(**)
c. 60E vs 60UL	100	0.020	0.049	0.002	0.004	0.555	-0.266	(*)	-0.596	(**)	-14.964	(**)

Note: Legend is at the end of Table 3.

prey; however, the converse is not true. For example, the 30 versus 60 prey comparison yields 100 percent overlap of 30 by 60, but only 50 percent overlap of 60 by 30. Thus, the effects of species richness

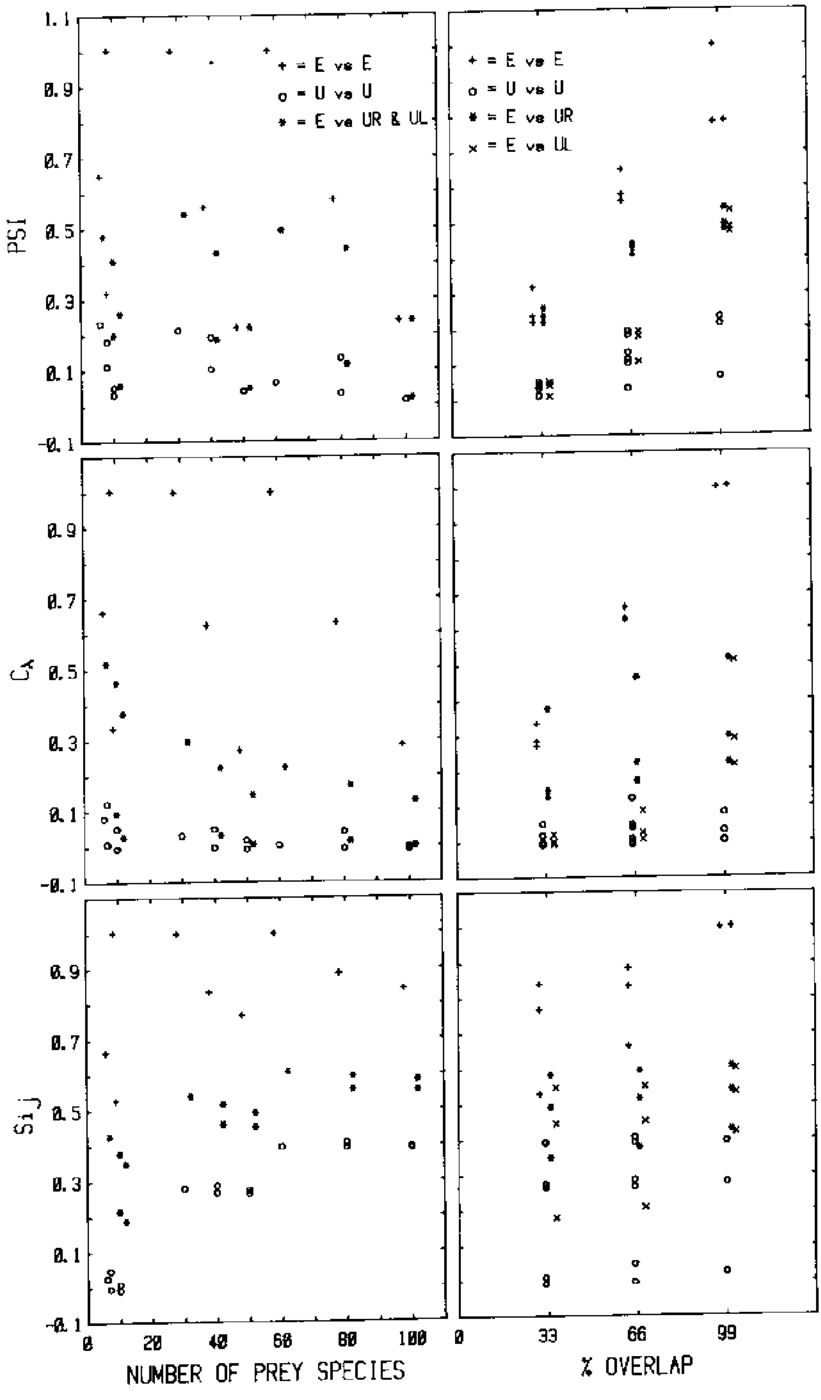

FIGURE 4: Values of 3 overlap measures against percent overlap.

and overlap can be difficult to separate.

Prey distribution (skew) did, however, have a discernible effect, with right versus right skew comparisons producing higher overlap values than left versus right or right versus left (Table 3). The left versus left skew comparisons produced similar overlap values as the right versus left with all measures. Four of these measures behaved quite similarly in this manner, while one (S_{ij}) exhibited a more narrow range of values.

TABLE 3: COMPARISON OF OVERLAP MEASURES AND CORRELATION COEFFICIENTS: UNEQUAL PREY

	---------Overlap Measures---------						--------Correlation Coefficients--------					
	n	PSI	R_o	C_λ	O_{xy}	S_{ij}	C_p		τ		r_s	
A. Even vs Even												
a. 30 vs 60	60	0.578	0.748	0.745	0.794	0.882	0.752	**	1.105	**	0.391	**
b. 6 vs 30	30	0.280	0.485	0.459	0.597	0.668	0.626	**	1.464	**	0.051	ns
c. 6 vs 60	60	0.138	0.303	0.249	0.422	0.627	0.473	**	2.118	**	-2.208	(**)
B. Uneven vs Uneven												
Right vs Right Skew												
a. 30 vs 60	60	0.850	0.959	0.969	0.987	0.882	0.987	**	1.057	**	0.786	**
b. 6 vs 30	30	0.710	0.839	0.939	0.990	0.782	0.995	**	1.507	**	0.139	ns
c. 6 vs 60	60	0.640	0.785	0.861	0.981	0.690	0.988	**	2.039	**	-2.100	(**)
Left vs Right Skew												
a. 30 vs 60	60	0.295	0.429	0.045	0.046	0.348	-0.033	ns	0.562	**	-0.509	(**)
b. 6 vs 30	30	0.230	0.358	0.098	0.103	0.163	0.014	ns	1.432	**	0.078	ns
c. 6 vs 60	60	0.200	0.340	0.101	0.115	0.211	0.064	ns	2.001	**	-2.121	(**)
Right vs Left Skew												
a. 30 vs 60	60	0.036	0.087	0.005	0.005	0.334	-0.078	ns	-1.057	(**)	-8.461	(**)
b. 6 vs 30	30	0.030	0.083	0.013	0.014	0.125	-0.085	ns	-1.507	(**)	-3.195	(**)
c. 6 vs 60	60	0.006	0.023	0.003	0.003	0.169	-0.055	ns	-2.039	(**)	-6.577	(**)
Left vs Left Skew												
a. 30 vs 60	60	0.036	0.097	0.008	0.008	0.336	-0.074	ns	-0.848	(**)	-7.812	(**)
b. 6 vs 30	30	0.030	0.083	0.013	0.014	0.125	-0.085	ns	-1.507	(**)	-3.195	(**)
c. 6 vs 60	60	0.006	0.023	0.003	0.003	0.169	-0.055	ns	-2.039	(**)	-6.577	(**)
C. Even vs Uneven: Right Skew												
a. Low Diversity Even												
1. 30E vs 60UR	60	0.564	0.801	0.386	0.515	0.635	0.440	**	1.069	**	0.775	**
2. 6E vs 30UR	30	0.400	0.665	0.585	0.601	0.577	0.528	**	1.526	**	0.132	ns
3. 6E vs 60UR	60	0.420	0.646	0.644	0.645	0.648	0.607	**	2.051	**	-2.102	(**)
b. High Diversity Even												
1. 30UR vs 60E	60	0.417	0.565	0.163	0.335	0.514	0.368	*	1.092	**	0.454	**
2. 6UR vs 30E	30	0.260	0.386	0.180	0.360	0.329	0.394	ns	1.445	**	0.063	ns
3. 6UR vs 60E	60	0.137	0.246	0.097	0.255	0.306	0.315	*	2.106	**	-2.206	(**)
D. Even vs Uneven: Left Skew												
a. Low Diversity Even												
1. 30E vs 60UL	60	0.360	0.107	0.010	0.013	0.536	-0.271	ns	-1.069	(**)	-8.502	(**)
2. 6E vs 30UL	30	0.030	0.098	0.023	0.024	0.351	-0.161	ns	-1.526	(**)	-3.198	(**)
3. 6E vs 60UL	60	0.006	0.026	0.006	0.006	0.412	-0.100	ns	-2.051	(**)	-6.578	(**)
b. High Diversity Even												
1. 30UL vs 60E	60	0.371	0.524	0.126	0.258	0.503	0.061	ns	0.633	**	-1.118	(**)
2. 6UL vs 30E	30	0.240	0.365	0.153	0.306	0.318	0.213	ns	1.375	**	-0.031	ns
3. 6UL vs 60E	60	0.133	0.238	0.082	0.226	0.302	0.204	ns	2.080	**	-2.226	(**)

Symbols: Distribution of prey: L = left skew; R = right skew; N = normal; E = even; U = uneven.

Significance levels: * = $P < 0.05$; ** = $P < .01$; ns = not significant; () = significance is for a negative correlation.

The important factor in unequal prey comparisons is the positioning of the overlap with respect to the dominant species (if any) of one or both prey arrays. If high ranks of both arrays are overlapped, high values will result (right versus right skew). If prey array overlap includes the dominant prey species of only one predator, the results will depend on the characteristics of the overlapping portion of the opposing prey array. For this array, the higher the relative importance of the overlapped prey, the higher the values of the indices. Thus, in our examples, the left skew, even and right skew distributions will result in the low, medium, and high values, respectively (see Table 3-B, right versus left; C, right skew, high diversity predator even (b); B, right versus right skew).

Correlation analyses of both equal and unequal prey comparisons indicated that all overlap indices were significantly positively correlated ($p < .001$), despite the differences noted above.

Correlation Coefficients

Equal Prey. In general, the conclusions from all three correlation coefficients and their significance levels agreed (Table 2). The conclusions from Spearman's (r_s) and Kendall's (tau) were the same in all cases but one (six even versus six uneven). Even in this case, however, the actual correlation coefficients were close. Also, the conclusions of the product-moment correlation coefficient (C_p) agreed in all but two cases with Kendall's and in all but one case with Spearman's coefficient. When these three approaches disagreed, the differences were most likely due to the small sample sizes involved.

In many comparisons, both Kendall's and Spearman's rank correlation coefficients were considerably larger or smaller than the normally prescribed range of -1.0 to +1.0 for correlation coefficients (Tables 2 and 3). Some prey arrays devised for this study contained high frequencies of tied ranks, particularly in those with high diversities and even distributions (Table 1). Comparisons between these arrays or between those in which there was a large discrepancy in the number of prey (i.e., six versus sixty) resulted in many tied ranks and both equations used, even when corrected for ties, are highly sensitive to numerous tied ranks. Close inspection of each equation (Siegel, 1956; Sokal and Rohlf, 1969) reveals that, as the number of ties at one rank approaches N (the total number of ranks), the denominator approaches zero. Thus, in cases where there are numerous species and hence a large number of ties, or where there was very low overlap and hence a large number of tied zero values, neither Kendall's nor Spearman's rank correlation coefficient is appropriate.

Unequal Prey. Here, the problems noted for the rank correlation techniques for equal prey are even more noticeable (Table 3) and disagreements among all three correlation coefficients were more numerous. The conclusions of Kendall's and Spearman's correlation coefficients disagreed in 14 of 27 comparisons, while those of the product-moment and either of the non-parametric measures disagreed only 7 out of 27 times (Table 3). Again, the effect of numerous ties, primarily due to non-overlap and high richness and evenness, causes both non-parametric rank correlation measures to provide unreliable results. Therefore, one must be extremely careful when interpreting correlation coefficients under these comparative circumstances.

Comparison of Overlap Measures with Correlation Coefficient C_p

The mean overlap values generally decreased with level of significance of the product-moment correlation coefficients in the test comparisons (Table 4). However, there were differences in the range of their mean values which may indicate something about their sensitivity. Four indices (RSI, R_o, C_λ and O_{xy}) were similar to each other. S_{ij}, however, had a very narrow range in mean values and did not produce low values in the negatively correlated category. In fact, the mean S_{ij} value there was larger than that for the non-significant category. Thus, S_{ij} once again appears to respond differently than the other four overlap measures.

TABLE 4: MEANS AND STANDARD DEVIATIONS FOR EACH OF THE FIVE OVERLAP MEASURES CORRESPONDING TO SIGNIFICANCE LEVELS OF THE PRODUCT-MOMENT CORRELATION COEFFICIENT

Significance Level	N	PSI Mean	PSI S	R_o Mean	R_o S	C_λ Mean	C_λ S	O_{xy} Mean	O_{xy} S	S_{ij} Mean	S_{ij} S
** or *	13	0.4698	0.2081	0.6538	0.2075	0.5257	0.2967	0.6242	0.2502	0.6344	0.1627
ns	47	0.1944	0.1723	0.2856	0.2078	0.1212	0.1730	0.1501	0.1927	0.3415	0.2005
(**) or (*)	6	0.1628	0.0819	0.2392	0.1055	0.1170	0.1292	0.1247	0.1243	0.5662	0.2235

Significance levels are ** = $P < 0.01$, * = $P < 0.05$ (positive correlation); ns = not significant; (**) = $P < 0.01$, (*) = $P < 0.05$ (negative correlation). See Tables 2 and 3 for further details.

Summary

In general the overlap measures analyzed resulted in similar conclusions about the degree of overlap in the test cases created. However, there were differences among them. In many cases, these differences could be related to their sensitivity to species richness and evenness, the influence of dominant and rare species (prey distribution), the amount of overlap or the inequality of prey arrays.

Of the three correlation measures, the non-parametric rank correlation coefficients reacted quite unpredictably and could not appropriately handle comparisons in which there were large numbers of ties, considerable non-overlap, or high richness and evenness. The product-moment correlation coefficient, however, seemed to agree, in most cases, with the values of the five overlap measures.

It is hoped that these results will serve to aid others in choosing appropriate overlap measures and in interpreting their results.

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The Use of Discriminate Analysis in the Study of Fish Food Habits

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The methods commonly employed in stomach content analysis of fish rely either on the numerical occurrence of the food item or a volumetric or gravimetric measurement of the various food organisms. Allen (1935) listed the number of fish in which each food item occurred as a percentage of the total number of fish examined (frequency of occurrence). In another paper by the same author (Allen, 1938), the total number of individuals of each food group was listed and their occurrence expressed as the percentage of the total number of organisms found in all the fish. The purely numerical approach was somewhat modified into a semi-quantitative method by Swynnerton and Worthington (1940) and later by Frost (1943) by weighing the value given to each food item through consideration of the size of the food item and its volumetric displacement. Hynes (1950) used a method similar to frequency of occurrence where the number of fish in which each food item occurred (as the most abundant food item) is expressed as a percentage of the total number of fish examined. The type of data which results from the aforementioned methods has been used to calculate such factors as food preference of fish (Hess and Rainwater, 1939), forage ratio (Hess and Swartz, 1941), effective food grade (Surber, 1941), and electivity (Ivlev, 1961). These factors are intended to reflect the relationship between the feeding habits of a fish and the occurrence of prey species in the environment.

Expressing the results from stomach analysis in terms of numbers alone would be adequate if the following conditions were true: all the food items eaten by the fish were of the same weight, volumetric displacement and nutritional value; and the fish, regardless of difference in age or size class, fed on the exact same size and type of food item. What is needed is a method by which the food species found in a fish diet may be ranked according to their relative nutritional value. Such a method would involve the enumeration and quantification of the prey in the gut so that weight of the food items previous to the effects of digestion, the reconstructed weight, may be estimated (Ricker, 1937). This information would then be used to select the proper size and weight of food organisms from the environment to analyze for percent composition of digestible matter (Windell, 1966), caloric and nutritional value. Supplied with such information it would be possible to rate the food items accordingly. (It should be noted that, ideally, some estimate of the energetic cost to the fish of obtaining the various prey items would be very helpful. However, the present state of technology would seem to preclude this.)

After listing the diets for two or more samples of fish by the above method, there are a number of nonparametric statistical methods by which the diets may be compared for degree of overlap or tested for statistical difference (Chi-square) or similarity (Spearmens rank-corelation coefficient). One of the shortcomings of these statistical procedures is the disregard for the variability or consistency with which the prey items occur within and between the samples being compared. It is these factors of within and between sample variability which is addressed by the use of discriminate analysis.

The problem of how to handle the stomach content data from the occasional fish that has fed extensively on a previously minor prey item is also dealt with in this statistical technique. A simple listing of the prey by numerical occurrence would misleadingly place such a food organism in a prominent position. The factor of low frequency of occurrence is compensated for by the dependence of the discriminate function and the resulting _F_ score on the within sample variance.

I first used discriminate analysis (Nie et al, 1970) in comparing the summer and winter diets of the mountain whitefish, _Prosopium williamsoni_, and the summer diets of the mountain whitefish and Eastern brook trout, _Salvelinus fontinalis_, found in the Little Walker River, Mono County, California (Ellison, 1977). I found the mountain whitefish to have a less diverse diet (relative diversity = .61) than the brook trout (relative diversity = .77). This was to be expected as the whitefish feeds largely on benthic prey items, whereas the brook trout feeds on both benthic and terrestrial organisms in the drift. Although there was obvious overlap in the diets, discriminate analysis showed the diets (using reconstructed weight of prey) to be significantly different at the 99.99% level of confidence. The summer and winter diets of the whitefish were also found to be different (_F_ = 10.87, _df_ = 17 and 78) probably due to the seasonal shift in prey abundance.

Recently while investigating embiotocid energetics at King Harbor, Redondo Beach, California, (Ellison and Stephens, manuscript), I used discriminate analysis to compare the diets (using calorific equivalent of prey) of 5 species of surfperch found along the harbor breakwater. Two species pair, _Embiotoca jacksoni_ x _Hypsurus caryi_ and _Hypsurus caryi_ x _Phanerodon furcatus_, exhibited a high degree of spatial overlap in feeding individuals and amphipods figured prominently in the diets of all three species. Although a significant difference at the 95% level of confidence was demonstrated for the diets of _E. jacksoni_ and _P. furcatus_, no difference was found between the diets of these species and _H. caryi_, indicating that _H. caryi_ may be a dietary intermediate (Table 1).

The type of data used in the calculation of the discriminate function may be limited to the numerical occurrence of the prey items in the diet.

However, this statistical method and others are considerably "strengthened" by the use of reconstructed weight as in the case of the whitefish and brook trout or calorific equivalents (see Table 2) as with the surfperch. The use of these factors will more accurately reflect the contribution of the various prey to the diets of the fish.

One of the underlying assumptions in any statistical method that relies on the use of the mean and variance is that the variables being measured are normally distributed. Figure 1 typifies the distribution of prey found in the diets of whitefish, brook trout, and surfperch. A similar distribution of food items in fish stomachs has been found by Sibert and Obrebski (1976). As can be seen, prey items in fish stomachs do not follow a Gaussian distribution. It is interesting to note, however, that the basic analysis of variance (ANOVA) statistic is robust with respect to the assumption of normality in the underlying populations and its validity is affected only slightly even by great deviations from normality (Zar, 1974). The multivariate or discriminate analysis for all its complexities is based on the ANOVA technique and is probably valid even in light of the aforementioned distributions.

An interesting aspect of the SPSS subprogram for discriminate analysis is that the variables are entered into the analysis in a stepwise fashion so that each one is assessed as to its contribution to the discriminate function. Variables found to contribute very little to the analysis (basically those variables which occur with the lowest frequency) are omitted in the final calculations. It has been my experience that out of 40 variables submitted approximately 7 to 10 are used in the final analysis.

Another subtlety of the SPSS subprogram is that only two samples should be compared in any one run. Theoretically the capability to run three or more samples through the analysis exists; however, the strength of the analysis is compromised when this done. The variables chosen in the subprogram to discriminate between three or more samples are not the best to discriminate between any two samples.

For the convenience of those who wish to use this technique in fish diet analysis, I have shown a sample deck set up in Figure 2. For the most part the lines are self-explanatory, but the following may be helpful: Lines 1 to 3 and 19 to 21 are part of the "mechanics" of the computer system and will vary with the type of computer and program package used; in Line 7, RVA and EMB refer to <u>Rhacochilus</u> <u>vacca</u> and <u>Embiotoca</u> <u>jacksoni</u> respectively, and the numbers in parenthesis indicate the number of data card sets (individuals in the sample) for each species; Line 8 indicates to the computer how the data is to be read off the cards; in Lines 10 and 11 note that the variables used in the analysis are a function of the number of prey items in each category (N1, N2... Nn) and their respective calorific equivalent, reconstructed weight or volumetric displacement; for Lines 13 to 16 reference should be made to Nie, et al (1970); Line 18 is a sample data card for a female <u>R</u>. <u>vacca</u> caught on April 15 at station 2 whose standard length was 175 mm, with the rest of the numbers indicating the number of food items in specific prey categories.

The number of fish necessary to achieve an adequate sample size needs to be mentioned. It should be recognized that the adequacy of the size of the sample is a function of the manner in which the prey are distributed in the environment and the feeding strategy and trophic level of the fish (predator). For example E. jacksoni feeds in a relatively indiscriminate manner (grazing), and its prey exhibit a fine-grained (even) distribution. This results in the stomach contents from one full E. jacksoni being a more adequate representation of the total diet for that species than the contents of one full stomach of a Paralabrax clathratus which is at a higher trophic level, has fewer food items per full stomach, and feeds on larger, less frequently encountered prey. The number of full or near full individuals needed to achieve an adequate sample size for E. jacksoni is less than that needed for P. clathratus. For any given species of fish, or the same species collected at different life history stage or location, the number which must be taken to attain an adequate sample will vary. For microcarnivors like the surfperch which may have the remains of over a thousand prey in their stomachs, I consider ten full or mostly full individuals to be the minimum needed for an adequate sample.

Discriminate analysis is potentially a very powerful and convenient tool for biologists who are involved in comparing animal diets. Hopefully as this technique becomes more widely accepted and used, it will be subjected to the critical analysis of those biologists with more extensive statistical backgrounds. Combined with other statistical methods for measuring niche breadth, diversity, similarity, and dietary overlap, discriminate analysis will help ecologists to gain a firmer grasp on the many intricacies involved in inter- and intraspecific trophic relationships.

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Figure 1. Histogram of the frequency of counts of a principal prey item in the stomachs of *Prosopium williamsoni*.

```
            20-
              -
              -      X
              -      X
              -      X
            15-      X
              - X    X
              - X    X    X
              - X    X    X
              - X    X    X
Number of   10- X    X    X
Fish          - X    X    X
              - X    X    X
              - X    X    X    X
              - X    X    X    X
             5- X    X    X    X         X
              - X    X    X    X         X
              - X    X    X    X         X
              - X    X    X    X    X    X    X    X
              - X    X    X    X    X    X    X    X                   X
             0----------------------------------------------------------------------
                0    1-   6-  11-  16-  21-  26-  31-  36-  41-  46-  51-  56-  61-
                     5   10   15   20   25   30   35   40   45   50   55   60   65
                               Larval Heptageniids/Stomach
```

Figure 2. Sample deck setup for discriminate analysis subprogram in SPSS system.

```
 (1)  // JOB FISHDIET (user number)
 (2)  // EXEC PROC=$$SPSS
 (3)  // EXEC SPSS
 (4)  RUN NAME          FOOD ANALYSIS
 (5)  VARIABLE LIST     SPECIES,DATE,STATION,SL,SEX,N1,N2, ... ,Nn
 (6)  INPUT FORMAT      CARD
 (7)  SUBFILE LIST      RVA (10), EMB (11)
 (8)  INPUT FORMAT      FIXED(A3,1X,F4,0,1X,A2,1X,F3,0,1X,A1/ etc.
 (9)  VAR LABELS        SL,STANDARD LENGTH/N1,DECAPODA-MISC/ ... /Nn
(10)  COMPUTE           V1=N1*131
        .                 .
(11)  COMPUTE           Vn=Nn*calorific equivalent
(12)  RUN SUBFILES      (RVA,EMB)
(13)  DISCRIMINANT      GROUPS = SUBFILES/VARIABLES = V1 TO Vn/
(14)                    ANALYSIS = V1 TO Vn/METHOD =MAHAL/
(15)  OPTIONS           3,6,7,10
(16)  STATISTICS        1,2,3,4,5,6
(17)  READ INPUT DATA
(18)  RVA 4-15 2 175 F  36      7            4 128          73 etc.
(19)  FINISH
(20)  /*
(21)  /&
```

Table 1. Results of discriminate analysis of the diets of five species of embiotocids from King Harbor, Redondo Beach, during the summer.

X = diets significantly different (*F*.95).

0 = diets not significantly different.

	Rhacochilus vacca	*Embiotoca jacksoni*	*Hypsurus caryi*	*Phanerodon furcatus*	*Micrometrus minimus*
Rhacochilus vacca	-	X	X	X	X
Embiotaca jacksoni	X	-	0	X	X
Hypsurus caryi	X	0	-	0	X
Phanerodon furcatus	X	X	0	-	X
Micrometrus minimus	X	X	X	X	-

Table 2. Calorific equivalents of prey items used in embiotocid diet analysis.

calorific category	calories/ individual	wt/individual (mg dry wt)
Microcrustacea (i.e. Isopoda, *Jaeropsis* spp; Amphipoda <4mm)	0.3	0.2
Small crabs (i.e. Pinnotheridae)	131.0	79.4
Hermit crabs (i.e. *Pagurus* spp)	11.0	4.0
Shrimp (i.e. *Alpheus* spp)	198.0	58.8
Isopoda, large (i.e. *Cirolana harfordi*)	3.0	1.7
Gammaridea (between 4mm & 10mm)	4.0	2.3
Gastropoda, medium (i.e. *Mitrella* spp)	36.0	32.5*
Gastropoda, small (i.e. *Barleeia* spp)	0.3	0.1*
Limpet-like gastropods (i.e. Acmaeidae & *Crepipatella lingulata*)	44.0	12.3*
Clams, medium (i.e. *Hiatella artica*)	52.0	10.2*
Clams, small (i.e. Lyonsiidae)	9.0	2.1*
Brittle stars (i.e. *Ophiothrix spiculata*)	16.0	15.8
Bryozoans (i.e. *Thalamoporella californía*)	38.0	51.9
Polycheates, medium (i.e. *Neanthes* spp)	2.0	0.6
Polycheates, small (i.e. *Armandia* spp)	0.4	0.1

* without shell

Multivariate Statistical Analysis Of Stomach Contents

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This paper was added to the proceedings because it resulted from discussions at the workshop.

A test of the stomach contents of two or more groups of fish may be desirable to determine if the diets of the groups are statistically different. If it is desirable to test for differences in more than one prey species then a multivariate test is mandatory. A multivariate test assumes multiple measurements on the same individual and includes the correlations between prey items in the analysis. Because of these considerations a multivariate test can find a highly significant difference when a series of univariate tests on the separate variables will not find a difference.

The paper will begin with the limitations of chi-square tests which have been used in stomach content analysis. The multivariate analysis of variance (MANOVA) is then introduced. Discriminant analysis is discussed as an extension of the multivariate analysis of variance. Principal components analysis (PCA) is explained both as a preliminary to MANOVA and as a clustering procedure. The extension of PCA to correspondence analysis is described. Finally, two methods of non-parametric MANOVA are compared. References for the multivariate techniques discussed are Anderson (1958) and Morrison (1976), the latter presenting a more readable discussion. Examples of the techniques are also contained in Blackith and Reyment (1971) and Atchley and Bryant (1975).

Chi-Square Tests

Both the chi-square test for independence and the chi-square test for goodness of fit have been discussed at this conference. A chi-square test for independence would consist of a two way (m x p) contingency table with the m rows representing predator species and the p columns representing prey items. A series of goodness of fit tests could be used to compare a series of predator species to one predator species which is used to estimate the expected number of the other species in each prey category. These tests can only be used for the dominant prey item in each stomach such that the sum of the observations is equal to the total number of stomachs examined. If the presence of each prey item in a stomach is used then the total number of observations in the cells of the tables will exceed the number of stomachs examined. In either case the list of prey items may be replaced by foraging modes so long as the sum of observations is equal to the total number of fish stomachs examined. In a chi-square test for goodness of fit the predator species used to estimate the expected frequencies must be based on a much larger sample than the predator species used for the observed frequencies such that the observed frequencies are normally distributed around the expected frequencies which are known without error, and have a known variance. The expected frequencies could also be based on the average of all stomachs of all species. However, in this case the test for independence is superior since no assumption of measurement without error is required. These tests are explained in Sokal and Rohlf (1969).

Multivariate Analysis of Variance (MANOVA)

MANOVA determines the probability that k groups of predators have the same mean stomach contents of each of p prey items, whereas the chi-square tests only considered the frequency of stomachs in each group for which a given prey species is the most important prey item. A multivariate analysis of variance assumes the following model:

(1) All individuals from a group are independent, random samples from the same population, and independent from the individuals in the other groups.

(2) The observations within the i^{th} group were sampled from a multivariate normal distribution with a 1 x p mean vector U_i and a within group p x p variance - covariance matrix Σ_i.

(3) All variance - covariance matrices are the same, $\Sigma_i = \Sigma$. The assumption of equal covariance matrices can be tested with Box's M-test (Morrison, 1976).

Method:

(1) From a sample of k groups of n individuals, a total of N individuals, construct the N x p data matrix X, and calculate the group means for each variable, $\bar{x}_{i.m}$, and the grand mean for each variable, $\bar{x}_{..m}$.

(2) Calculate the p x p within group pooled error matrix, E, containing the within group sum of squares of each variable on the diagonal

$$SSE_m = \sum_{i=1}^{k} \sum_{j=1}^{n} (x_{ijm} - \bar{x}_{i \cdot m})^2$$

and the within group sums of cross-products between each pair of variables (l and m) on the off diagonal elements

$$SSP_{lm} = \sum_{i=1}^{k} \sum_{j=1}^{n} (x_{ijl} - \bar{x}_{i \cdot l})(x_{ijm} - \bar{x}_{i \cdot m}).$$

(3) Calculate the p x p between group hypothesis matrix, H, containing the between group sums of squares on the diagonal

$$SSH_m = n \sum_{i=1}^{k} (\bar{x}_{i \cdot m} - \bar{x}_{\cdot \cdot m})^2$$

and the between group sums of cross-products on the off diagonal elements

$$HCP_{lm} = n \sum_{i=1}^{k} (\bar{x}_{i \cdot l} - \bar{x}_{\cdot \cdot l})(\bar{x}_{i \cdot m} - \bar{x}_{\cdot \cdot m}).$$

These two matrices are distributed in a Wishart distribution with k(n-1) and k-1 degrees of freedom.

(4) The test statistic is a function of the eigenvalues (λ_i) of the p x p matrix HE^{-1}. If the probability level associated with the test statistic is too low the null hypothesis is rejected and the groups are statistically different from one another. A wide variety of test statistics for MANOVA have been developed. The one which appears to have the best characteristics in terms of both power and robustness (Olson, 1974) is Pillai's trace (Pillai, 1955)

$$V = \sum_{i=1}^{r} \frac{\lambda_i}{1 + \lambda_i}$$

where r is the rank of HE^{-1}. For two groups MANOVA reduces to Hotellings T^2 test. If more than two groups are compared linear contrasts may be used to determine which of the groups are different.

Unfortunately, the assumptions of this test are not very applicable to stomach content data. The multivariate analysis of variance assumes homogeneity of variance - covariance matrices and a multivariate normal distribution. The test is not robust to departures from the homogeneity assumption and the lack of robustness is most severe when sample sizes are unequal (Olson, 1974). Since sample sizes are rarely equal in stomach content data, the common sample size is limited to the least abundant group. Also the covariance matrices are unlikely to be equal in stomach content work, especially when one prey species is absent from one group, resulting in zero variances and covariances and making the pooled covariance matrix nonrepresentative.

Discriminant Analysis

Discriminant analysis is similar to the multivariate analysis of variance in that it also uses the eigenvalues of HE^{-1} and assumes homogeneity of covariance matrices. Discriminant analysis calculates the eigenvectors of HE^{-1} (l_i) and calculates a new set of discriminating variables (z_i), also called canonical variables, which are products of the original data and the eigenvectors ($z_i = Xl_i$). The new discriminate variables have the following properties: (1) they are orthogonal to each other (i.e., cov(z_i, z_j) = 0) and (2) the discriminate variable associated with the largest eigenvalue explains the most variability and most adequately discriminates between the groups.

Discriminate analysis has three major uses: (1) to identify the variables in which the groups differ (i.e., which of the original variables have high correlation with the discriminate variables), (2) to identify modes of difference (i.e., feeding modes of the fish, groups of prey species with high correlations on the same discriminate variable), and (3) to predict in which group an unidentified individual belongs. Discriminate analysis makes three assumptions: (1) linear functions, (2) homogeneous covariance matrices, and (3) orthogonal dimensions. A fourth assumption of normality is required to calculate probabilities of misclassification. Some discriminate analysis computer programs also calculate a significance level for the difference between groups. This is calculated by a multivariate analysis of variance and is subject to the same limitations. Furthermore, when a stepwise discriminate program is used a significance level is calculated at each step. This means that at the first step the most significant variable is chosen. At the second step the variable which most complements the difference exhibited by the first variable is added. If 100 variables were measured on k identical groups, 5 variables would be expected to be significantly different due to chance alone. Since the variables selected in a stepwise discriminate program are selected _a posteriori_ the results of the significance tests must be interpreted with care. Comparing significance levels is a good way of selecting a discriminate function with few variables and high discriminating power, but a poor way of testing for significance. The proper way to test is to select variables _a priori_, test for a difference with a multivariate analysis of variance, and then check for which prey items have discriminating power and what feeding modes are present through discriminant analysis. The last step is also referred to as canonical variate analysis (Blackith and Reyment, 1971). Discriminate analysis is more robust than multivariate analysis since no testing is involved. The main use of discriminate analysis is as an aid in the interpretation of the results. To this end the results of the analysis can also be plotted to observe the group separation.

Discriminate analysis is starting to be used in food habit analysis (Ellison, this conference and Desselle et al., 1978). However, neither author discussed the interpretation of the eigenvectors and little appeared to be learned from the exercise. Unless the analysis provides improved interpretation of the results, the exercise has little benefit.

Principal Component Analysis (PCA)

One way of getting around the restrictive assumptions of MANOVA is to do a principal component analysis (PCA) before doing a MANOVA. This is done by calculating a single variance - covariance matrix on the pooled data (T) ignoring the group identifications. The eigenvalues and eigenvectors of T can then be calculated. The relative magnitudes of the eigenvectors indicate the relative amounts of variability explained by its associated eigenvector. If the group membership is responsible for the major portion of the variability then the principal eigenvectors will tend to separate the groups. If the within-group variability is responsible for the major portion of the variability but the groups are still distinct, then the secondary eigenvectors may provide maximum group separation. The eignevectors can then be used to reduce the dimensionality of the system. New variables, called component variables, are calculated as in discriminant analysis by multiplying the original observations by the eigenvectors ($z_i = Xl_i$). Usually only a small number of new variables are necessary to capture a large percentage of the total system variability. These new variables can now be used in a multivariate analysis of variance to test for group differences. The new variables have the following advantages over the original variables: (1) There will be fewer variables in the analysis which will make the analysis more robust, (2) because the new variables are linear combinations of the original variables their within-group covariance matrices, E_i, should come closer to being homogeneous than the covariance matrices of the original variables, and (3) because they are linear combinations of random variables the distributions of the new variables will tend to approximate a multivariate normal distribution more closely than the original variables. Thus, the component variables will come closer to meeting the assumptions of a multivariate analysis of variance than the original variables. Becuase principal component analysis does not identify treatment groups it does not purposefully select components which have the best group discriminating power as in discriminant analysis where the groups are determined a priori. Since the selection of the new variables is "independent" of group discriminating power the new variables can be used in the subsequent statistical analysis to test for differences between groups, unlike discriminate analysis which uses group discriminating power as the criteria for selecting the eigenvectors.

PCA is also used as a clustering technique which can be helpful in the analysis of functional feeding groups or for the elimination of outliers. Since PCA attempts to explain most of the variability in a data set in one or two dimensions a plot of the component variables will often reveal the presence of abnormal individuals whose stomach contents do not fit into any pattern present in the rest of the data. An investitor may wish to remove these from the remainder of the data set. PCA clustering may also be used to group the stomachs into similar feeding categories ignoring species classifications. If the species classifications account for a large portion of the variability then the stomachs will be clustered by species. If some other grouping accounts for most of the variability then the stomachs will be grouped by that criteria. If there is not a significant grouping of the data then none should be apparent from the analysis. This topic of a posteriori grouping is discussed further in the following paper.

Correspondence Analysis

When PCA clustering is used an extension of PCA called correspondence analysis is sometimes useful (David et al., 1974, Chardy et al., 1976). In correspondence analysis the data is transformed as follows:

$$S = \sum_{i=1}^{N} \sum_{j=1}^{p} x_{ij} ; \; w_{ij} = x_{ij} / S ; \; w_{i.} = \sum_{j=1}^{p} x_{ij} ;$$

$$w_{.j} = \sum_{i=1}^{N} x_{ij} \; ; \; y_{ij} = \frac{w_{ij}}{w_{i.}\sqrt{w_{.j}}}$$

The new N x p data matrix is Y, and principal components are calculated for the p x p matrix Y^TY. The new variables are then plotted on the new axis defined by the eigenvectors just as in PCA. However, now each prey species can also be plotted by multiplying the j^{th} element of the i^{th} eigenvector by the square root of the i^{th} eigenvalue and using this number as the coordinate for the j^{th} prey species along the i^{th} axis. Thus the plot will have the N data points representing each stomach, and p prey points representing each prey species. The resulting plot provides the following information. (1) Stomach points close to each other are from fish with similar prey composition, (2) clusters of stomachs represent fish with similar feeding habits and may represent a feeding guild, (3) prey points close together represent prey items which tend to be found in the same stomach, and (4) a group of prey points close to a cluster of stomachs will identify the prey items which that feeding guild is utilizing. The stomachs associated with a feeding guild can then be identified by species, size, location, etc., to determine the characteristics of fish feeding in a guild.

Non-parametric Multivariate Analysis of Variance

A non-parametric test allows an investigator to avoid the assumptions of normality and homogeneity of a parametric analysis. Unfortunately, it does this by discarding some of the power and information content of a parametric analysis. However, a non-parametric analysis can be used to test for equality of group medians when the assumptions of a parametric test are not met.

If there are more than two groups there is no provision for comparing some groups with others or comparing pairs of groups. These comparisons must be done in separate tests. Two non-parametric analysis of variances have been developed, one by Mantel and Valand (1970) and another described in Koch (1969). Each will be briefly described here along with its application to gut analysis.

Method 1: Mantel and Valand (1970).

(1) Assign ranks ($r_{\alpha i}$) for each individual (i=1,n) on each variable (α=1,p).

(2) Use some function $f_\alpha(r_{\alpha i}, r_{\alpha j})$ to describe the similarity between any two individuals for any variable α. f_α may be different for each variable but must be symmetric around zero.

(3) Calculate a similarity index

$$Y_{ij} = \sum_{\alpha=1}^{p} f_\alpha(r_{\alpha i}, r_{\alpha j})$$

to represent the closeness of any two individuals over all p variables.

(4) Create a dummy variable X_{ij} which is equal to unity when i and j are in the same group and is equal to zero when i and j are in different groups.

(5) Calculate

$$Z = \sum_{i=1}^{n} \sum_{j=1}^{n} X_{ij}Y_{ij}$$

The smaller Z the larger the difference between groups. Z is in the form of a Hoeffding (1948) U statistic and as such it is asymtotically normally distributed. Thus, $t = [Z - E(Z)]/Var(Z)$ is distributed as a student's t-distribution where E(Z) and Var(Z) are the permutational expectation and variance of Z. t can be compared to a tabled value to determine the probability that there is no difference between groups.

If the reader is familiar with non-parametric statistics, the ranking method used in the Mann-Whitney U-test, mid-ranks, probably comes immediately to mind. This complex method is not recommended when using this test for fish gut work where most stomachs will not contain any prey items from most prey categories. A simpler method is recommended and described in Table 1.

TABLE 1

	Raw Data	Mid-rank Method	Recommended Ranking
1	0	4.5	0
2	0	4.5	0
3	0	4.5	0
4	0	4.5	0
5	0	4.5	0
6	0	4.5	0
7	0	4.5	0
8	0	4.5	0
9	1	9	1
10	2	10	2
11	10	12	3
12	10	12	3
13	10	12	3
14	20	14	4
15	30	15	5

Notice in the U-test ranking observation 9 is app. as close to a count of 20 as it is to zero, whereas in the recommended ranking it is closer to zero.

This analysis also permits weighting factors to be used in the calculation of f_α. Weighting factors allow the recognition of important versus unimportant prey species in the calculation of a similarity index. If weighting factors are not used and a large number of rare species are included in the prey categories they may dominate the simularity index and produce anomolous results.

Method 2: Koch (1969).

(1) Assign ranks using the mid-rank method.
(2) Use the ranks to calculate T as in PCA using N instead of N-1 for degrees of freedom.
(3) Use the ranks to calculate h which is a (px1) vector of $(\bar{r}_{\alpha i.} - \bar{r}_{\alpha ..})$, where $r_{\alpha i.}$ is the mean rank of the i^{th} group.
(4) $L = (\frac{N-1}{N}) \sum_{i=1}^{k} n_i h_i^T T^{-1} h_i$ where L is approximately distrubed in a central chi-square distribution with p(k-1) degrees of freedom when the null hypothesis is true, and N is large.

Method 1 does not require the use of mid-ranks but is considerably more expensive to run. The expense of method 1 increases exponentially with the total number of fish, N, (e.g., for N=100 p=34, a run required 35.4 system record units (SRU) whereas for N=120 p=34, a run required 63 SRU). The cost of method 2 increases exponentially with the number of prey categories, p, since the p x p matrix T must be inverted. The need to invert T can also cause numerical problems when T is ill-conditioned or singular, which frequently occurs with small sample sizes.

Discussion

Computer Programs.

The statistical package for the social sciences (SPSS) contains programs for several of the methods cited: chi-square test for goodness of fit (CROSSTABS), multivariate analysis of variance (MANOVA), discriminate analysis (DISCRIMINATE), and principal components analysis (FACTOR using TYPE=PA1). Jerome Pella at NMFS, Auk Bay has a program for non-parametric MANOVA using the Mantel and Valand technique. I am unaware of existing programs for the remaining techniques outside of the original authors

Chi-square tests are limited to the most dominant prey item in each predator class and as such do not investigate the differences between predators as thoroughly as multivariate tests. MANOVA is theoretically appropriate, but is not robust against the deviations from its assumptions frequently found in stomach content data.

The recommended procedure for testing for a statistical difference between populations would involve one of the two non-parametric techniques or a MANOVA run on the component variables produced by PCA. When the MANOVA is run, the sample sizes should be as close to equal as possible to ensure robustness.

Interpretation via discriminate analysis assumes that the group breakdowns assigned *a priori* are the most meaningful, or the most important to the investigator. Interpretation via cluster analysis, such as PCA or Correspondence Analysis allows a natural, *a posteriori*, grouping of similar samples which hopefully corresponds to samples affected by the same processes.

However, the comparison of mean vectors may not be the only question which is of interest to the investigator. A comparison of generality versus specificity may be important. There are two types of generality, (1) each individual has a variety of prey items in its stomach (true generalist), and (2) each fish has different prey items in its stomach (opportunist). If clustering is done the true generalists will be in their own cluster along a component which has correlations with several prey groups, although this may be a secondary axis (an axis which does not account for a large portion of the variability). However, an opportunist may have individuals clustered into several groups of specialists. The chi-square test for independence should be very good at displaying differences between generalists and specialists but not differences between types of generalists. Differences between types of generalists can be obtained by calculating a diversity index for each stomach and comparing diversity indices in a univariate test. A parametric test can be used relying on the robustness of the test with equal sample sizes, or else a non-parametric test could be used.

The determination of diet overlap and analysis of potential competition is often the focal point of food habit studies. The statistical tests proposed do not attempt to assess competition, especially since two species can have statistically different diets with significant diet overlap. Furthermore, the tests do not assess the degree to which food is limiting. However, since the degree of overlap and not the difference in mean vectors is the important aspect in competition, the misclassification probabilities from discriminate analysis may be useful in assessing overlap. A misclassification probability represents the proportion of fish in species A which appear to be feeding as a member of species B.

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A Technique of Guild Analysis

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This paper was added to the proceedings because it resulted from discussions at the workshop.

Several speakers at this conference have talked of the need for methods to identify species which have similar feeding habits. The aspect of different size classes of the same species foraging in distinct feeding stanzas has also been mentioned. The possibility of fish of the same species, in the same size class having more than one foraging strategy also exists and needs to be considered. A method of guild analysis should identify the similar feeding strategies and feeding stanzas of each species. Cluster analysis is a numerical technique which may have application in this area. A clustering algorithm ignores any preconceived classification of the fish stomachs such as species or size of fish, and only looks at the gut contents of each individual. It then attempts to group similar stomachs together. A tightly clustered group of stomachs could then be considered a foraging guild and species and size classes of fish in that guild could then be identified.

The difficulty with using a clustering algorithm is the lack of any criteria for deciding what is a group. If a sample of 100 stomachs is entered into the algorithm it sorts the data into groups, either starting with one group of 100 stomachs and going to 2,3,4...100 groups, or starting with 100 groups with 1 stomach each and going to 99,98,97...1 group. It is left to the user to determine which number of groups is the most significant. An elaborate and expensive method for making this decision is described here. After the clustering program has sorted the data into groups, perform a multivariate analysis on each set of groups to calculate the probability that each set of groups are samples from the same population. The set of groups with the smallest probability level represents the most significant grouping of the data. The probability level should not be used as a test for significance, but only as an index of within group cohesion and inter-group distinction. This is most effectively graphed by plotting the negative logarithm of the alpha level versus the number of groups. This will produce distinct, sharp peaks in the plot. After the most significant groups are identified, the stomachs in each group should be identified according to species and size class. After this the feeding guilds may be obvious. Prey guilds may be identified in a similar manner by determining the prey species and size classes a feeding guild eats. The identification of prey guilds may aid in clarifying the concepts of prey availability, selectivity, electivity, and avoidance.

It is quite possible that the plot of $-\ln \alpha$ versus the number of groups may have multiple peaks representing a hierarchy of feeding guilds with guilds being broken down into subguilds. For example, the first peak may represent a breakdown into top, mid-water, and bottom feeding species, the second peak may further divide these into finer, more specialized groups.

The basic tool of this analysis is clustering, about which volumes have been written and computer programs abound. Unfortunately, few hard rules about how to select a clustering procedure or how to choose the correct number of groups exist. The procedure suggested here is based more on intuition than on hard facts. Some of the options available are, hierarchical versus non-hierarchical, agglomerative (bottom-up) versus degenerative (top-down), the use of a large array of similarity indices (Bray-Curtis, mean difference, euclidean distance, etc.), and different clustering algorithms (nearest neighbor, farthest neighbor, etc.). Principal Component Analysis or Correspondence Analysis may be used to cluster the points instead of a clustering procedure but the investigator must determine the group cluster boundaries and assign stomachs to guilds.

If forced to make a recommendation at this time, I would suggest one of the following: (1) a top-down, non-hierarchical, farthest neighbor clustering, using the non-parametric multivariate analysis of variance (Method 1, Crow, this volume) to test the number of groups, and using the same simularity index as the testing procedure; (2) identify clusters from a principal components or correspondence analysis, testing the number of groups using MANOVA or one of the non-parametric techniques.

SESSION 2 Statistical Analysis
Discussion

Cailliet questioned Tyler regarding his use of chi-squared values. Tyler explained that the second use of his technique is to look for heterogeneity effects. After one finds significance then one sees how heterogeneity increases and the detection of this plateau is left as a subjective decision. Tyler said that he usually rejects the idea of a plateau unless it is really very obvious so that it becomes an event to describe feeding stanzas. If the fish changes its natural diet gradually over a size range then the problem is more ambiguous. In a similar manner one could test between and among different species of predators to determine homogeneous groups. Once the homogeneous groups of predators in a feeding stanza are defined, then comparisons could be made between other groups and the established feeding stanzas. What if the fish are feeding on 20 or 30 food items? Tyler responded that the program has a trap in it to reject all prey items that are not frequent enough to perform a decent chi-square test. It is rare to come across a fish that does not have a narrow range of important diet items supplemented by miscellaneous items. Tyler then described a piscivore occurring off the East Coast which is a large ambush-type predator with no principal prey. It preyed upon such a bewildering variety of fish that there were no real groups of prey that were main constituents of the diet. To find what was making up 80 percent of the diet one came up with a whole list of species. This technique would not apply to that kind of a predator.

Sibert asked about multiple switches and wondered if the chi-square test was sophisticated enough to separate multiple groups. Tyler was affirmative in this supposition although he had not encountered such a predator in his study. Atlantic cod, for example, go through about four feeding stanzas but he had encountered usually only two of them at any time. Sibert commented that an interesting map could be constructed of the local chi-square maxima in fish that exist in several size classes throughout the year.

Feller spoke out in opposition to diversity indices and suggested that Hoffman could have learned the diversity of different prey items being consumed by a fish in a more direct manner by plotting the cumulative number of prey encountered in the ordinate versus the number of stomachs examined on the abcissa. He told her she would have the same shaped curve as she did with the diversity indices. Hoffman had tried that approach but felt that the diversity index also incorporated proportion, which can mean a large difference when comparisons are made for significant differences. She was not interested simply in the number of species but also in what proportions the species made of the total diet. Feller reiterated comments from the first session by emphasizing that it all depends on what one is asking about a group of fishes.

Word brought out that he had used many indices of diversity and looked at replicates and found some of the formulae easier to use than Pielou's method. Levy asked Hoffman that, if her statistical tests showed a leveling at 25 or 30 fish to give a representative sample, did that indicate that in the next month she could go out and confidently sample 25 or 30 stomachs? He suggested that the formula will not work that way as all variables change with time. Hoffman replied that she looks for the optimum sample size with each sample to ensure taking enough fish because there is considerable change in diet even over a month's time. She calculates this as she goes and terminates stomach examination when she is confident that the curve has leveled.

Lipovsky asked how empty stomachs were sampled as this was a problem encountered in Columbia River fish being sampled. Hoffman said that she threw them out but Lipovsky argued that this would bias results towards those fish that were eating and eliminated important conclusions which could be drawn from observation of empty guts. The theme of specific questions again arose when Hoffman stated that she wanted to know what the fish were eating and fish which were not eating could not help her to answer the questions; empty fish were noted but because of several valid reasons they were not incorporated in the analysis, but simply mentioned in the summarization. Feller theorized that then she may need to open a hundred fish to find 40 with food in the stomachs. Hoffman replied that she encountered very few fish with empty stomachs. Tyler helped to emphasize her position by stating that "those are fish that are not eating--she wants to look at fish that are eating." It was argued that the empty stomachs were still a part of the sample to which Hoffman defended that the data was not being discarded from the total analysis but simply not incorporated into the diversity indices.

Word asked Hoffman to give him an idea, based on the use of diversity indices to calculate minimum acceptable sample size in studies with the sockeye and stickleback, what the number of stomachs examined was. Anywhere from 20 to 40 sockeye were studied and about 80 of the age two stickleback.

Gabriel's talk generated a brief discussion regarding the assumptions of her statistical approach. For maximum efficiency of the formula, N_1 and N_2 should be the same--in that way comparisons are strictly across board. However, the sticky situation occurs when one sampler is a box core and the other sampler is fish stomachs. Sibert asked if the ideal was to have the same number of worms collected by box cores as the number consumed by fish; the reply was "yes." The problem, Gabriel explained, was when to know when one has a number of fish stomachs equivalent to the sampling of a box core--in some ways it is related to the problem of knowing when one's sample size is adequate. Sibert asked Gabriel if this test was better than a chi-square and she explained that for descriptive purposes it is much easier to interpret; the results between the two methods of testing are consistent, however.

Cailliet suggested that Gabriel's test might be better suited to comparing prey arrays between predators of equal size in that way one could confidently compare equal numbers of stomachs from each predator. Gabriel explained that the test was developed by medical statisticians to determine if the proportion of schizophrenics being admitted to hospitals was the same in New York as in London--which assumes that all schizophrenics are the same. The problem to resolve is, she summarized, "Is a worm in a box core the same as a worm in a fish stomach?" Crow commented that equal sample size is usually for maximum efficiency but questioned if it was really limiting the value of the test to have unequal sample sizes. It is going to affect the standard error, replied Gabriel, and she agreed that the problem of equalizing N_1 and N_2 is a debatable question.

Several questions were raised after Cailliet's presentation. One had to do with rank correlation coefficients and when to use them. Cailliet preferred not to recommend anything without more background information but did make a qualified statement based on the assumption that his results were correct. If one has equal prey categories--two predators with ecual prey--the rank correlation technique would be valid and also acceptable to reviewers. However, there are probably 60 to 100 of these predators with equal prey--not very many. Another point to consider is that correlation coefficients may not be inherently interpretable. There are nonparametric coefficients with some overlap measure which are suited to Cailliet's purposes. PSI is a simple technique.

Levy wondered what Cailliet thought about comparing within-group PSI's with between-group PSI's, to which Cailliet gave an adamantly affirmative response. He has not had a chance to try it but cited a paper by Mary Stober who reported the technique. He suggested that it may be <u>the</u> way to take into consideration variability among guts--Stober compared the diatoms in salp stomachs to compare composition among salps and between salps and between salps and in the water column. What one gets is a mean PSI, then one can calculate some sort of variability around the mean PSI level.

Feller asked Ellison how he obtained his data for caloric equivalents--were they actual measures or literature values. Ellison replied that they first determined units, such as a whole amphipod or a bite of bryozoan. Some of the data was then derived by them with a bomb calorimeter, taking samples of invertebrates and scrapings of the bryozoans, etc. They had an adaptor for the calorimeter so that smaller samples could be run.

Crow and Ellison entered into a complex debate over semantics of the statistical technique used by Ellison and it soon became obvious why it is important that we define our techniques and use the proper nomenclature to prevent confusion. Crow asserted that Ellison did not use discriminate analysis as Ellison claimed but rather the SPSS program discriminate, which is a multivariate analysis of variance and not discriminate analysis. Ellison confirmed that he had sought the advice of a professor at California State University at Long Beach who gave him the SPSS program and affirmed that it was a technique for discriminate analysis. Crow then quoted various SPSS commentaries and again suggested that Ellison had actually employed multivariate analysis of variance. Discriminate analysis would allow a person to classify an unknown stomach but does not itself test, which a multivariate analysis of variance does do. The multivariate analysis of variance makes two assumptions:

1. It assumes a multivariate normal distribution.
2. It assumes a homogeneous variance-covariance matrix.

One needs to be lucky to have both those conditions. Ellison explained that a number of people who are authorities in statistics have examined his treatment of the data.

Smith asked for us to think about what models we were trying to develop. What is the effectiveness of one's measure in the first place--a statistical exercise or a useful measurement of a fisheries, for protection of a conservation species, etc? Smith emphasized the need for data to substantiate and help with management decisions. Mearns agreed and suggested that we have a discussion about what questiors researchers and managers are asking. Cailliet asked Mearns to give an example of a question he is asking. Mearns replied that, for example, he would like to know if fish around wastewater outfalls are in some way deriving any fo their energy from waste discharges and, if so, through what routes. Are they direct or are prey animals eating wastes and so on and so forth. Mearns said that he picks up some hints of new things to try that he might never have thought about before attending the GUTSHOP. Part of the value in attending a workshop such as this is to learn new methods or to hear something that sets off a chain reaction of thought which might eventually lead to some important information. Word backed Mearns and added that another question they ask is if a population of individuals is absent from an area because it is feeding on a species not near the outfall or if because of a specific toxic response to some pollutants in the environment. Word again emphasized the need for careful questions before one attempts to gather any data.

Smith picked up Mearn's lead and said that his specific interest is to figure out how to use information on feeding relationships in multi-species management models. He wondered if feeding studies were really approaching the problem with the kinds of data and measures that may not be useful to a modeler.

Cailliet entered the discussion by posing two alternative routes of research. One, a fine resolution approach, is to look at a very specific detail on the feeding habits and prey availability and so on. The second approach, a broader, coarser resolution perspective, is to do the system kind of thing where you want to find out something about the feeding habits of all the fishes that are very abundant; this is one which, given the stomachs available, limits the data on individual species but rather characterizes the system in general.

Mearns projected that one objective common to all our studies somewhere down the line is the need to better our abilities to predict and forecast. Chess argued that it is necessary to understand relationships before one can forecast. Mearns reminded Chess that one must decide the question of forecasting early in the game and then to design studies to give sufficient data to meet that goal. Chess still argued for the idea of taking the broad view first then refining it and emphasized that it is the specific questions that lead to the ability to predict. Cailliet asserted with the ecological research one must perform some type of survey to get an idea of what kinds of things to look at, then focus on those selections.

Cailliet described a lunchtime conversation with Crow who had an idea of using discriminate analysis to define feeding guilds of fishes and suggested that the group would benefit from a review of that discussion by Crow. Crow expresses himself well and, while perhaps not word for word, the following is the lengthy comment by Crow as transcribed from the tape:

> "My comment comes as more of an eight-minute lecture than a one-minute comment. I was thinking over the question at lunch and what I came up with was to group predators and prey into guilds so we can say with respect to Word's idea about ecological groups and when ecological groups of predators and ecological groups of prey. Well, when I did this I thought it would be guild analysis. What you do is to take all your stomachs--go to a cluster analysis--and find out which groups of stomachs are most similar. The problem of cluster analysis, as you probably all know, is that cluster analysis does not know when to stop. It starts off, say with a group of 500 stomachs, starts with 500 groups and goes to one group. You do not know at which level one is a "significant" group. What you could do is go to discriminate analysis or to an analysis of variance that John (Ellison) talked about. Take what looks like the best groups into a multivariate analysis of variance and it will give you an alpha level for the significance of those groups. How significantly different are they? That depends on the assumptions that are not met. It means that the alpha level is garbage in terms of probability. But still it is a good index of difference and unlike most other indices it takes into account both within group variability and between group differences so that you can use the cluster analysis to find out what your groups are and you will get groups of six or five or 20, then stick your groups into an analysis of variance and that will tell you how good that grouping is. And essentially you can draw a plot with the number of groups versus your alpha level and that it is going to look something like this (draws plot on blackboard) and I would argue that right here is the most distinct number of groups and you can say that, if this is 8, I have 8 guilds of predators. You then look at the compositions of the guilds. One guild may be a, b, c, and another b, c, d, e. One species of fish may be in a different guild, or a species may change guilds as it grows. You could then identify prey categories with feeding guilds. Finally, you can identify which prey produce the groupings and you can get what I propose as a reasonable approach to ecological groups of predators and ecological groups of prey fairly objectively with a statistically straight forward procedure. And that is what I thought up over lunch."

Word commented that the formula used to cluster data and to made dendrograms affects the outcome and at what points one determines a cluster. Crow agreed that caution must be employed with the formulae. Feller asked what parameters are used to cluster groups, for example with similarity of gut contents; does one define gut contents to species level or to prey category? Crow suggested that by looking at the guilds one could determine the appropriate levels of identification to which Feller responded that he saw the potential for an interesting exercise with clustering. Cailliet promoted identification to species level whenever possible. As mentioned before, once data is lumped it can never be separated but if the raw data is available at the species level then it can be grouped and regrouped whichever way one desires. Feller mentioned that, practically speaking, it sometimes wastes time and money to go to species but Cailiet still maintained that it is important. It was suggested that perhaps organizations could cooperate with each other and share expertise.

Cailliet recalled that there is a formula for figuring instantaneous mortality of fishing gear related to fishing effort. Can a similar formula be applied using fish as the fishing gear? Crow affirmed this, as long as the fish does not change foraging behavior or morphology with time.

Sibert, the challenger, argued the concept of availability. He asserted that it is a word in ecology that we often use but we still end up spending a lot of time trying to search for a meaning for it. Everything in a fish stomach is available to that fish, and thus indicates a minimum estimate of availability. Yet it seems intuitive that more is "out there" than is available. Gabriel suggested substituting the term accessability. If a polychaete has a tube or a mollusc a shell then it may be inaccessible to certain kinds of fish. After a brief discussion between Sibert and Gabriel, Cailliet asked if they were suggesting that there is some way of weighing all variables to come up with a definition of availability. Perhaps prey and predators can be matched on a one to one basis. One examines the suite of prey present and then pair each fish's physical capacity to catch that prey. Perhaps what it can catch is what it will eat. Levy observed that once again we are involved in a problem of semantics. He explained a paper by Hyatt(?) who had recently published in a series on fish physiology a paper about factors affecting acquisition of natural foods by fish. He referred to three kinds of availability: realized availability, apparent availability, and potential availability. Realized availability is the set of prey actually present in the stomach. Potential availability is the set of organisms fish can search for, detect, ingest, and assimilate in a given time interval. Apparent availability is those organisms which investigators think a fish can search for, detect, ingest, and assimilate in a given time interval. How does one select the definition to use? Tyler suggested that after one has a defined hypothesis then the selection of a definition will be easier. Eggers suggested that maybe we should define availability as a null hypothesis.

Hixon reinforced the idea of selection by describing an experiment in which divers followed predator fish around and caught food items that were spit out in a little dip net. In that way they were able to identify rejected food items, something we do not see in the laboratory setting with preserved guts. Cailliet commented that that was a behavioral approach to selectivity. After an attack against the word selectivity Levy suggested that we substitute the phrase "density-dependent prey acquisition," which might not bias a reader who has preconceived ideas of a definition of selectivity.

Thus ended a lively discussion period.

SESSION 3

Trophic Structure

SESSION LEADER
Wendy L. Gabriel

PARTICIPANTS
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Pollutant Flow Through Marine Food Webs

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Documenting pollutant pathways is cited as one of the most important reasons for conducting fish food habits studies. Indeed, in some ecosystems, there are strong relationships between what an organism eats and the concentrations of some contaminants in an organism's tissues (such as for DDT and for many substances in laboratory experiments). However, during the past decade the results of numerous chemical analyses of biota in both contaminated and uncontaminated coastal ecosystems show that bioaccumulation through marine food changes may be an exception rather than a rule, especially for trace metals. The reasons for this are poorly understood. It is possible that some metals, such as chromium, are discharged in insoluble biologically inactive forms and thus cannot enter the food web (Mearns and Young, 1977). Other organic materials such as chlorinated benzenes are apparently so volatile that they also do not enter the food web (Young and Heesen, 1978). Others, such as polycyclic aromatic hydrocarbons, polychlorinated biphenyls (PCBs) and DDT isomers do enter food webs and may be transferred, concentrated, or metabolized. Finally, it may be that, unlike terrestrial and freshwater systems, ocean food webs are so complex that that averaging of pollutant concentrations across trophic levels becomes a distinct possibility (Isaacs, 1972, 1973, and 1976).

Faced with these uncertainties, how can we determine the importance of food habits studies in documenting or forecasting pollutant flow in marine food webs?

At SCCWRP, we are taking several approaches to this problem. For several years we have attempted to document the physical-chemical form of some pollutants in the ocean to see what fraction might be in biologically available forms (Jan and Young, 1978 and Mearns and Young, 1977). Some of the metals studied to date appear to be tightly bound to particulates and largely unavailable to organisms. DDTs and PCBs appear to be highly associated with particulates and are therefore more accessible to the benthic food web than to pelagic food web at contaminated sites (Young et al., 1976). More recently, however, we have begun to make use of natural pollutant analogues to examine coastal fish and shellfish to see what potential they have for bioaccumulation.

Cesium as a Pollutant Analogue

One such analogue appears to be the trace alkali element cesium (Cs). As summarized by Young (1970), cesium has a number of attributes which make it useful in tracing food chains. There are no substantial point sources of cesium in coastal waters, yet it occurs in low unchanging concentrations in the oceans (0.3 µg/L). It can be shown than an animal's cesium content is mainly the result of food intake, not seawater. Physiologically, cesium follows potassium into an animal's cells, but has a biological halflife about two to three times longer than potassium. It is concentrated mainly in muscle tissue rather than in the liver or other tissues. Finally, both stable and radio cesium have been shown to undergo bioaccumulation in terresterial and freshwater linear food chains including caribou → wolf (two- to three-fold increase), food → pigs (two-fold increase), food → bluegill sunfish (3.3-fold increase), small mixed fish → perch (1.5-fold), and perch → pike (3.5-fold).

In 1970, Young demonstrated that in the simple nearly linear marine food chain of the Salton Sea (Figure 1), cesium and the ratio of cesium to potassium (Cs/K)) increased in tissue concentration as one moved up the food chain from phytoplankton and detritus to a 7 kg predator, the orangemouth corvina (Cynoscion xanthulus). There was about a six-fold increase over three trophic steps (Table 1). However, when the same species from the open and more complicated ecosystem in the northern Gulf of California was examined, no bioaccumulation was evident (Table 1). These results suggested to Young, Isaacs, and others that (1) cesium and perhaps other alkali metals might be a useful addition to studies attempting to document the existence or lack of chemical structure in marine food webs, and (2) that marine food webs may in fact be so complex they are chemically unstructured.

During the past year, we begin a project to examine the relationships between food habits, pollutants, and pollutant analogues in coastal food webs. Our objective is to determine whether or not southern California marine organisms show chemical evidence of trophic separation and, if they do, to determine which if any of various classes of contaminants follow the indicated trophic position.

Methods

Several kinds of projects were initiated. First, our chemistry team spent several months modifying chemical recovery techniques so that cesium could be measured safely in small samples with the Project's atomic absorption spectrophotometer. The modified method uses small tissue samples (3 to 6 g), standard addition of pure cesium, digestion in nitric acid, concentration on ammonia-12 molybdophosphate microcrystals (AMP), dissolution in ammonium hydroxide, and analysis using carbon furnace atomic absorbtion spectrometry (AAS). In addition, potassium is analyzed by flame AAS.

Second, we returned to the Salton Sea to confirm whether or not previous results could be repeated and to make measurements of pollutants. Gillnetting and beach seining in March 1978 produced a collection of orangemouth corvina (*Cynoscion xanthulus*), croaker (*Bardiella icistius*), sargo (*Anisotremus davidsoni*), threadfin shad (*Dorosoma petenense*), sailfin molly (*Peocilia latipinna*), longjaw mudsucker (*Gillichthys mirabilis*), pile worms (*Neanthes succinea*), barnacles (*Balanus amphitrite*), ditritus, sediments, and water, but no mullet (*Mugil cephalus*). To date, five of the fishes plus sediments and water have been measured for Cs, K, seven trace metals, DDTs, and PCBs.

Third, we collected fishes, invertebrates, and plants from two southern California marine communities. In July 1978, we collaborated with Dr. Michael Horn (California State University, Fullerton) in a collection of fishes from Newport Bay, a major backbay of southern California which harbors a fauna not unlike the Salton Sea. Included in these collections were striped bass (*Roccus saxitilis*), spotted sand bass (*Paralabrax maculatofasciatus*), yellowfin croaker (*Umbrina roncador*), striped mullet (*Mugil cephalus*), longjaw mudsucker (*Gillichthys mirabilis*), topsmelt (*Atherinopsis affinis*), and California killifish (*Fundulus parvipinnis*). We also made use of previously collected samples of important sea food organisms collected near a coastal water waste discharge site. These included bacaccio (*Sebastes paucispinis*), California scorpionfish (*Scorpaena guttata*), Pacific sanddab, (*Citharichthys sordidus*), ridgeback prawn (*Sycionia ingentis*), yellow crab (*Cancer anthonyi*), purple hinge scallop (*Hinnites multirugosus*), and black abalone (*Haliotis cracherodii*).

All animals were carefully dissected according to an established protocol for trace contaminant analyses. White muscle tissue was excised and chemically analyzed for cesium, potassium, all or part of a suite of trace metals (Ag, silver; Cd, cadmium; Cr, chromium; Cu, copper; Ni, nickel; Zn, zinc; and others) (Jan et al., 1977); and Hg, mercury, (Eganhouse and Young, 1978); and for chlorinated hydrocarbons (DDTs and PCBs) (Young et al., 1976). For large specimens one sample from minimum of three specimens of similar sizes were analyzed. For smaller organisms, three composites from a larger number of organisms were used.

We considered that a detailed investigation of food habits was justified if analyses showed marked chemical differences in these preliminary samples. Gut contents were examined in all organisms dissected and a large separate collection of each species was preserved for detailed food habits analysis. There are a considerable number of reports on the feeding habits of many prominent fishes in southern California. To begin our work then, we assigned tentative trophic levels to each organism based on literature and unpublished stomach content data which contained information at least on frequencies of occurrence of food items.

Based on this general knowledge of feeding habits, we then attempted to assign each organism to one of five trophic categories:

I Plants including phytoplankton
II Herbivores, Zooplankton
III Primary carnivores, including some infaunal feeders
IV Secondary carnivores (many fishes)
V Tertiary carnivores (e.g., large predatory fishes and sharks)

Most organisms and samples did not fit this scheme well and were then assigned intermediate levels. For example, Salton Sea detritus was composed of dead phytoplankton (I) and zooplankton (II) and therefore was assigned trophic level I-II. Similarly, we found both algae (I), suspension feeding bryozoans (II-III) amphipods and small crabs (perhaps III) in stomachs of yellowfin croaker; since there is no evidence that these fish are able to digest the algae, we assigned these fish to trophic level III-IV.

Results

Replicate (≥ 3) samples of four fishes (plus single specimens of shad and mudsuckers) have been chemically analyzed from the Salt Sea collections. As shown in Table 1 median Cs/K ratios ranged from 10 to 33 with the highest ratio (33) found in the corvina (at lease a secondary carnivore, trophic level IV-V) and next highest (19 and 20 respectively) in sargo and croaker (primary carnivores, trophic level III-IV). The single shad (zooplankton feeder, trophic level III) so far analyzed produced a Cs/K ratio of 10 while sailfin mollies (assumed detrital feeders, trophic level II-III) had a higher ratio of 14.

With the exception of the sailfin molly, these results generally agree with the considerably more extensive analysis done in 1967 (Young, 1970, Table 2). In the 1967 survey, all fishes showed somewhat higher values ranging from 15 to 58 for shad, croaker, sargo, and corvina. Sailfin molly was not analyzed in 1967, but a confirmed diatom feeder, the striped mullet, yielded a Cs/K ratio of 9. Also in that study, the polychaetes produced ratios of 4 to 8; algae, 4; and water, 3.5. Detailed stomach content analysis of the sailfin mollies is obviously justified and may help confirm whether or not it belongs at a higher trophic position. Another difference is that our 1978 orangemouth corvina had considerably lower average cesium concentrations than the 1967 fish analyzed by Young (1970). Several of our recent fish contained polychaetes (Neanthes succinea) as well as fish remains and it is possible polychaetes are now a more important food item for this fish.

Examination of the new data on trace metals (also in Table 1) reveals a striking lack of any pattern. In fact, except for mercury, no trace metal showed evidence of biomagnification through this food chain. For example, copper concentrations ranged from 300 μg/wet kg in the sailfin molly and mudsucker to 1340 μg/wet kg in threadfin shad; intermediate levels occurred in the sargo, croaker, and corvina. In contrast, total DDT and total Hg did show muscle concentrations that might generally be related to trophic level; Hg was two to three times higher in corvina than in the sailfin molly or the croaker. If threadfin shad were deleted, DDT would also follow this pattern.

While analyses of Newport Bay organisms are still in progress, preliminary results are extremely interesting (Table 3). First, tissue values of Cs/K are considerably lower than in the Salton Sea, ranging from 3.6 in small striped mullet (II) to 5.5 in yellowfin croaker (III-IV). This is probably caused by different water concentrations of Cs and K in these two ecosystems (Young, 1970). More importantly, any trend of increasing values of the ratio with trophic position appears to be very minimal. In contrast, total Hg undergoes a 20- to 40-fold increase between striped mullet (II; .010 and .017 mg/wet kg) and striped bass (IV-V; 0.37 mg/wet kg). However, preliminary results from the other trace metals indicate no correlation with trophic position (e.g., for large striped mullet and spotted sandbass; Cd 20 and 3 μg/kg; Cr, 16 and 14 μg/kg; Cu, 550 and 260 μg/kg; and Zn, 3.3 and 4.3 mg/wet kg, respectively).

In the open coastal sea food organisms collected near the waste discharge site, a third set of chemical conditions is apparent. As shown in Table 4, Cs/K values are higher than in Newport Bay, ranging from 5.5 in filter feeding purple hinge scallops to 16.6 in predatory bocaccio. There is also some tendency for Cs/K to be higher in higher trophic level organisms. However, as in the Salton Sea and in Newport Bay none of the trace metals except Hg show evidence of higher values associated with higher trophic position; in fact, Cd, Cr, and Zn occur in highest concentrations in organisms assigned the lowest trophic positions, a condition partially due to concentration of sewage-origin metals into lower trophic levels (Jan et al., 1977). An apparent biomagnification of mercury is also obvious in these data, but inspection of other data shows similar patterns away from discharge sites. For DDT, the trophic level relationships (on a wet weight basis) are only somewhat apparent.

Conclusions

It is obvious that relationships between trophic level and pollutant concentrations in marine organisms are not at all simple and that all potential pollutants do not automatically concentrate "up the food web." These data, as well as many past studies--such as on Columbia River radionuclides (Osterberg et al., 1964)--indicate that classes of potential contaminates must be considered on a case-by-case basis with respect to their ability to concentrate through marine food chains. More importantly, even without detailed food habits analyses, our data already suggest that food habits studies cannot be the only criteria for explaining variations in pollutant concentrations in marine organisms or in forecasting pollutant concentrations in marine organisms or in forecasting pollutant trajectories. Neither are we convinced that food chain studies in enclosed experimental conditions (such as Aubert et al., 1972) provide a realistic appraisal of pollutant transfer conditions in the marine environment.

We are continuing our analyses by focusing more directly on marine predator-prey pairs, on more definitive food habits studies, and on analyses of other kinds of marine habitats and food webs. We are also not particularly pleased with our preliminary rules for trophic-level assignments and may well modify our approach in the near future. The conclusions reached by Wyatt (1976) regarding marine food chains may be most useful.

Acknowledgments

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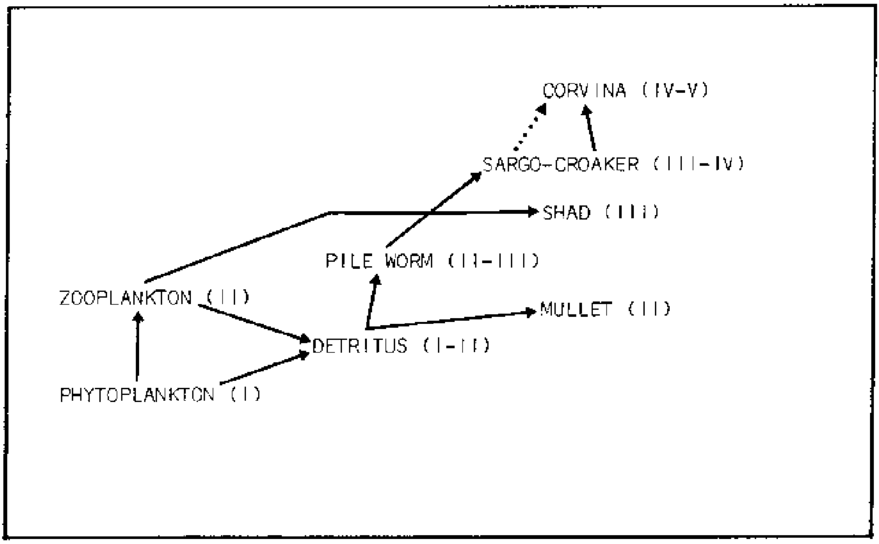

Figure 1. Food chain links in the Salton Sea determined by food habits studies (Young, 1970; Walker, 1961).

Table 1. Summary of median concentrations of cesium (Cs), the ratio of cesium to potassium (Cs/K) and median concentration of seven trace metals and total DDT and total PCB in fishes, sediments, and water from the Salton Sea, collected March, 1978.[1]

Common Name	Trophic Assignment	Cs µg/kg	Cs/K x 10^6	Ag	µg/kg wet weight Cd	Cr	Cu	Ni	Hg	mg/kg wet weight Zn	DDT	PCB
Fishes:												
Corvina	IV-V	116	33.3	<3	2	15	170	<40	0.016	3.0	0.02	0.016
Bardiella	III-IV	84.6	20.3	2	1	18	460	<26	0.009	3.2	0.064	0.009
Sargo	III-IV	76.8	18.6	2	1	28	620	<25	0.005	3.5	0.19	0.015
Mudsucker	III-IV	50.3	13.6	<3	6	<17	300	<55	NA	6.9	0.040	0.009
Shad	III	35.6	10.0	<2	1	<10	1340	35	NA	3.9	0.48	0.053
Molly	II-III	43.7	13.7	2	2	30	300	<25	0.005	5.3	0.040	0.058
Water, filtered[2] µg/l	--	0.48	0.0029	<0.02	0.35	1.4	0.45	0.93	NA	0.28	0.98	<2.6
Sediments, µg/dry kg	--	1480	266	69	110	18300	14800	19600	NA	48400	0.005	0.014

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1 - NA = Not analyzed

2 - DDT and PCM = ng/l in unfiltered water

Table 2. Summary for mean concentrations of cesium (Cs) and the ratio of cesium to potassium in muscle tissues of fishes from the Salton Sea and the Gulf of California. Concentrations based on wet weight. From Young (1970).

Common Name	Scientific Name	Trophic Assignment	Cs µg/kg		K g/kg		$Cs/K \times 10^6$	
			Sea	Gulf	Sea	Gulf	Sea	Gulf
Orange Mouth corvina	*Cynoscion xanthulus*	IV-V	202	39	3.52	4.70	58	8
Gulf croaker	*Bardiella icistius*	III-IV	98	54	3.43	4.20	29	13
Sargo	*Anisotremus davidsoni*	III-IV	84	36	3.58	4.10	24	9
Threadfin shad	*Dorosoma petenense*	III	46	--	3.07	--	15	--
Striped mullett	*Mugil cephalus*	II	30	51	3.38	4.03	9	13

Table 3. Summary of median concentrations (n = 3) of cesium (Cs), potassium (K), ratio of the two (Cs/K), and total mercury (Hg) in muscle samples of fish from Newport Bay, California, collected July 1978. Trophic level assignments tentative.

Common Name	Trophic Level	Size kg	Cs µg/wet kg	K g/wet kg	Cs/K $\times 10^6$	Total Hg mg/wet kg
Striped bass	IV-V	0.25[1]	21.7	4.39	4.94	0.37
Spotted sandbass	IV-V	0.31[1]	22.6	4.10	5.51	0.20
Yellowfin croaker	III-IV	0.21	19.8	3.58	5.53	0.050
Topsmelt	III	0.05	12.4	3.36	3.69	0.051
Striped mullet	II	2.7	16.8	3.76	4.47	0.010
Striped mullet	II	0.59	16.1	4.49	3.59	0.017

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[1] = viscera removed

Table 4. Summary of median concentrations of cesium (Cs), the Cs/K ratio, and median concentrations of seven trace metals, total DDT, and total PCB in fishes and invertebrates from the Palos Verdes coastal shelf, samples collected 1975-1976.

Common Name	Trophic Assignment	Cs µg/kg	Cs/K × 10^6	µg/kg					mg/kg			
				Ag	Cd	Cr	Cu	Ni	Hg	Zn	DDT	PCB
Boccacio	IV-V	77.4	16.6	8	<2	<10	0.15	58	0.14	4.7	0.61	0.11
Scorpionfish	IV-V	54.4	13.6	22	4	36	0.15	154	0.38	3.9	3.5	0.45
Sanddab	III-IV	48.1	12.1	5	3	32	0.19	56	0.081	3.2	6.1	0.46
Yellow crab	III-IV	21.1	6.5	95	4	80	7840	261	0.064	25	1.5	0.23
Prawn	III-IV	37.3	11.2	<4	32	<19	1970	<28	0.080	9.8	0.15	0.086
Scallop	II-III	21.4	5.3	<3	800	250	240	46	0.056	20	0.16	0.014
Abalone	II	24.3	7.5	28	41	950	3350	680	0.010	6.1	0.001	0.027

Trophic Spectrum Analysis of Fishes In Elkhorn Slough and Nearby Waters

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Introduction

Many studies have been designed to determine how fish assemblages in near-shore waters are structured, but few have stressed functional relationships between these fish assemblages and their benthic food sources. Indeed, Mills (1975) contended that "benthic studies are of vital importance to our understanding of marine productivity, particularly the fisheries". Several earlier studies by Darnell (1961, 1970) approached "community nutrition" for the fishes occupying Lake Pontchartrain, Louisiana by summarizing results of his food studies using a technique he called the "trophic spectrum". This approach requires a knowledge of the dominant fishes which are members of a particular system and detailed information about their feeding habits, usually based on stomach content analysis.

Information on the habits and life histories of the prey that these fishes consume is also important, since the fish predators are then categorized according to the general kinds of prey consumed. Darnell (1961) used the following categories of prey: (1) fishes; (2) macro-bottom animals; (3) micro-bottom animals; (4) zooplankton; (5) phytoplankton; (6) vascular plant material; and (7) organic detritus. He then placed each species of fish, and sometimes different life stages of the same species, into one grouping of these categories, and expressed the relative proportion that each general prey category contributed to the diet of the fish graphically by plotting the "percent volume of food observed in the particular food category". Thus, a great deal of functional data could be presented in a visually understandable manner, allowing the various food web interactions to be more easily understood.

In 1974, we started accumulating a quantitative data base of distribution and abundance information on benthic invertebrates, fishes and zooplankton inhabiting Elkhorn Slough, California (Nybakken, et al., 1977), thus making a similar kind of study possible for this coastal ecosystem. Since the habits and various aspects of life histories of benthic invertebrates were studied in some detail and the feeding habits of the more common fishes in the slough and nearby waters were analyzed, it was possible to investigate ecological interactions among fish species and their prey and to assess their importance in structuring the communities in this ecosystem.

The accumulation of this large data base stimulated several questions that could now at least be qualitatively approached. First, what is the food base utilized by fishes living in Elkhorn Slough and nearby waters? Second, does the food base used by slough fishes differ from that used offshore? Finally, if there are differences in food bases inshore and offshore, do they reflect differences in the food base available in these two habitats? To answer these questions, we have modified Darnell's trophic spectrum analysis technique so that it could be applied to the assemblages of fishes in Elkhorn Slough and nearby waters. The main objective of this paper is to present this ecosystem-level technique as we have modified it, and to demonstrate the kinds of information that can be gathered from such an analysis. A more thorough presentation of our specific results is forthcoming.

Materials and Methods

Elkhorn Slough is a shallow coastal embayment located in the center of Monterey Bay, California, which has a long history of scientific faunal studies, beginning with the work of MacGinitie (1935). During a two-year period starting in August of 1974, fishes were sampled monthly at three locations in the slough and at two locations in the ocean, north and south of the harbor mouth (see Nybakken, et al., 1977 for detailed map). A small otter trawl with a 16-foot headrope and 1-1/2 inch stretch mesh liner in the codend was towed behind a 16-foot Boston Whaler into the tidal flow. All species of fishes and macroinvertebrates were identified, counted, measured and weighed, and all catch data were standardized to catch in numbers and biomass (weight) per ten-minute tow. At the end of the two-year study, all catch data for each of the four stations were combined, producing overall mean abundances, percent by number and ranks of species collected (see Figures 1 and 2). For this study, "common" species were defined as those that comprised at least one percent, by number, of the total otter trawl fish catch at each location. To assess similarity of species composition among locations, two similarity indices were used. One, species similarity, is based on presence and absence data, and is calculated by dividing two times the number of joint occurrences of species in two locations by the product of the number of species occurring in each location. The other, percent similarity, is calculated by summing the smallest percent by number of each species pair between both locations (Odum, 1971). It is recognized that otter trawls do not adequately sample all species and therefore, this analysis is limited to fishes caught by this sampling technique solely.

Subsamples of each common species were preserved for stomach content analysis, and stomachs of these species were analyzed from each station, forming the baseline information used in the trophic spectrum analysis. In some cases, only a few individuals of a species at a specific location were available for stomach content analysis. In general, however, sample sizes were quite large (see Figures 1 and 2). Prey from fishes selected for analysis were identified to the lowest possible taxa and counted. The percent by volume of each prey group was subjectively estimated. Two indices of prey importance were calculated: the numerical importance of each prey taxon was evaluated as the proportion of its abundance to the total abundance of all items found in this species, and the volumetric importance was determined as the average percent volume. Ultimately, it would be desirable to express dietary value in terms of biomass and numbers of calories per gram of prey. Nevertheless, by expressing the prey used by each fish species, both in numerical and volumetrical terms, it is possible to more comprehensively evaluate the actual importance of that prey item to the predator involved.

Prey categories were then established subsequent to observations with investigators studying the food organisms such as zooplankton and invertebrates in this ecosystem (see Nybakken, et al., 1977). These prey categories were based upon knowledge of the habits of the prey species, their potential availability to the fish predators and the likelihood that they would suggest behavioral features typical of the fish while feeding. Our categories bear a striking resemblance to those proposed by Darnell (1961); however, we feel that the differences better fit the fishes that comprise our assemblages. Categories were divided into four general types: (1) mobile fauna (including fish and cephalopoda, crustacea and zooplankton); (2) epifauna (including polychaetes, crustacea, molluscs, echinoderms and eggs from both fish and invertebrates); (3) infauna (including "worms" such as polychaetes, nemerteans, phoronids and echiuroids, molluscs and foraminifera); and (4) flora (including algae, vascular plants and detritus).

The stomach content data were then combined for each fish predator in order to determine which categories best described that fish's feeding habits. These fish predators were then arrayed from plankton feeders to infaunal, epifaunal and mobile epifaunal feeders. The proportion of the diet that was contributed by each general prey category was expressed by a rectangle, with the percent by volume being the vertical dimension and the percent by number being the horizontal dimension of the box (see Figures 1 and 2). This technique allows the relative importance of each prey category to be visually assessed for each fish predator. Since this paper is intended only to introduce an analytical technique, the trophic spectra from only two locations are presented.

We decided that it would be fruitful to extend the analysis beyond the scope originally proposed by Darnell (1961, 1970) and attempt to compile total system trophic spectra, lumping all fish predators within each location in order to determine the food base utilized by all fishes occupying an area. In our first attempt, a total system trophic spectrum (Figure 3) was constructed, combining the results of all fish species by location. Here, the relative contribution of each prey category to all of the fishes at each location was expressed as percent volume. Second, since the more numerically dominant species of fish are probably more important in energy turnover than are rare species, an adjusted total system trophic spectrum was constructed, which weighted the percent volume of each prey category consumed by the relative numerical abundance of the fishes which consumed it (Figure 4). Finally, since ranking the fishes by their relative biomass might be a more apt way of expressing functional interrelationships, a third total system trophic spectrum was constructed which weighted the percent volume of each prey category consumed by the relative biomass of the fishes which consumed it (Figure 5). These trophic spectra were then compared to determine which prey categories formed the major components of the food base in each of the four particular habitats.

Finally, since the invertebrate studies were in progress at the same locations during the same time periods, a rough index of prey category availability could be estimated. Benthic invertebrates were sampled both intertidally and subtidally near the stations sampled for fishes, using cores of either 0.018 m^2 or 0.005 m^2 surface areas (Nybakken, et al., 1977). Samples were screened using 0.5 mm square mesh sieves, relaxed in propylene phenoxetol and then preserved in 10% formalin. Organisms were stained with rose bengal, sorted and identified to the lowest possible taxa. Invertebrate prey species were placed into the general categories used for prey in the fish feeding study and the percent by number from these core samples were plotted on graphs similar to the total system trophic spectra (Figure 6). Since several prey categories were not sampled by these cores, no estimate of their availability could be made. These categories included fish and cephalopoda, mobile crustacea, fish and invertebrate eggs, foraminifera and all flora.

Results and Discussion

During this two-year survey, 209 otter trawl samples were taken, which collected a total of 15,323 fish. In all, 81 species of fish were captured, of which 24 were "common". The number of common species varied little among stations, but the densities (numbers and weights per tow) varied considerably, with the bridge station having the highest and the ocean station producing the lowest values (Table 1). Both indices of species similarity indicated that the fish fauna within the slough were more similar to each other than any slough station was to the ocean location (Table 2). This suggests that the food bases might differ between the inshore slough habitats and the nearby ocean habitats.

TABLE 1: SUMMARY OF CATCH STATISTICS FOR THREE SLOUGH AND SINGLE OCEAN STATION

	Ocean	Bridge	Dairies	Kirby Park
Total number of species	33	38	38	26
Number of "common" species	13	14	15	12
Dominance index	0.12	0.26	0.19	0.27
Total numbers	949	7326	3245	3803
Mean number per tow (95% C.I.)	12.5 (4.1)	209.2 (257.6)	66.2 (47.0)	98.9 (53.4)
Mean biomass per tow (95% C.I.)	1044.4 (890.9)	16258.7 (7978.9)	2412.4 (724.4)	1911.2 (760.8)
Number of tows	76	35	49	49

TABLE 2: TWO MEASURES OF SPECIES SIMILARITY FOR ALL COMPARISONS OF FISH ASSEMBLAGES BETWEEN SLOUGH AND OCEAN STATIONS

SPECIES SIMILARITY

	OCEAN	BRIDGE	DAIRIES	KIRBY PARK	
OCEAN		0.26	0.24	0.26	
BRIDGE	0.52	--	0.76	0.59	PSI
DAIRIES	0.50	0.90	--	0.50	
KIRBY PARK	0.48	0.77	0.89	--	
		SS			

Stomach content analyses were performed on 2,451 individuals of the 24 common species of fishes occupying all locations. Since only the trophic spectra from the ocean and Kirby Park slough stations will be presented here, the total number of stomachs analyzed totaled 1,390; these data are for nineteen species of fish.

Differences in the food bases of the two locations were apparent when the trophic spectra were studied. The ocean trophic spectrum was comprised of four zooplankton feeders, two infaunal "worm" feeders, four epifaunal crustacea feeders, one mobile crustacea and infaunal worm feeder and three larger, mobile crustacea or fish feeders (Figure 1). Kirby Park, the most inland slough station, had a trophic spectrum with fish species, one that consumed algae, two that ate zooplankton or eggs, six mixed feeders that consumed infaunal "worms" and molluscs along with epifaunal crustacea and molluscs, one strictly mollusc feeder and three smaller fish that were primarily epifaunal crustacea feeders (Figure 2).

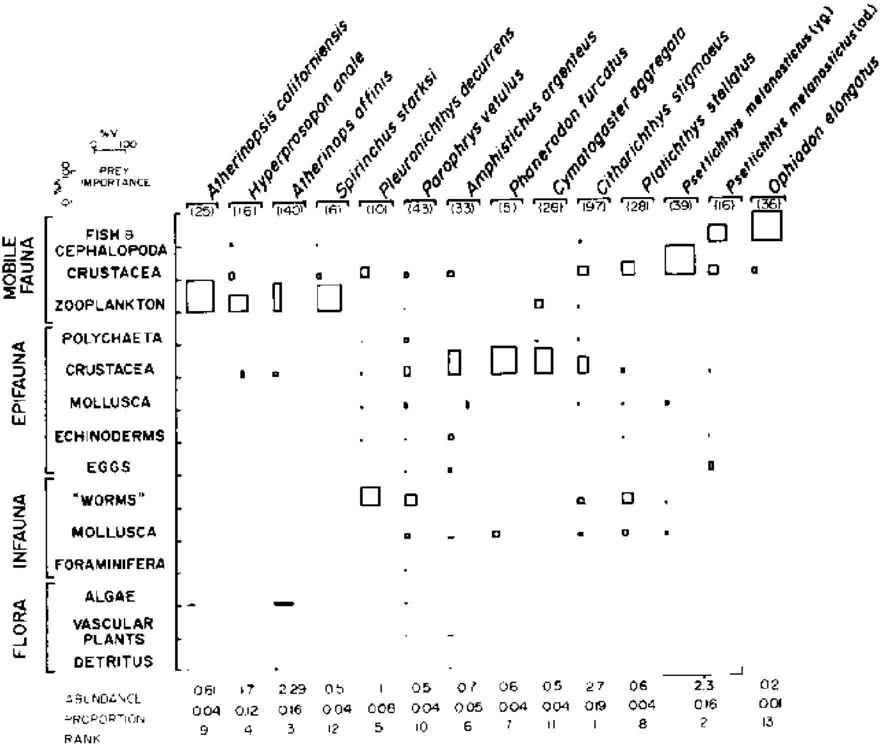

Figure 1: Trophic spectrum of the fish assemblage found at the ocean station, Monterey Bay, California.

Modification of Darnell's original trophic spectrum approach to include both numerical and volumetric measures has enabled the recognition of previously unimportant prey categories. For example, at the ocean station, Atherinops affinis, which ate few but voluminous bits of algae (Figure 1), would have been categorized as a planktivore, whereas it actually appears, on the basis of prey volume, to be an algae feeder.

Similarly, at the Kirby Park station, both species of atherinids would be categorized as egg and infaunal "worm" feeders by numerical prey importance values, but when judged by volume, algae again appear to be the major prey item (Figure 2). Since other organisms occurred in the diet of these fishes, it could be suggested that they consume algae, in part, for the organisms that associate with the algae.

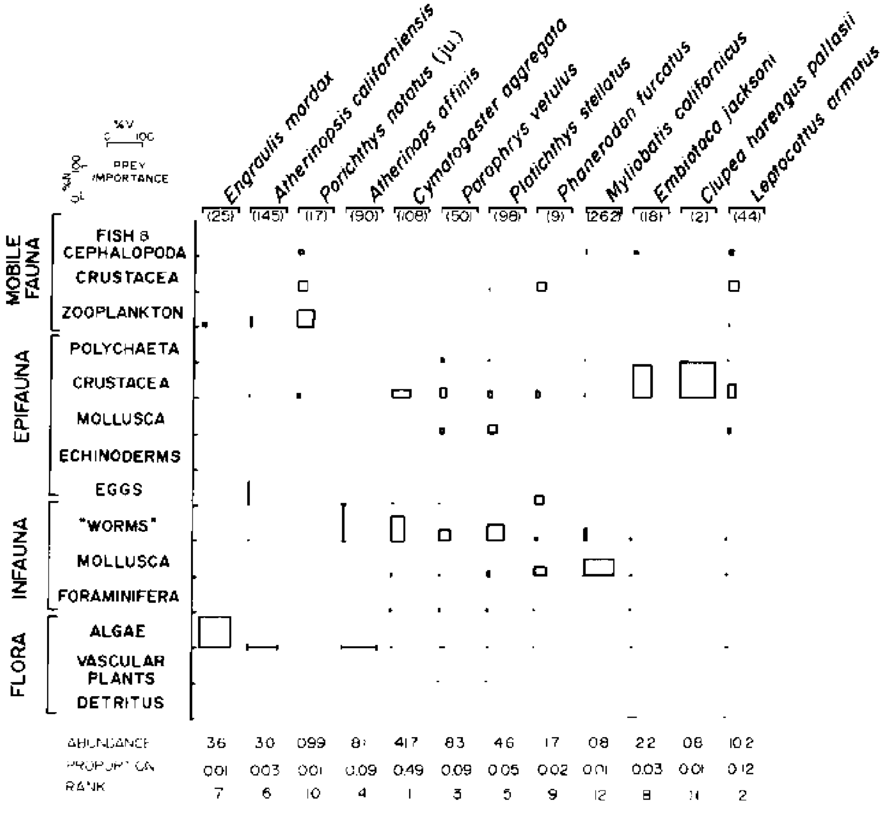

Figure 2: Trophic spectrum of the fish assemblage found at the Kirby Park station in Elkhorn Slough, California.

In contrast with the trophic spectra already presented, the unadjusted total system trophic spectrum did not reflect the apparent differences between the ocean and slough habitats (Figure 3). The relative contribution of prey categories at the ocean station appeared quite similar to that found for slough fishes, with mobile crustacea, epifaunal crustacea, infaunal "worms" and mollusca and algae being dominant. However, when adjusted by the relative numerical abundance of fish predators, the total system trophic spectrum (Figure 4) uncovered a striking difference in the food base utilized by the fishes in these two habitats. At the ocean station, the more numerous fishes consumed primarily

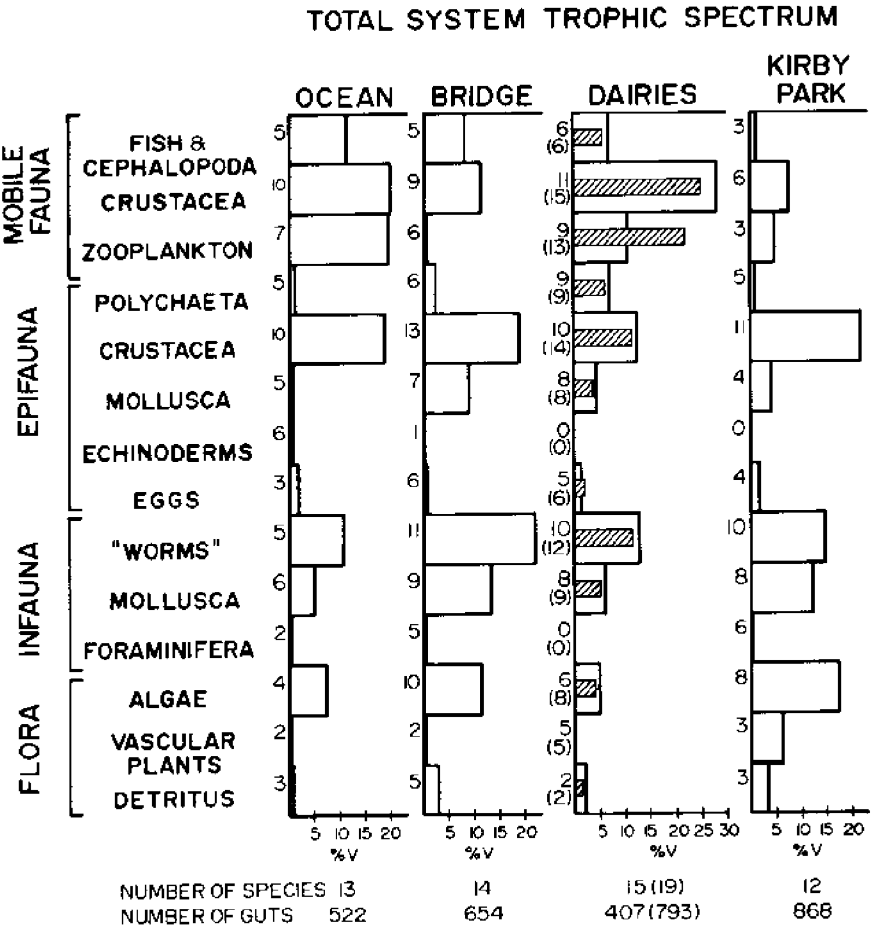

Figure 3: Total system trophic spectrum for three slough and one ocean station near Elkhorn Slough, California. Values in each spectrum are the mean percent by volume values of each prey category for all fish species, unadjusted by relative abundance or biomass.

mobile, epifaunal crustacea and echinoderms. In contrast, fishes from all three slough stations had consumed predominantly epifaunal crustacea (mostly amphipods) and infaunal "worms". The total system trophic spectrum adjusted by relative biomass or the fish predators further strengthened these results (Figure 5). Again, offshore, mobile crustacea dominated the diets of these fishes, but echinoderms became less and infaunal "worms" became more important to these fishes. Inshore, similar prey categories were contributing to the fishes' diet, dominated by epifaunal crustacea, infaunal "worms" and mollusca, with the mobile crustacea fraction decreasing substantially.

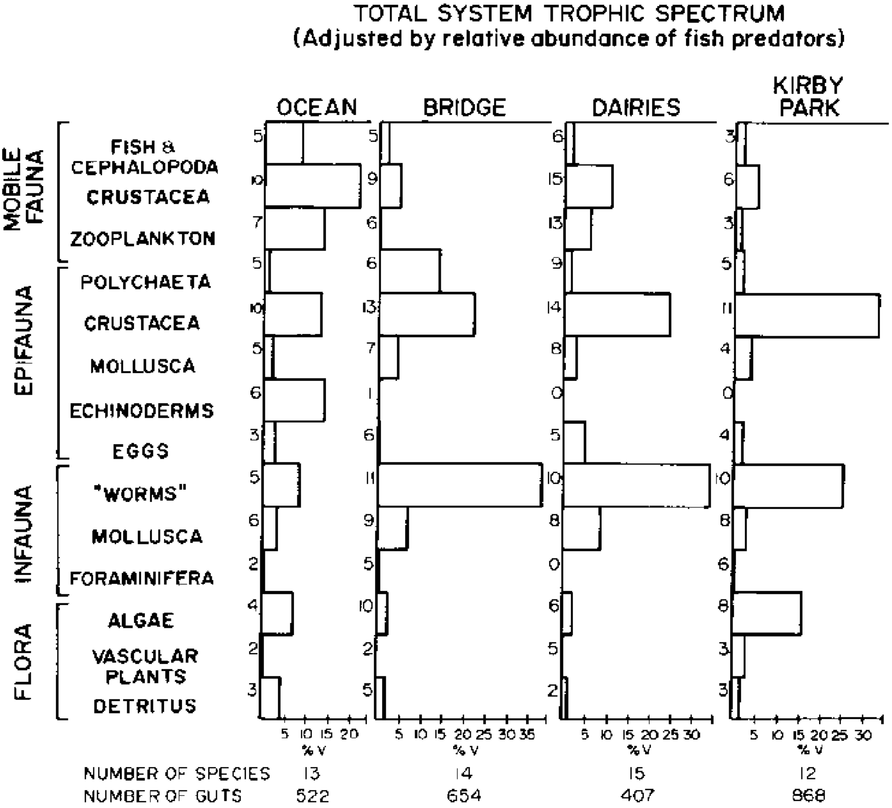

Figure 4: Total system trophic spectrum adjusted by relative abundance of fish predators for the three slough and one ocean station near Elkhorn Slough, California.

Finally, the admittedly rough availability data from the subtidal and intertidal core samples indicate that the apparent difference in the food base for fishes between habitats may indeed be due to differences in prey availability (Figure 6). These limited samples indicate, for those prey species sampled, that epifaunal crustacea and echinoderms dominated the sediment offshore, while infaunal "worms" and some epifaunal crustacea were more important, and hence perhaps more available, inshore.

It is intended that this paper merely present an approach to studying the feeding habits of an entire fish assemblage in relation to the available prey species and their behavioral and life history characteristics. This approach appears to serve a useful function in a preliminary assessment of the various factors that structure nearshore communities. It also suggests that a great deal of the structure seen in

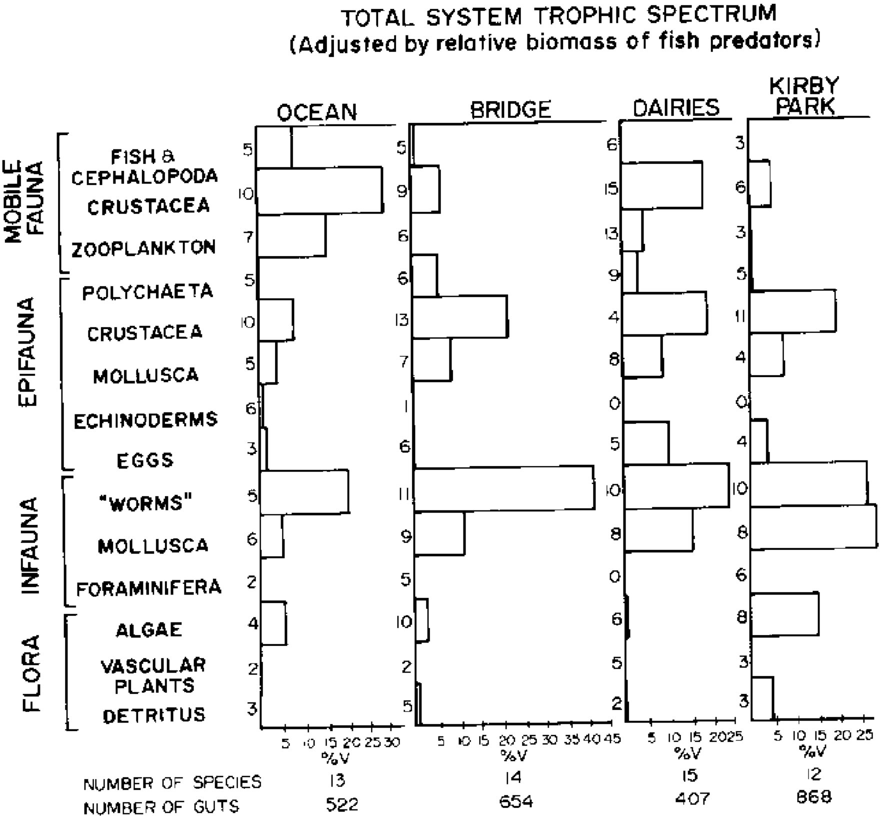

Figure 5: Total system trophic spectrum, adjusted by relative biomass of the fish predators, for the three slough and one ocean station near Elkhorn Slough, California.

otter trawl-caught fish assemblages in Elkhorn Slough and the nearby ocean waters is reflected in real differences in the food base available and being utilized. With more time and sufficient effort, a better understanding of the functional relationships described can be achieved. It is hoped that this paper stimulates others to use this kind of ecosystem-level approach to studying the feeding ecology of fishes and its role in structuring communities.

Acknowledgements

We are indebted to the invertebrate research team at Moss Landing Marine Laboratories, especially C. Jong and J. Nybakken, for their tireless aid in identifying invertebrate prey fragments and for providing the data used in estimating availability. The data on feeding habits of two atherinid species were contributed by A.A. Ruagh. Special thanks go to Lynn McMasters for preparing the illustrations. M. Yoklavich reviewed

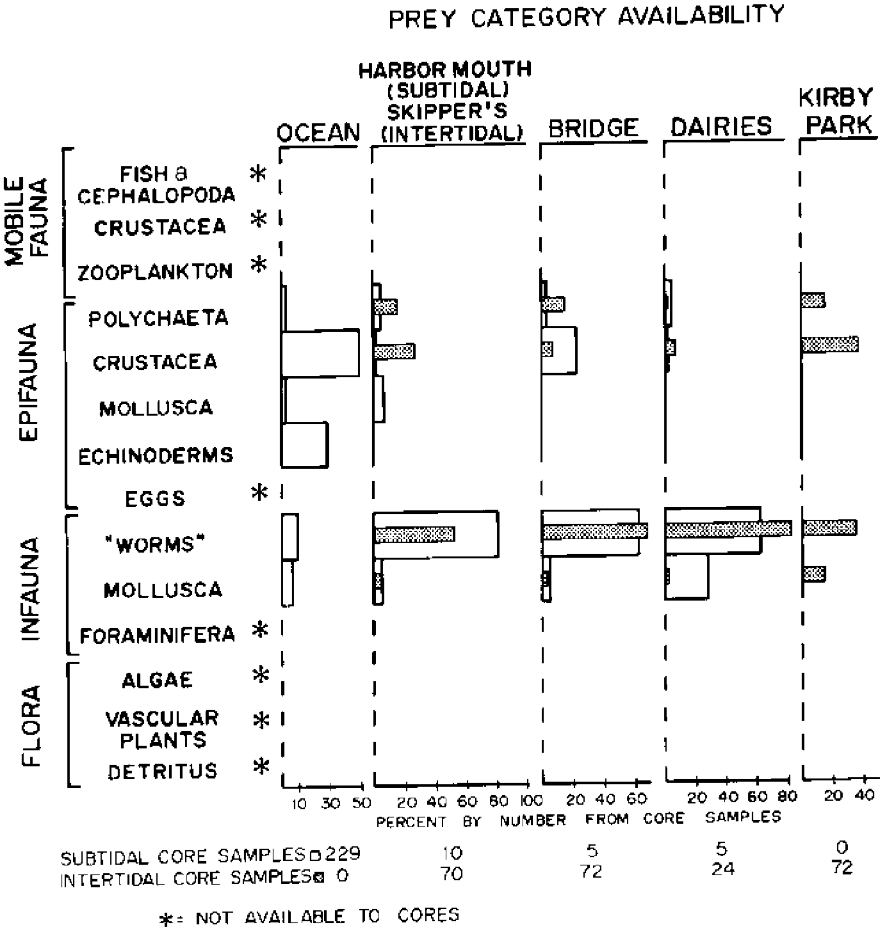

Figure 6: Prey category availability for four slough and one ocean station near Elkhorn Slough, California.

the manuscript. This research was supported in part by the Pacific Gas and Electric Company and the NOAA Office of Sea Grant, Department of Commerce. Finally, we wish to thank the California Coastal Commission for stimulating interest in funding this research.

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Feeding Selectivity of Dover Sole Off Oregon

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Abstract

Factors influencing the selection of food by Dover sole were investigated by analyzing stomach contents of fish and serially sectioned box core samples for benthic invertebrates. Samples were taken in two areas of high Dover sole abundance on the central Oregon continental shelf (Sea Grant Station 29: 119 W, SGS 10: 426 m) in July, 1976. Thirty-five principal prey taxa (taxa occurring in at least 10% of stomachs containing food) were identified from fish sampled at 119 m. Twenty-five principal taxa were found at 426 m. Relative abundances of prey taxa in stomachs and box core samples were compared using the Ivlev index of electivity for each principal taxon and chi square tests.

At both locations, polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weight and numbers. Polychaetes and ophiuroids were generally positively selected at both locations, i.e., they were more common in fish stomachs than in box core samples. Molluscs were generally negatively selected at both locations. Crustaceans were positively selected at 426 m, and were consumed non-selectively at 119 m. The box core samples may, however, underestimate crustaceans and hence give artificially higher values of electivity.

An interative chi-square test, based on differences in frequency of occurrence of prey items consumed by different size-classes of predators, was used to determine the dependency of diet on fish size. Fish were divided into two size groups (feeding stanzas) which differed significantly in frequency of occurrence of a prey species. Significant changes in occurrence with fish size occurred for 27 of the principal prey taxa at 119 m and five of the principal prey taxa at 426 m. These changes indicate that composition of fish diet varies with size.

Electivity indices for prey species which increased in frequency with increased fish size were compared between feeding stanzas for each prey. The larger the fish size at which the significant difference in prey frequency occurred, the larger the increase in electivity across the interval. This implies increased selectivity by larger sized predators.

Body size of a prey taxon was positively correlated with fish length at which the significant difference in prey frequency occurred: larger fish consumed large sized prey. However, successful capture of prey also appeared to vary with size of predator: the mean depth of a prey taxon within the sediment was positively correlated with the length of the fish at which a significant increase in prey frequency occurred. It may be energetically advantageous for larger fish to extract a few large prey from below two cm in the sediment as opposed to consuming many small superficially occurring prey. Alternatively, small fish may be physically unable to extract prey from deep within the sediment.

Few size-related changes in diet were found at SGS 10. Environmental abundance of a preferred taxon, polychaetes, was lower at SGS 10 than SGS 29. Therefore, Dover sole may change its feeding strategy from a specialized predator whose feeding habits vary with its body size to more of a generalist consuming more types of preferred prey regardless of prey size. Because vertical distribution of prey within the sediment at SGS 10 was shallower than at SGS 29, the advantage afforded large fish in removing deeply buried prey may be eliminated.

(This abstract has been taken from a Master's Thesis by the author entitled "Feeding Selectivity of the Dover Sole (*Microstomus pacificus* Lockington) off Oregon (1979, School of Oceanography, Oregon State University). A manuscript is in preparation.)

Preliminary Observations on the Distribution, Abundance, And Food Habits of Some Nearshore Fishes in the Northeastern Gulf of Alaska (Abstract)

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Abstract:

The marine fishes are an important component of the inshore fauna of the northeastern Gulf of Alaska. Direct observations of fishes living in both exposed and protected habitats of the Gulf have been made while diving during the years 1974 to 1978. The shallow water fish communities of this region are represented by at least 50 species which are typically found in the nearshore zone. Sixteen percent (8/50) of the fishes identified to date were previously unreported in these waters, and as such represent northern range extensions in the eastern Pacific.

To date, a total of 4,200 square meters of sea floor has been examined for fish density and vertical distribution along randomly or haphazardly placed transects. Another 2,310 square meters of underwater terrain was surveyed within fixed transect bands. Most of the counts were replicated to account for differences in tidal height and current direction, time of day and the activity patterns of the individual fish. The rockfishes (Scorpaenidae); greenlings (Hexagrammidae); wolffishes (Anarhichadidae); and ronquils (Bathymasteridae) dominated the rocky exposed habitats, while more protected locations were numerically dominated by sulpins (Cottidae); pricklebacks (Stichaeidae); sand lances (Ammodytidae); righteye flounders (Pleuronectidae); greenlings (Hexagrammidae) and codfishes (Gadidae).

Samples from these fish populations have been taken for the purpose of describing their food habits, thus leading to a better understanding of tropic interaction and energy flow in the coastal zone. Most of the specimens were collected during daylight hours with spears and hand nets. The remainder were either caught in gillnets or taken on hook and line. The stomach contents of 275 specimens, comprising 24 species, have been examined for food items. Dietary trends have been identified for some species. However, with a number of others, more samples are

needed in order to attain a higher resolution of understanding. Important prey of the bottom feeders included gammarid amphipods, brachyuran crabs, caridean shrimps, ophiuroids, caprellid amphipods, gastropods, mussels and fish eggs. Whereas, fishes that feed and spend a great deal of time in the water column preyed heavily upon zooplankters such as calanoid copepods, megalops crab larvae, tomopterid polychaetes, chaetognaths, small fishes, and amphipods.

Patterns of habitat utilization are also being studied in relation to a few key parameters which seemingly effect spatial distributions and contribute to resource partitioning. Emphasis has been placed on studying the characteristic or representative important species in these habitats. Fishes have been included in this category on the basis of their numerical importance, commercial value or functional role in the maintenance of the natural system.

A series of color, 35 mm slides were made for the purpose of recording on film the different kinds of habitats and ichthyofauna present in each study area. This has been done so that even the uninformed or casual observer can view these assemblages as they occur in nature.

The Feeding Behavior of Three Myctophid Species in the Eastern Subarctic Pacific

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Introduction

Myctophid fish are conspicuous and abundant components of the mesopelagic fauna worldwide, but little is known about their biology. Much of the research to date on these fish has concerned their relationships with sonic-scattering layers. As part of a project whose intent was to comprehend for predictive purposes the occurrence, intensity and vertical distribution of sound-scattering layers, I conducted an intensive study of the relationships between the feeding behavior of several species of myctophid fish and their vertical distributions and diel migrations, especially as related to the vertical distributions and migrations of their zooplankton prey. Specifically, I was interested in whether the vertical distributions and diel migrations of these fish were affected by the distribution and availability of forage organisms.

It has long been assumed that the primary reason for the diel migrations performed by some species was to enable the fish to feed during the night in the upper layers of the ocean where their prey, predominantly zooplankton, is most abundant. Inhabiting mesopelagic depths during the day presumably provides these fish a refuge from larger predators. These are only assumptions, however, and in fact, little is known of the feeding behavior of myctophids. Although there are a number of reports in the literature on the feeding behavior of myctophids, most have only described the diets of the fish, and few have attempted to correlate aspects of feeding behavior with the vertical distributions of the prey organisms.

One of the most comprehensive studies of mesopelagic fish feeding behavior was that of Merrett and Roe (1974). Although they utilized zooplankton samples taken concurrently with their fish samples, their interpretations of the results were hindered by the fact that all of their fish were collected below 200 m depth, so that migrating fish were not caught throughout the day and night. They concluded by saying that "a more extensive study made from collections at a variety of selected depths designed to sample the species under investigation throughout the 24 hour period would be a valuable contribution". This is what I attempted to do.

Methods

The mesopelagic community in the subarctic North Pacific was chosen for intensive investigation for several reasons. Previous investigations had shown that myctophids were abundant in the area and that they were distributed more shallowly than in lower latitude regions. This would simplify sampling. In addition, both the zooplankton and micronekton communities were characterized by low diversity, and this would facilitate interpretations of trophic relationships. Finally, a great deal was already known about the zooplankton in the subarctic due to sampling from the Canadian weather ships at Station P. Sampling for this study was performed in the central Gulf of Alaska, away from coastal effects, during two cruises in the summers of 1974 and 1975.

In order to analyze the relationships between vertical distributions, migrations, and feeding behavior of the fish, it was necessary to sample the fish and their zooplankton prey nearly simultaneously, using trawls which provided vertically stratified, uncontaminated samples over short intervals of depth and time. Opening-closing zooplankton and micronekton trawls were designed for this purpose (Frost and McCrone, 1974). Scattering layers were observed using a 12 kHz echosounder and replicated day and night vertical series were taken with both trawls to at least 50 m below the non-migratory sound-scattering layer. In order to study the feeding chronology of the myctophids, time series samples were taken throughout 48-hour periods both in the scattering layer during the day and near the surface at night.

Many of the previous studies of myctophid stomach contents were not very comprehensive. Often, the stomach contents of fish of greatly different lengths were lumped together although there were almost certainly size-related differences in diet. For this reason, I took replicate fish (usually 10 unless fewer were available) only from within a given size class for each sample. I removed the stomachs from the fish and placed the contents in glycerine on a microscope slide. I identified prey items to species whenever possible, and then counted and recorded them. It was very important that prey items be identified to species in order to show any relationships between aspects of the feeding behavior of the fish and the distribution of the prey organisms. In many previous studies, prey were only identified to major taxa (copepods, euphausiids, etc.) so such interpretations could not be made. Another problem with many previous studies was that the investigators attempted to study feeding chronology without taking time series samples at one location. Often samples from different times of the day or night were compared between days, seasons, even years in some cases. It is not surprising, therefore, that it usually was not possible to answer the question of when the fish were feeding. My samples were taken from closely spaced time series trawls designed to follow the fish throughout their migrations during 48-hour periods in each year.

Results

The mesopelagic fish community was indeed a simple one. Three myctophid species, Stenobrachius leucopsarus, Diaphus theta, and Protomyctophum thompsoni, comprised 80% or more of the total fish catch in the vertical series. These three species had the same rank order of abundance in each year. Stenobrachius leucopsarus and Diaphus theta performed diel vertical migrations over a depth range of 250-400 meters. These fish spent the day between 300-450 m depth and at night migrated into the upper 50 m. Protomyctophum thompsoni inhabited the 250-400 m depth stratum both day and night and did not migrate to the surface. Thus, all three species spent the day at similar depths. It was fortuitous that of the three abundant myctophid species, two were migrators and one was not, as this permitted me to compare and contrast the feeding strategies of migratory and non-migratory fish which inhabited the same depths during the day.

I identified a wide variety of prey organisms from the stomachs of the myctophids. These included calanoid, cyclopoid, and harpacticoid copepods, amphipods, decapods, euphausiids, isopods, ostracods, chaetognaths, larvaceans, pteropods, squid, fish, polychaetes and nauplii. Nearly every species found in the plankton samples was found in the fish stomachs. There was considerable overlap in the occurrence of individual prey items; many of the prey species were found in each of the three myctophids.

The feeding chronology of these fish was investigated by following the change in the number of prey items per stomach with time through the 48-hour sampling periods. The numbers of prey per stomach were normalized with a logarithmic transformation. A one-way analysis of variance then showed that for most of the size classes of each species considered, there were significant differences in the number of prey present in the stomachs at different times of the day-night period. For most of the size classes of Stenobrachius leucopsarus and Diaphus theta, the lowest numbers of prey occurred late in the afternoon or early in the evening, and then the numbers of prey rose through the night after the fish had migrated into the surface layer, reaching a peak just before the fish returned to depth. This suggests that these migratory fish fed most intensively during the night near the surface, but may have fed at a reduced rate during the day at depth.

To investigate the feeding chronology of the non-migrator, Protomyctophum thompsoni, it was necessary to combine the results from trawls taken on a number of different days. For all sizes of Protomyctophum thompsoni, the lowest numbers of prey occurred during the night and the highest numbers during the day. This suggests that feeding for the non-migratory myctophids occurred primarily during the day.

As the stomach contents for a given fish species and size class were being analyzed, one of the most striking differences between samples taken at different times of the day-night cycle was the variable composition of the prey items. At one time, the stomachs might contain primarily euphausiids, while at other times copepods might have been the dominant prey items. The proportions of the various prey species were normalized with an arcsin transformation. A one-way analysis of variance then showed that there were significant differences through time in the proportion of certain prey categories. Prey such as juvenile euphausiids and the copepod Pseudocalanus, whose distributions were shallow, occurred in highest proportion in the stomach contents of the migratory fish while the fish fed at night near the surface. Prey such as males of the copepod Metridia lucens and ostracods, whose distributions were primarily deep, occurred in highest proportion in the stomach contents of the migratory fish during the day at depth, and were absent from the stomachs during the night. The diet of these fish obviously depended to a large extent on what was available at a given depth and time. The ingestion of deep-dwelling prey demonstrated conclusively that feeding did occur at depth, although on a biomass basis prey eaten near the surface made up the bulk of the diet of the migratory myctophids.

Although the total list of prey species in the diets of these fish was quite long, most of the prey categories were rare. Often as few as four or five prey species made up 80% or so of a diet. By combining some rare categories, I found that I could collapse the prey list to an array of only 20 categories without sacrificing much information. This facilitated summarization and description of the diets of these fish.

Figures 1-3 detail the diets of individual size classes of the three myctophid species. In each, the prey categories are grouped by depth of habitat. Species that occurred primarily in the near-surface layer are found in the top groups. Species that inhabited the near-surface layer only at night, but migrated to greater depths during the day are found in the next group. Beneath that is a group of primarily deep-dwelling prey species. Finally, at the bottom is a group of prey categories that could not be assigned to one distribution or another. Within each group, the prey categories are arranged in order of decreasing size, the largest prey organisms located at the top, smallest at the bottom. Beneath each column are two numbers: the first is the number of fish examined; the second is the number of prey items identified. Below these numbers are the lengths of fish considered for each size class. The diets of each size class are represented as percent of the total number of identifiable prey items.

The diets of five size classes of Diaphus theta in 1974 are presented in Figure 1. It is readily apparent that the diets of these fish were dominated by a small subset of the available items. The dominance of shallow-dwelling prey in all size classes substantiates the earlier suggestion that feeding occurred primarily near the surface at night for the migratory species. There was a marked shift in the size of prey items utilized as the fish increased in size. Metridia lucens, which was the dominant prey species in the smallest fish, progressively decreased in importance, while the proportions of the larger euphausiids and the amphipod Parathemisto pacifica increased. The largest fish also had higher proportions of deep-dwelling prey in their stomachs, reflecting the deeper depth distribution of this size class.

The diets of five size classes of the other migrator, Stenobrachius leucopsarus (Fig. 2), were dominated by the copepod Metridia lucens over a wide size range, and euphausiids and Parathemisto pacifica never took on the importance they did for Diaphus theta. Except for the difference in importance of euphausiids and amphipods, however, there was considerable overlap in the diets of these two migratory myctophids.

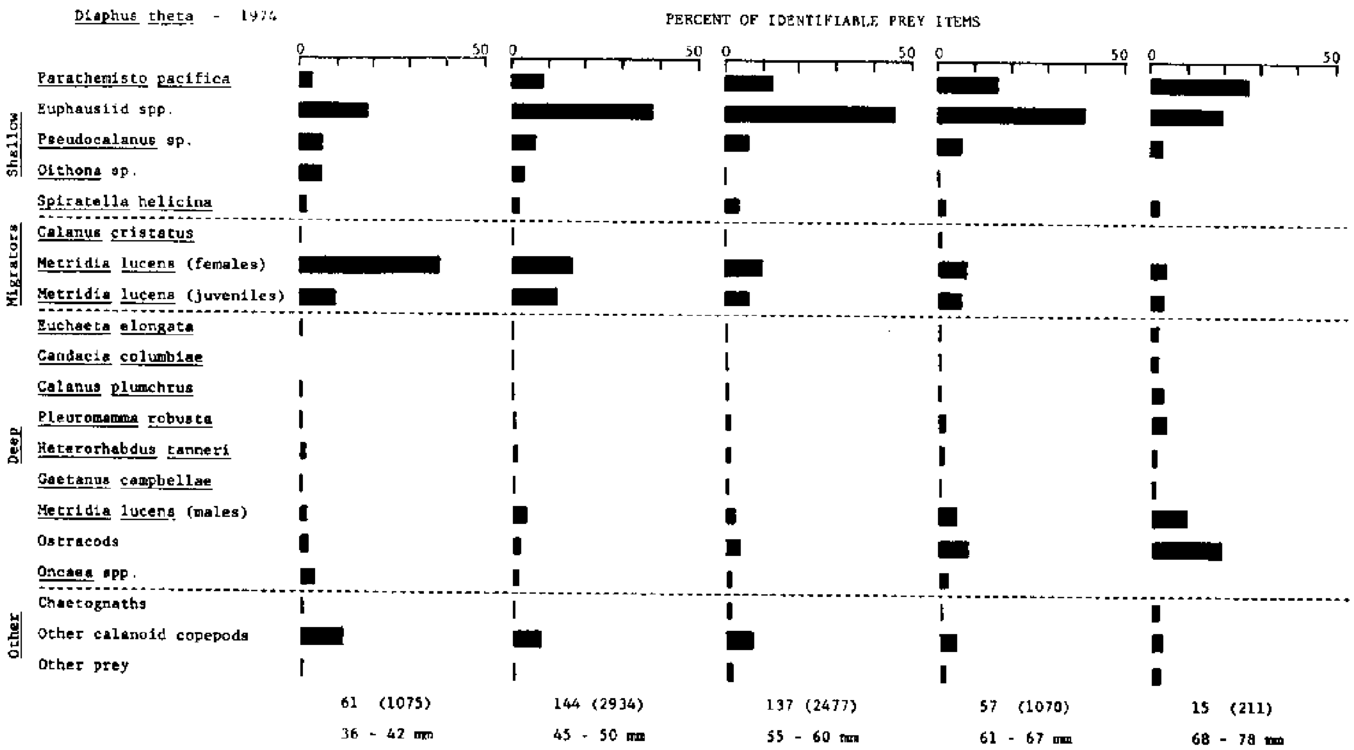

Figure 1. The diets of five size-classes of Diaphus theta during the 1974 cruise.

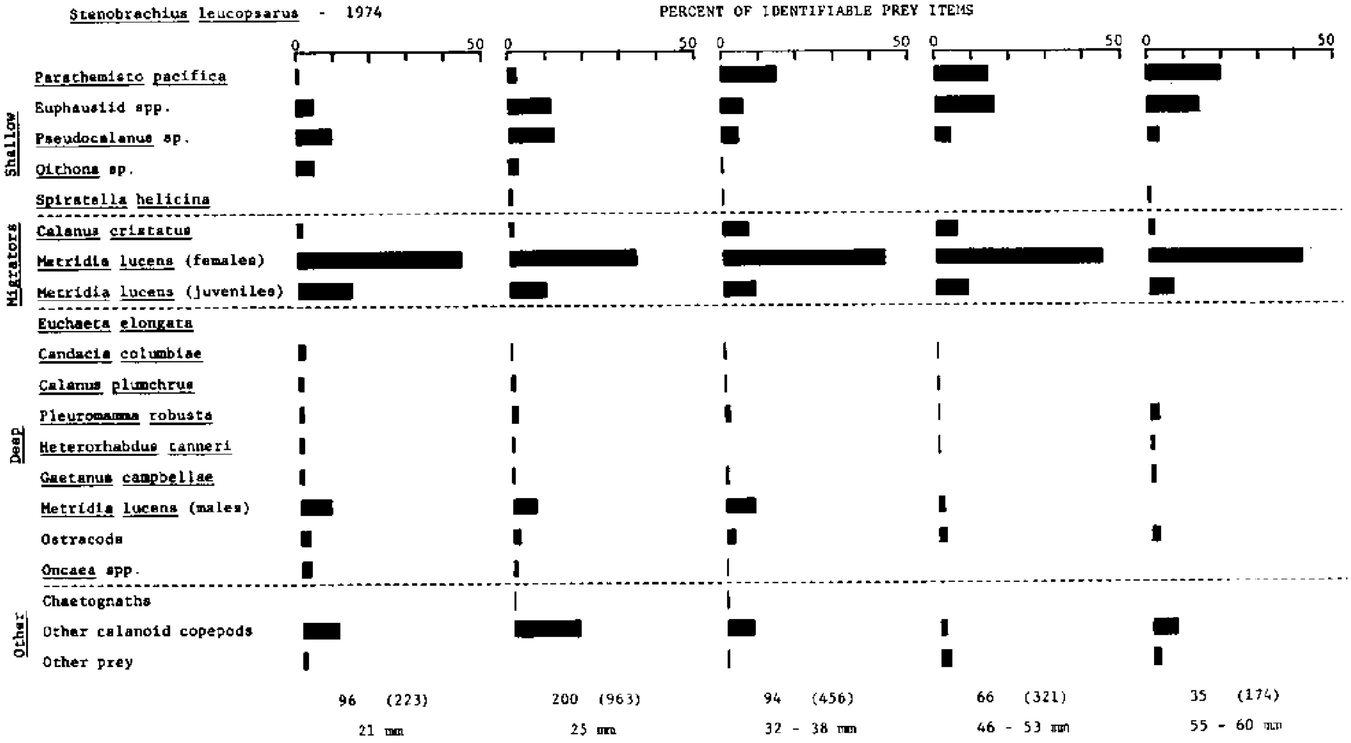

Figure 2. The diets of five size-classes of Stenobrachius leucopsarus during the 1974 cruise.

The diets of the three size classes of the non-migratory myctophid, Protomyctophum thompsoni (Fig. 3), were characterized by very low abundances of the prey species that were primarily shallow-dwelling, and a preponderance of deep-dwelling prey. There was little overlap, therefore, between the diets of the non-migratory myctophid and those of the two migratory myctophids. There was a shift in the size of prey ingested, as the most abundant prey in the smallest fish was the small cyclopoid Oncaea, whereas the larger fish had more of the larger species of deep-dwelling copepods.

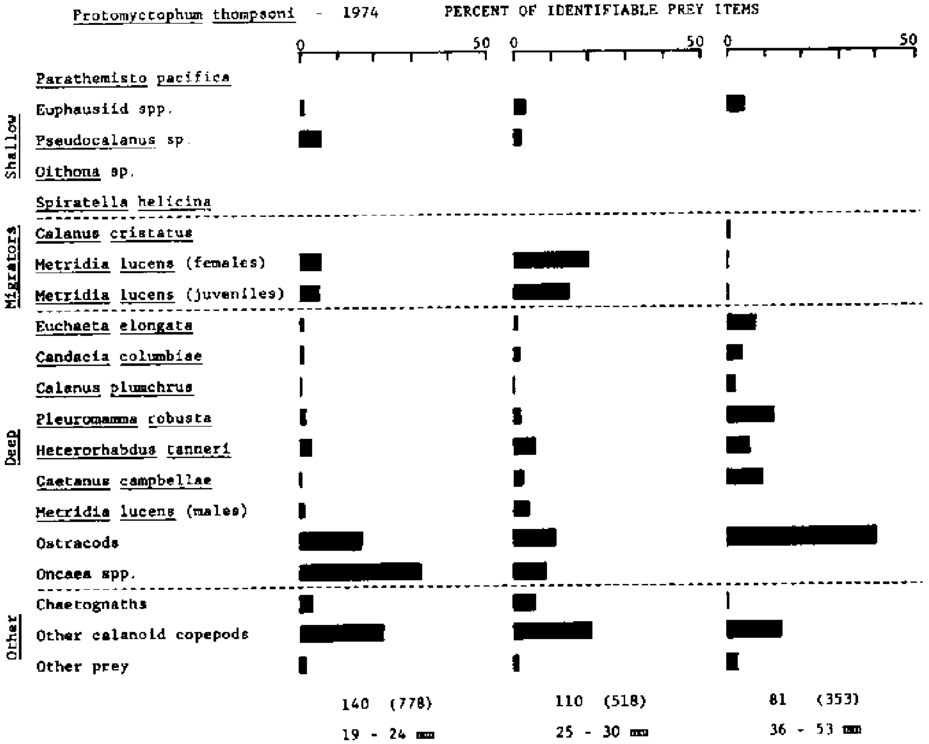

Figure 3. The diets of three size classes of Protomyctophum thompsoni during the 1974 cruise.

During the 1974 cruise, the near-surface zooplankton community was dominated by juvenile euphausiids and the copepod Metridia lucens, both of which were important prey items for the migratory myctophids. During the 1975 cruise, euphausiids were much less abundant and the zooplankton community was dominated by the large copepods Calanus plumchrus and Calanus cristatus. Calanus cristatus had been present the previous year but was much less abundant. Calanus plumchrus in 1974 had already begun overwintering at depths greater than 400 m.

In 1975, Diaphus theta, which had ingested many euphausiids in 1974, ingested very few. It did not shift to utilizing the abundant Calanus plumchrus and Calanus cristatus, but was largely dependent on Metridia lucens and ostracods. Stenobrachius leucopsarus, however, was taking advantage of the increased abundances of Calanus plumchrus and Calanus cristatus. These two copepods together made up nearly 50% of the identifiable prey items in its diet. These differences in diet between the two migratory myctophids cannot be explained on morphological or distributional grounds, and I can only surmise that there is some behavioral difference that affects the observed prey selection.

Discussion

The migratory fish did spend the night where zooplankton prey were most abundant, but during the day they migrated to deeper depths. Could their day depths be correlated with the distributions of preferred prey species? Metridia lucens females and Calanus cristatus were representative of prey species that performed diel migrations, but typically the fish migrated to much greater depths during the day, so they did not seem to be aggregating in a layer where these prey were abundant. Most of the deep-dwelling prey were broadly distributed at depth, so it is doubtful that the fish were keying in on their distribution. Other species, such as Calanus plumchrus which was preyed upon heavily when in the surface waters, have a haven from the fish when they overwinter at depth, and there did not seem to be a deepening of the fish distributions to take advantage of this overwintering population. Only a few species of zooplankton had vertical distributions that could be correlated with the vertical distributions of the fish, but these were never important prey items. The extensive co-occurrence of the three myctophid species in the daytime suggests that the 300-450 m depth stratum was inhabited for reasons unrelated to feeding. Light is the obvious suggestion for what determines the daytime depth of these fish, but it was surprising that they would not override this cue and adjust their vertical distributions to take advantage of aggregations of preferred prey.

In summary, the migratory and non-migratory myctophid species in the subarctic North Pacific exhibited pronounced differences in diet. Although the three abundant species inhabited similar daytime depths and ingested similar sizes of prey, the difference in timing of feeding resulted in a spatial separation during feeding and consequently differences in the prey items utilized. There was considerable overlap in the diets of the two migratory myctophids, but there were distinct differences in a few of the major prey categories, such as euphausiids, amphipods, Calanus cristatus, and Calanus plumchrus. There were ontogenetic changes in diet for all three species of myctophid, which reflected not only prey selection on the basis of size, but differences in the prey spectrum available to the fish at the depths they forage.

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Feeding Patterns of Juvenile Chum In the Skagit River Salt Marsh

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Studies of wild and hatchery stocks of Pacific salmon have shown that mortality during the marine phase of the life cycle is inversely related to body size at the time of entrance into salt water (Mathews and Buckley, 1976; Ricker, 1976). Much of the mortality apparently occurs during the first few weeks in salt water; Parker (1968) estimated that average daily losses of pink salmon fry varied from 2 to 4% during the first 40 days in coastal waters. Parker (1962, 1971) has suggested that instantaneous mortality rates decline as the growing fry become too large to be eaten by many predators. If mortality during early marine life is inversely related to body size, it follows that foraging success in estuarine and coastal marine habitats will be a major determinant of survival, particularly for pink, chum, and (fall) chinook fry, which migrate to sea within the first few weeks or months of life. This hypothesis has recently served as the rational basis for a computer simulation model of early marine mortality developed by Walters, Hilborn, Peterman and Staley (1978).

The first estuarine habitat encountered by seaward migrating fry from many river systems is salt marsh. A growing literature deals with the residence and diet composition of juvenile chum salmon in salt marsh and shallow estuarine habitats (Mason, 1974; Sibert, Brown, Healey, Kask and Naiman, 1977; Sibert and Kask, 1978; Levy and Levings, 1978). Only Mason (1974) has reported observations on diel changes in feeding activity and diet composition. He found that chum fry in a small Vancouver Island marsh fed successively on freshwater, estuarine, and marine organisms during a tidal cycle.

The Skagit River is the largest river in the Puget Sound basin and produces major runs of chum, chinook, coho, and pink salmon. Juvenile chum and chinook are abundant in the Skagit salt marsh from March through mid-May. The present study was undertaken to determine the diet composition, feeding areas, and feeding chronology of juvenile chum salmon in the Skagit marsh. It was the first phase of a continuing study on the role of marsh residence in the early life history of Skagit River chum salmon.

Materials and Methods

The study site was a salt marsh drainage channel about 500 meters north of Freshwater Slough, on the South Fork of the Skagit River. The channel varied in width from 6 to 8 meters and in depth from 0.2 to 1.5 meters. The surrounding vegetation was predominantly sedge, *Carex* sp., and bulrush, *Scirpus americanus* and *Scirpus maritimus*.

Samples of five to ten chum fry (fork lengths 36 to 52 mm) were collected by beach seine at two- to three-hour intervals throughout a 24-hr period. Two of these 24-hr sampling series were completed in 1977, and one in 1978. Each of the two 1977 series was broken into two periods separated by a 24- to 48-hr interval; sampling was continuous in 1978. Fish samples were preserved in 20% buffered formalin and later transferred to 40% isopropanol and the contents removed, sorted, and identified to the lowest possible taxon. Individuals in each prey category were counted, dried to constant weight at 80°C, and weighed to the nearest microgram. After measuring fork length to the nearest millimeter, fish carcasses were dried to constant weight at 80°C and weighed to the nearest 0.1 milligram.

Two indices were used to quantify the relative importance of the various prey organisms found in chum stomachs. The percentage by weight contributed by each prey category was estimated for each of the 10 to 12 fry samples taken during a 24-hr period, and an overall average percentage by weight was then determined for all samples combined. Similarly, the percentage of stomachs in each sample containing items of a given prey type was estimated, and an overall average frequence of occurrence was determined for all samples combined.

To provide an index of relative prey availability in the water column, samples of organisms carried into the study area by tidal flow were collected with drift samplers. The samplers had a 230-cm^2 rectangular mouth, flaring to a 484-cm^2 opening. The net was constructed of 300-micron mesh nylon netting and was 115 cm in length. Samples were removed by everting the cod-end of the net through a zippered opening. Accumulated organisms and debris were rinsed into a jar and preserved in a solution of 10% buffered formalin to which 0.01% by weight Phloxine B stain was added. One pair of nets was fished at the surface and a second pair on the bottom. The nets were usually emptied at high slack and low slack tide, but more frequently on some occasions so that samples taken during early and late phases of the incoming or receding tidal flow could be compared.

To examine diet composition during different stages of the tidal cycle, stomach samples were classified according to the following criteria:

Nominal tidal stage at time of ingestion	Time of collection
low	1 hr after low tide to beginning of incoming flow
early flood	1 hr after beginning of incoming flow to 1 hr before high
high	high tide to one hr after low tide

These intervals were selected after stomach fullness curves had been constructed and feeding periods identified. This method only partially discriminates between food items eaten at different times, since some items eaten during any interval will still be present in the stomach during part or all of the following interval. However, the turnover of stomach contents should be sufficiently rapid to allow recognition of marked changes in diet composition. At temperatures similar to those prevailing in the marsh during this study (10 to 20°C), 20 to 30 cm brown trout fed on live amphipods and chironomid larvae evacuated 50% of their stomach contents in 1.5 to 4.5 hours (Elliot, 1972).

Results and Discussion

Feeding chronology

The mean dry weight of the stomach contents of chum fry, expressed as a percentage of dry body weight, fluctuated widely and peaked once or twice during each 24-hr period (Fig. 1). Analysis of variance indicated highly significant differences between the mean weights of stomach contents at different times during the diel cycle ($p < 0.01$ for each of the three dates). The weight of the stomach contents reached a maximum value from 3 to 4 hours after a high tide and subsequently declined; minimum values occurred late in the period of low slack water. There was no evident increase for as long as 2.5 hours after the beginning of incoming flow.

The fry fed most intensely during periods of marsh submergence, which lasted 4 to 5 hours. During this time they were captured on the flats in water 0.3 to 1.0 meters deep. The marsh flats were usually inundated 1.5 to 2 hours before high tide, and were exposed again 2 to 2.5 hours after high tide. After the marsh was exposed by the receding tide, schools of chum fry could often be observed in small side channels, feeding on both benthic and drifting organisms as they slowly moved back toward the larger, deeper channels where they resided during the period of low water. The peak in stomach contents occurring 3 to 4 hours after high tide roughly coincided with the time the fry would have re-entered the low tide holding areas. At low tide the fish were concentrated in areas of suitable depth and temperature, and feeding intensity greatly decreased.

Diet composition

Diptera adults and pupae made up 81.4% by weight of the diet of chum fry in early May, 1977 (Table 1). By far the most important dipterans were Chironomidae adults and pupae (the two forms could not be reliably distinguished when partially digested) which were found in almost all stomachs and made up 67.1% of the diet by weight. The next most important dipteran group was Ceratopoganidae pupae, although they contributed only 8.1% by weight. Miscellaneous insect parts, the third most important category, were made up almost entirely of chironomid appendages and abdomens. Non-dipteran categories were of minor significance; none was greater than 2.4% of the diet by weight, and only harpacticoid copepods had an overall frequency of occurrence greater than 15% (36% F.O.).

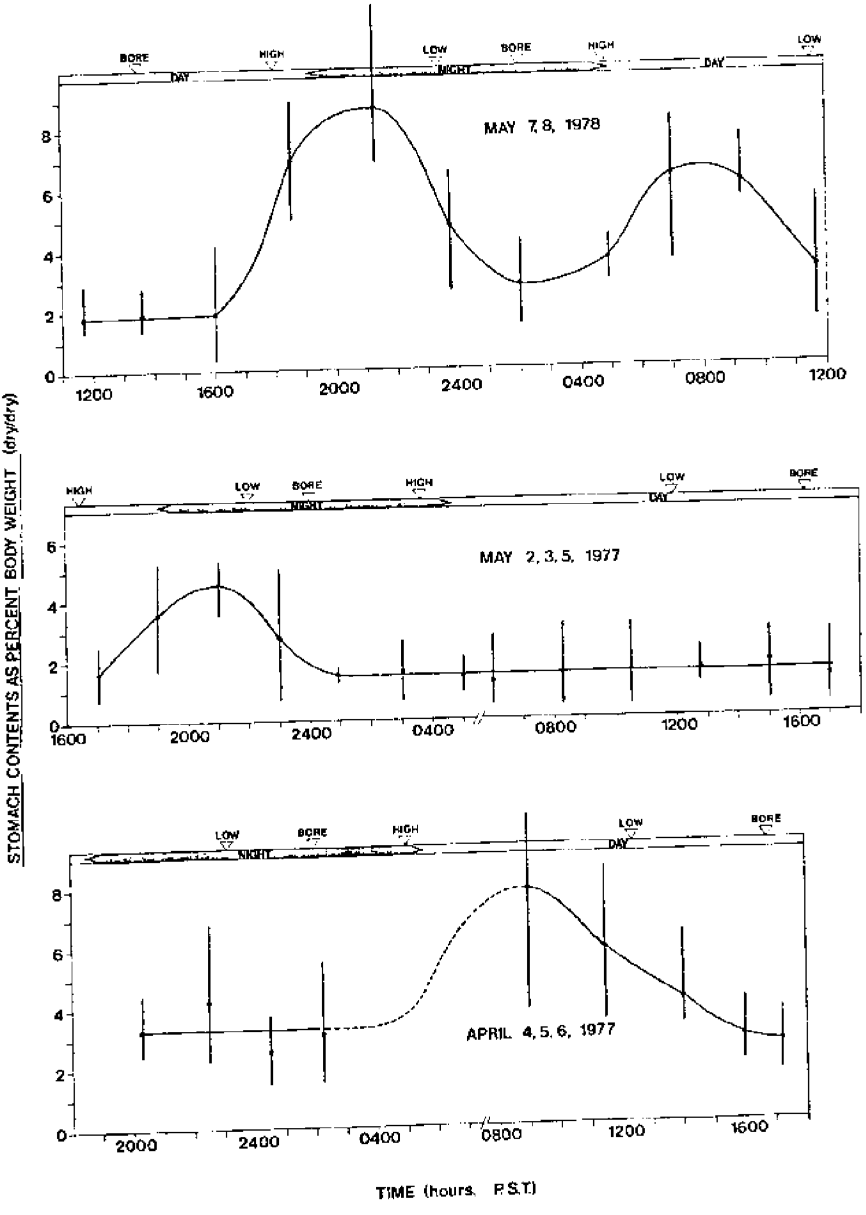

FIGURE 1. Diel changes in mean weight of stomach contents of juvenile chum salmon, expressed as a percentage of body weight (both weights on dry basis). The vertical bars represent sample ranges (n = 5 to 10 fish).

TABLE 1. Mean indices of importance for prey eaten by juvenile chum salmon over two 24-hour periods.

May 7, 8 - 1978
(10 samples, n = 45)

PREY CATEGORY	PREY WEIGHT (mg/g fish)	% Total	%F.O.
Chironomidae pupae, adults	20.3	45.4	100.0
Oligochaeta	12.8	28.6	42.2
Misc. Insecta parts	2.0	4.5	23.5
Anisogammarus	1.7	3.8	51.1
Ceratopogonidae, adults	1.6	3.6	66.7
Unid. Amphipoda	1.2	2.7	12.2
Ceratopogonidae pupae	1.0	2.2	27.2
Unid. Diptera adults	0.9	2.0	22.2
Mysidae	0.7	1.6	4.4
Hemiptera	0.5	1.1	25.6
Chironomidae larvae	0.4	0.9	58.9
Corophium	0.4	0.9	9.3
Harpacticoida	0.3	0.7	37.2
Hymenoptera	0.3	0.7	2.2
Cyclorrapha larvae	0.2	0.4	4.6
Unknown material	0.2	0.4	4.4
Coleoptera adults	0.1	0.2	3.3
Other	0.1	0.2	-
Total	44.7	99.9	
All Diptera pupae, adults	25.8	57.7	100

May 2, 3, 5 - 1977
(12 samples, n = 60)

PREY CATEGORY	PREY WEIGHT (mg/g fish)	% Total	
Chironomidae pupae, adults	14.1	67.1	98.5
Ceratopogonidae pupae	1.7	8.1	19.5
Misc. Insecta parts	0.8	3.8	16.8
Corophium	0.5	2.4	1.7
Unknown material	0.5	2.4	5.0
Anisogammarus	0.4	1.9	13.2
Unid. Diptera adult	0.4	1.9	16.5
Unid. larvae	0.4	1.9	9.1
Unid. Amphipoda	0.4	1.9	5.9
Cyclorrapha larvae	0.3	1.4	4.6
Collembola	0.3	1.4	10.3
Mysidae	0.3	1.4	1.7
Harpacticoida	0.3	1.4	36.0
Chironomidae, larvae	0.2	0.9	28.3
Ceratopogonidae, adult	0.1	0.5	15.7
Hemiptera	0.1	0.5	13.1
Other	0.2	0.9	-
Total	21.0	99.8	
All Diptera pupae, adults	17.1	81.4	98.5

In May 1978, dipteran adults and pupae made up a smaller percentage of the diet than a year previously, but still contributed 57.7% by weight (Table 1). Chironomid adults and pupae were 45.4% of the diet by weight and occurred in stomachs of all fry sampled. Although chironomid adults and pupae were a smaller percentage of the total diet by weight in comparison with May 1977 (45.4 vs 67.1%), the average quantity present in fry stomachs was greater in 1978 (20.3 vs 14.1 mg/g). The decreased percentage by weight for chironomid adults and pupae in 1978 was largely due to the relatively large contribution made by Oligochaeta in that year (28.6% by weight); this prey item was of negligible importance in 1977. Other than oligochaetes, the only non-dipteran category adding more than 2% by weight to the diet in 1978 was the amphipod *Anisogammarus confervicolus* (3.8% by weight). Harpacticoid copepods again had a high frequency of occurrence (37.2%), but made up less than 1% of the diet by weight.

Diet composition data for fry collected in early April 1977 have not been summarized, because adequate numbers of stomachs were not analyzed for all sample periods. However, chironomid adults and pupae made up 85% by weight of the diet of fry (n = 10) collected following the prominant morning feeding period (Fig. 1), and 63% by weight of the diet of fry (n = 9) collected at low water. Other important food items were *Neomysis mercedis* (9.4% by weight at high water, 12.5% at low water) and chironomid larvae (4.1% by weight at high water, 13.6% at low water).

Diel changes in diet composition

Dipteran adults and pupae were the dominant food items in chum fry stomachs at all stages of the tidal cycle and during both day and night hours (Table 2). Oligochaetes were important in high-water samples on May 7 and 8, 1978, but not in early flood or low-water samples. Since food consumption was highest during periods of high water, the prevalence of dipterans in early flood and low-water samples was at least partially due to carry-over of high-water stomach contents into subsequent periods.

Several organisms always occurred more frequently in low-water stomach samples than in high-water samples. This was true of *Anisogammarus confervicolus* and Harpacticoidea. More individuals of these groups may have been eaten at low water than at any other time because they were more available in the marsh channels than on the marsh flats, or because preferred prey items (dipterans) were not always available in the channels, forcing the fry to accept alternative prey. Harpacticoid copepods contributed more to the weight of stomach contents during daytime low-water periods than during night-time low-water periods. Their small size (< 600 microns) may have made it difficult for the fish to see them at night.

Comparison of drift composition and diet composition

Dipteran pupae and adults were very uncommon in the drift: total catches for the four drift nets ranged from zero to seventeen individuals. Preliminary analysis indicated no significant differences between bottom and surface nets, so the data were summarized as average catch per net (Table 3). Catches were highest during receding flows in the late afternoon, indicating that drifting dipterans were derived from the marsh rather than from river water pushed into the marsh by the incoming tide.

TABLE 2. Diet composition at different stages of tidal cycle on two dates.

May 7, 8 - 1978

1. LOW (Daylight)
1140, 1340 hr (n = 8)

	%WT.	%F.O.
Diptera adults, pupae	47.9	100.0
Anisogammarus	26.8	100.0
Unid. Amphipoda	12.6	25.0
Harpacticoida	4.2	87.5
Diptera larvae	3.7	75.0
Hemiptera	2.1	25.0
Other	2.6	-

2. EARLY FLOOD (Day)
1600 hr (n = 5)

	%WT	% F.O.
Diptera adults, pupae	50.5	100
Hymenoptera	14.1	20
Hemiptera	11.4	40
Anisogammarus	11.4	60
Oligochaeta	4.9	20
Harpacticoida	4.3	100
Arachnida	1.6	20
Unknown material	1.1	20
Polychaeta	0.5	20

3. HIGH (late daylight - early night)
1830, 2115 hrs (n = 10)

	%WT	%F.O.
Diptera adults, pupae	65.7	100
Oligochaeta	24.6	80
Mysidae	4.4	10
Anisogammarus	1.5	30
Hemiptera	1.3	70
Diptera, larvae	1.3	70
Corophium	0.5	30
Coleoptera, adult	0.5	10
Other	0.1	-

4. LOW (night)
0200 hr (n = 5)

	%WT	% F.O.
Diptera adults, pupae	87.1	100
Diptera, larvae	5.4	100
Anisogammarus	4.6	80
Corophium	1.8	40
Harpacticoida	0.4	60
Other	0.7	-

5. HIGH (early daylight)
0700, 0915 (n = 10)

	%WT	%F.O.
Oligochaeta	50.8	90
Diptera adults, pupae	43.8	100
Unid. Amphipoda	1.5	10
Corophium	0.6	10
Diptera larvae	0.5	50
Anisogammarus	0.3	30
Unknown material	1.6	10
Other	0.8	-

May 2, 3, 5 - 1977

1. HIGH (late daylight to early night)
1900, 2100 hr (n = 10)

	% WT.	%F.O.
Diptera adults, pupae	78.2	100
Corophium	8.4	20
Mysidae	3.7	10
Diptera larvae	1.0	50
Collembola	0.5	10
Arachnida	0.2	10
Unknown material	7.4	30
Other	0.5	-

2. LOW (night)
2300 hr (n = 6)

	% WT.	%F.O.
Diptera adults, pupae	81.6	100.0
Unid. Amphipoda	10.5	33.3
Unid. larvae	3.1	50.0
Diptera larvae	2.0	16.7
Anisogammarus	1.4	66.6
Harpacticoida	0.3	66.6
Hemiptera	0.3	33.3
Other	0.7	-

3. EARLY FLOOD (Night)
0100, 0300 hr (n = 7)

	%WT	%F.O.
Diptera adults, pupae	98.1	100
Anisogammarus	1.9	14.3

4. HIGH (early daylight)
0600, 0815, 1030 hr (n = 16)

	% WT.	%F.O.
Diptera adults, pupae	71.8	93.8
Unid. larvae	8.7	12.5
Collembola	6.0	12.5
Diptera larvae	4.0	25.0
Unid. Amphipoda	2.7	6.3
Harpacticoida	2.0	43.8
Coleoptera larvae	0.7	6.3
Hemiptera	0.7	50.0
Other	3.4	-

5. LOW (daylight)
1245, 1500 hr (n = 11)

	%WT.	%F.O.
Diptera adults, pupae	85.9	100
Harpacticoida	7.6	81.8
Diptera larvae	2.9	63.6
Anisogammarus	1.2	9.1
Arachnida	1.2	9.1
Corophium	0.6	9.1
Other	0.6	-

TABLE 3. Mean drift net catch ($\bar{X} \pm$ S.D.; n = 4) for four selected taxa throughout two tidal cycles.

	INCOMING	OUTGOING		INCOMING	OUTGOING	INCOMING
Prey Category	Daylight	Late daylight	Early night	Night	Early daylight	Daylight
			May 2, 3, 5 - 1977			
Diptera adults, pupae	-	4.3 ± 5.2	0	0.5 ± 0.6	0.5 ± 0.6	2.0 ± 2.2
Anisogammarus	-	4.8 ± 4.9	53.5 ± 41.0	173 ± 92.6	2.3 ± 1.5	9.5 ± 11.2
Corophium	-	0	2.8 + 3.8	4.8 ± 4.1	0	0.25
Mysidae	-		23.2 ± 15.6	52.2 ± 52.4	0.3 ± 0.5	53.7 + 12.7
			May 7, 8 - 1978			
Diptera adults, pupae	1.5 ± 0.6		2.8 ± 2.6	0.3 ± 0.5	0.3 ± 0.5	-
Anisogammarus	66.8 + 44.0		385 + 144	429 + 234	32.8 ± 31.7	-
Corophium	7.0 + 5.5		41.5 + 26.4	4.0 ± 7.6	19.5 ± 23.9	-
Mysidae	2.5 ± 2.1		0.8 ± 1.5	0	0	-

The evening peaks also suggest a possible diel rhythm in emergence timing. Sampling with emergence traps confirmed that both chironomid and ceratopogonid adults were emerging in the study areas (unpublished data). Although insects are generally stenohaline, the Chironomidae include a number of intertidal marine species (Hashimoto, 1976), and in laboratory tests some chironomid larvae can tolerate undiluted sea water (Foster and Treherne, 1970). Smith (1977) reported that chironomid larvae in sediments of the Snohomish delta, 30 km south of the Skagit delta, increased in density with increasing tidal elevation. He found few or no larvae near mean lower low water (MLLW) and up to several thousand per m^2 at 1 to 2.5 m above MLLW.

In view of the dominance of dipterans in the diet of chum fry, the small catches of dipteran adults and pupae in drift nets were surprising. The chironomids eaten must have been taken from the bottom or from plant stems, rather than from the water column.

Anisogammarus appeared in greatest numbers in the drift samples during the night. This species is nocturnally active; many individuals could be observed swimming near the surface of the water at night during both high- and low-water periods. Nevertheless, the occurrence of *Anisogammarus* in chum stomachs seemed more closely correlated with tidal stage than with light: both percentage by weight and frequency of occurrence were highest following periods of low water (Table 2). The catch rate for *Anisogammarus* was three- to seven-fold greater in May 1978 than in 1977, and the average weight in the stomachs of chum fry was correspondingly higher in 1978 than in 1977 (1.7 mg/g fish vs 0.4 mg/g fish). Catches of *Corophium salmonis* and *Neomysis mercedis* also differed between years, but these differences did not correlate with changes in rates of consumption by chum fry.

Conclusions

(1) Chum fry fed most intensely during high water, when they moved out of marsh channels and onto the marsh flats.

(2) Dipteran adults and pupae, predominantly species belonging to the

family Chironomidae, were the dominant prey on all dates. Dipteran adults and pupae made up 58 to 81% of the diet by weight and occurred in all but one of the 124 chum stomachs examined. Dipteran larvae contributed 1 to 4% by weight. Non-dipteran categories individually making up 2% or more of the diet by weight were oligochaetes, the amphipods *Anisogammarus confervicolus* and *Corophium salmonis*, and the mysid *Neomysis mercedis*.

(3) Although individuals of *A. confervicolus*, *C. salmonis*, and *N. mercedis* were fairly abundant in the tidal drift at times, few chironomid pupae or adults were captured in the drift samplers. This suggests that most chironomids eaten by chum fry were on the substrate or attached to plant stems, rather than free-floating.

(4) The relatively large quantities of food in stomachs of chum fry following feeding periods, the absence of empty stomachs at all times, and the predominance of prey items originating from the intertidal marsh flats all indicate that the Skagit marsh is important foraging habitat for outmigrating chum fry. Future studies will determine residence periods and growth rates for juvenile salmon in the marsh.

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SESSION 3 Trophic Structure
DISCUSSION

Cailliet observed that, judging from cursory examination in simple systems that are semi-closed, one can get nice trends but when one gets offshore in more complicated zones then that is when you start getting results.

Feller asked Congleton if he had observed Anisogammarus being attracted to the drift nets and hiding under the box part of the net. Congleton said they did not have too much of that particular problem. Feller also wondered if they found Anisogammarus clinging to the outside of the net; Congleton replied no.

Koski asked Congleton to define the size range of the tomcod he examined; most of them were 35 to 50 mm and occasionally as large at 60 mm. The average was about 42 mm. Koski hypothesized that they were not of a size range to be expected to eat mysids. Rosenthal asked how big a salmon run the Skagit had and how much of the marsh has been compromised by urbanization and industrialization in the past 100 years. Congleton replied that the outmigration in 1977 was about 12 million chum salmon fry and the previous year was about 2 million; he had not received the estimate for 1978. The outmigration is very typical--the emergence is delayed and the fish moved downstream about a month late. Although much (80 percent) of the original marsh has been reclaimed for farmland, the marsh is building out all the time.

Sibert asked Congleton if the area received fresh water all the time. Congleton responded no, and, in that respect, it is not a natural estuarine situation. Simenstad asked what proportion if any of the fish were feeding up on the flat at high tide. According to Congleton, all of the fish feed up on the flat at high tide as the fish were caught with full stomachs at high tide.

Congleton surmised that the fish were picking chironomids off the surfaces and not feeding on organisms floating around. Most of the insects were late advanced pupae. It is a difficult taxonomic problem because of the effects of digestion on adults and pupae. To sample them, makeshift emergence traps were utilized to trap the chironomids as they came out of the marsh sediments. More along this line of research will be done later. Someone mentioned that Don Rogers has some very fine techniques in this area. The problem was then discussed of knowing when chironomids pupate and how long the larval stages last.

Ellison asked if Congleton had an idea of what proportion of fish take up residency in the marsh, what proportion remain in the river and what proportion are moving through. Congleton succinctly stated, "We need more money!" They need to know what is happening upstream and what is happening in Skagit Bay.

Cardwell asked McCrone what fish prey upon myctophids. McCrone replied that they are eaten by a large variety of oceanic predators such as salmon. Cardwell rephrased his question to what predators ate myctophids regularly such that depended on them. McCrone replied that there is a theory that migrating groups of myctophids that move around for feeding may get swept off the continental shelf; then, when they move back down the water column, they become available to predators, such as rockfish; Pearcy has shown this to be the case off the Oregon coast. Sometimes one cannot account for the populations of demersal fish just off the continental shelf where production does not indicate such a high occurrence. This "wash down" process may explain it. Smith added that squid are also predators of myctophids. McCrone replied that squid did not appear in the nets too often.

Eggers questioned if McCrone noticed any difference in growth rates between the migrating versus non-migrating myctophids that would suggest better efficiency in either of the two strategies. McCrown replied that size frequency was the only indicator of growth rates. Migratory fish seem to live longer, however. Eggers asked how the fish were aged and the reply was that somebody else had aged them from otoliths.

Feller asked how many of the prey items eaten by myctophids were luminescent. McCrone replied that most of the abundant items were--euphausiids, Metridia. There may be a selection for luminescence but limited sampling prevented a definitive statement. Furthermore, in the same layer some myctophids were eating Calanus cristatus but avoiding Eucalanus which may indicate something. Chess asked what were the smallest calanoids. The smallest were Pseudocalanus about 1 mm and, of course, the smaller stages of larger calanoids. There may be a visual breaking point at or about 1 mm. Chaetognaths and sergestid shrimps also eat copepods.

Mearns asked what temperature range the animals were experiencing. McCrone replied that it was not much--about six degrees, e.g., four degrees to 10 degrees. Cailliet asked about the population structure. McCrone was not sure if he was sampling the same population summer after summer; he suggested that perhaps it is not too important since they behave similarly.

SESSION 4
Competition

SESSION LEADER
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Comparative Analysis of Stomach Contents Of Cultured and Wild Juvenile Salmonids In Yaquina Bay, Oregon

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Introduction

The comparative food habits of hatchery and wild juvenile salmonids in estuaries are relatively unknown. The purpose of my paper is to present a preliminary report on an investigation, currently in progress in Yaquina Bay, Oregon, that deals with this subject. After presenting some background information on this investigation and the populations of hatchery and wild salmonids in the Yaquina system, I present a comparative analysis of the stomach contents of juvenile hatchery and wild coho salmon (Oncorhynchus kisutch) from samples taken in the estuary. This is followed by a discussion of the significance of these findings in terms of competition, life history strategies, and management decisions.

In 1971 the Oregon State Legislature authorized the establishment of private hatcheries in Oregon. To date, the Oregon Fish and Wildlife Commission has granted 20 permits for private salmon hatcheries. With the advent of salmon ranching by private aquaculture companies in Oregon, concern has been expressed by legislators, biologists, and fishermen about the impact that releases of large numbers of cultured salmon smolts may have on populations of wild fish and fish already being released from public hatcheries. These concerns are based, in part, on knowledge of the limited rearing capacity of estuarine systems for juvenile salmonids (Reimers, 1973; Baily, et al., 1975; Reimers and Concannon, 1977; Reimers, 1978).

The Oregon Department of Fish and Wildlife Policy Relating to Liscensing and Operation of Private Salmon Release and Recapture Facilities (adopted July 16, 1976) stipulates that fish are authorized for release provided necessary monitoring of fish in the estuary will be funded by the permittee (Oreg. Dept. Fish Wildl., 1977). To fulfill this requirement, an investigation was initiated in Yaquina Bay, Oregon, in July 1977 to provide information necessary for the evaluation of problems related to overlapping utilization of an estuarine environment by privately cultured and wild juvenile salmonids. The study was funded by Weyerhaeuser Company, conducted by Oregon State University, and monitored by the Oregon Department of Fish and Wildlife.

Background Information

Yaquina Bay located 115 miles south of the Columbia River, is the fifth largest estuary in Oregon, covering 3,910 acres of land at mean high tide (Oreg. Div. State Lands, 1973). Species of anadromous salmonids occurring naturally in the Yaquina watershed include fall chinook salmon (Oncorhynchus tshawytscha), coho salmon, chum salmon (O. keta), winter steelhead trout (Salmo gairdneri), and sea-run cutthroat trout (S. clarki).

The Yaquina watershed has 66 tributary streams which are utilized by anadromous salmonids (Smith and Lauman, 1972). The most recent study estimated an annual spawning escapement of 12,600 coho salmon, 2,300 winter steelhead trout, and 2,100 fall chinook salmon (Smith and Lauman, 1972). These populations are considered to be low when compared to other estuarine river systems (Percy et al., 1974).

In addition to native fish, juvenile salmonids reared in state hatcheries have been released into the Yaquina system as recently as 1974 (Fish Comm. Oreg., 1972-1974). Oregon Aqua Foods, now a subsidiary of Weyerhaeuser Company, began liberation of fish into the Yaquina system from their Wright Creek Hatchery in November 1973, and from their South Beach site in April 1975.

In 1977 approximately 1.4 million privately cultured salmon smolts were released into the Yaquina system. About 96% of these were coho salmon, 3% were spring chinook salmon, and 1% were chum salmon. Although data is not complete, over 7 million cultured juvenile salmonids will have been released directly into Yaquina estuary in 1978. Most of these are coho salmon, although spring and fall chinook salmon, and chum salmon, are also being released. Projected annual releases of cultured juvenile salmonids into Yaquina Bay by Oregon Aqua Foods are 9.5 million coho salmon by 1978, 10.6 million chinook salmon by 1980, and 20 million chum salmon by 1981.

Methods

Four beach (Sites 1, 2, 3, and 4, located 3.1, 3.8, 5.1, and 16.1 km, respectively, from the mouth of the bay) and two channel study areas (Sites 5 and 6, located 8.8 and 3.4 km from the mouth of the bay) are sampled for juvenile salmonids. Sampling at the four beach study areas began in July 1977. Biweekly samples were taken during periods of large releases of cultured smolts in July, August, and September of 1977 and 1978. Weekly samples were taken in October 1977 and June 1978, and bimonthly samples were taken throughout the remainder of the year. Sampling at the two channel study areas began in March 1978 and has continued on a bimonthly basis. Juvenile salmonids are captured at the four beach study areas with a 100- X 3-meter varied mesh beach seine similar in construction to that described by Sims and Johnsen (1974). A 221-meter long lampara net is used to sample the two channel study areas.

Samples or subsamples of juvenile salmonids captured at the study areas are injected and preserved with 10% buffered Formalin. In the laboratory, stomachs are dissected from each specimen, contents are separated into categories under a dissecting microscope, and the wet weight of all food categories having a biomass greater than .01 gm is measured.

Pooled weights of each food category are divided by the pooled weights of total stomach contents of each sample or group of fish to be compared to give a measure of the proportion of the biomass of all stomach contents represented by each food category.

An empirical measure of overlap is calculated using a simplified form of Morisita's (1959) index of overlap presented by Horn (1966). The index, $\hat{C}_\lambda$ is:

$$\hat{C}_\lambda = \frac{2 \sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where x_i and y_i are a measure of the proportion of biomass of all food items in samples x and y that are represented by food item i. This index varies from 0 when samples x and y have no food items in common to 1 when they are the same in terms of proportional composition of stomach contents (Horn, 1966). Food categories representing 1% or more of the total biomass of stomach contents in either group of fish being compared were included in the calculation of the index.

Results

To demonstrate the types of comparisons and results that will be made from this investigation, an analysis of stomach contents data obtained from hatchery and wild coho captured in 22 samples taken at the six study areas from April 15, 1978 through May 29, 1978 is presented.

During this period populations of hatchery and wild coho salmon were present in the estuary. Approximately 250,000 yearling hatchery coho were released into the estuary on April 6, 1978. Analysis based on recapture of hatchery coho marked with flourescent pigments indicated that most of this release group had left the estuary by May 13, although some remained in the estuary for over two months. Wild coho were first captured in the estuary in samples taken on April 15, 1978. Numbers of wild coho in the samples peaked in the upper estuary (Site 4) on April 29, and in the lower estuary on May 13.

Because sample sizes of hatchery and wild coho captured during this period were small, data obtained from samples taken at the beach and channel study areas, respectively, was pooled to provide an overall picture of comparative stomach contents between hatchery and wild coho. Graphical representations of the percentage composition by weight of major food types in the pooled stomach contents of hatchery and wild juvenile coho salmon captured at beach and channel study areas are shown in Figures 1 and 2. At beach study areas, juvenile fish, primarily anchovy (<u>Engraulis mordax</u>), surf smelt (<u>Hypomesus pretiosus</u>),

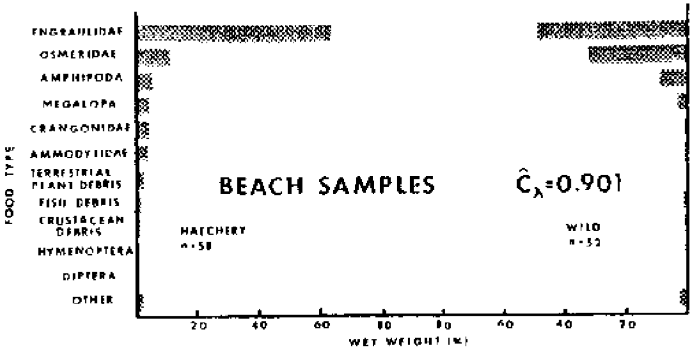

Figure 1. Percentage composition by weight of major food types in the pooled stomach contents of 58 hatchery and 52 wild juvenile coho salmon (Oncorhynchus kisutch) captured by seine at four beach study areas in Yaquina Bay, Oregon, from April 15, 1978 through May 27, 1978.

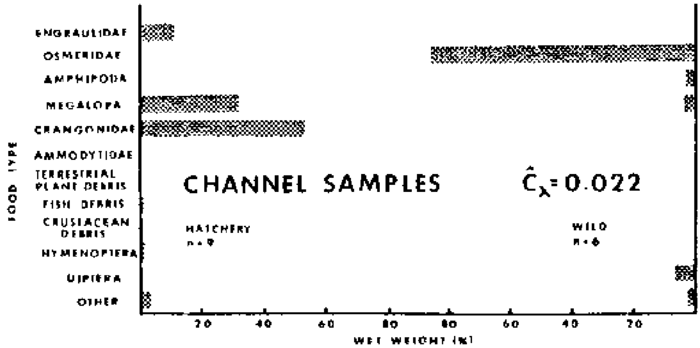

Figure 2. Percentage composition by weight of major food types in the pooled stomach contents of 9 hatchery and 6 wild juvenile coho salmon (Oncorhynchus kisutch) captured by lampara net at two channel study areas in Yaquina Bay, Oregon, from April 18, 1978 through May 29, 1978.

and sand lance (Ammodytes hexapterus), accounted for approximately 80% of the total biomass of stomach contents of hatchery coho and 73% of the total biomass of stomach contents of wild coho. At the channel study areas, crustaceans, primarily crangonid shrimp and megalopa larvae of Dungeness crab (Cancer magister), accounted for approximately 85% of the total biomass of stomach contents of hatchery coho, and juvenile surf smelt represented 86% of the total biomass of stomach contents of wild coho. The index of overlap calculated for these data shows a high degree of similarity ($\hat{C}_\lambda$ = .901) in the stomach contents of hatchery and wild coho captured in the beach study areas, and almost no similarity ($\hat{C}_\lambda$ = .022) in the stomach contents of hatchery and wild coho captured in the channel study areas.

Because the similarity in the stomach contents of hatchery and wild coho appeared to vary with respect to broad habitat differences, the index of overlap was also calculated for individual sample sites (Table 1). Although the index of overlap calculated for the individual samples sites shows that the stomach contents of hatchery and wild coho captured at the same study areas in beach habitat are more similar than dissimilar (i.e. $\hat{C}_\lambda > .5$), the degree of overlap varies considerably with sample site. A high degree of similarity ($\hat{C}_\lambda > .9$) was found only in the stomach contents of hatchery and wild coho captured in the upper estuary (Site 4), where juvenile anchovy accounted for 89% and 86%, respectively, of the total biomass of stomach contents of hatchery and wild coho salmon. Although the small sample sizes of hatchery and wild coho captured at the two channel study areas make generalizations questionable, indices of overlap calculated for the individual sample sites were similar to that calculated for the pooled data in that there was almost no similarity in the stomach contents of hatchery and wild coho at either Site 4 or Site 6 (Table 1).

Table 1. Overlap ($\hat{C}_\lambda$) in stomach contents calculated for the indicated sample sizes of hatchery (n_H) and wild (n_W) coho salmon (Oncorhynchus kisutch) captured at four beach and two channel study areas in Yaquina Bay, Oregon, from April 15 through May 29, 1978.

Index of Overlap ($\hat{C}_\lambda$) and Sample Size (n)	Study Area					
	Beach				Channel	
	1	2	3	4	5	6
$\hat{C}_\lambda$	.779	.536	--*	.995	.051	.003
n_H	15	13	3	27	6	4
n_W	26	11	0	15	2	4

* No index was calculated as no wild coho were captured at this site.

In order to determine if the similarity in stomach contents of hatchery and wild coho varied with time, indices of overlap were calculated for samples of hatchery and wild coho captured on the same date, regardless of sample site (Table 2). Stomach contents of hatchery and wild coho

Table 2. Overlap ($\hat{C}_\lambda$) in stomach contents calculated for the indicated sample sizes of hatchery (n_H) and wild (n_W) coho salmon (Oncorhynchus kisutch) captured in Yaquina Bay, Oregon, on eight different sample dates from April 15, 1978 through May 29, 1978.

Index of Overlap ($\hat{C}_\lambda$) and Sample Size (n)	Date							
	4/15	4/18	4/29	5/1	5/13	5/15	5/27	5/29
$\hat{C}_\lambda$	.942	--*	.907	.962	.162	--*	.946	--*
n_H	45	6	8	4	3	0	2	0
n_W	3	0	9	1	19	2	21	3

*No index was calculated, as hatchery and wild coho were not both captured on this date.

captured on the same date were found to have a high degree of similarity (i.e. $\hat{C}_\lambda > .9$) on all dates except May 13, 1978. On this date, sand lance composed 70% of the total biomass of stomach contents of hatchery coho, while 76% of the total biomass of stomach contents of wild coho was juvenile surf smelt and anchovy.

During this period, only seven samples were taken in which both hatchery and wild coho werepresent at the same sample site at the same time. Indices of overlap calculated for these samples (Table 3) show a high degree of similarity (i.e. $\hat{C}_\lambda > .9$) in the stomach contents of hatchery and wild coho in four out of seven cases.

Table 3. Overlap ($\hat{C}_\lambda$) in stomach contents calculated for the indicated sample sizes of hatchery (n_H) and wild (n_W) coho salmon (Oncorhynchus kisutch) captured at the same sample site on the same date in Yaquina Bay, Oregon, from April 15, 1978 through May 27, 1978.

Sample Site, Index of Overlap ($\hat{C}_\lambda$), and Sample Size (n)	Date						
	4/15	4/15	4/29	5/1	5/13	5/13	5/27
Sample Site	2	4	4	5	1	2	1
$\hat{C}_\lambda$	.486	.995	.943	.954	.052	.776	.945
n_H	10	23	4	2	2	1	2
n_W	1	2	9	1	9	8	17

Discussion

The above analyses demonstrate, in many cases, a high degree of similarity in the stomach contents of cultured and wild juvenile coho salmon in the estuary, although the amount of overlap can vary considerably with time, space, and habitat. Indices of overlap calculated from data pooled over time, space, and habitat varied from .003 (almost no similarity) to .995 (almost identical). A large part of this variability may be attributable to small sample sizes, although low abundance of hatchery and wild coho at the study areas during this period made avoidance of this problem difficult.

At low population densities such as those found during the period from April 15 through May 27, 1978, similarity in stomach contents of hatchery and wild coho salmon is probably more indicative of the presence of abundant food resources or the equal availability of limited food resources, than of competition between these two groups. The calculated indices of overlap ($\hat{C}_\lambda$) were usually highest when the stomach contents of hatchery and wild coho in the samples being compared were composed of similar proportions of one or two food categories having a large biomass (e.g. anchovy and surf smelt), or large proportions of one food category having a small biomass (e.g. megalopa larvae). Therefore, a high degree of similarity indicates that food resources were abundant or, at least, equally available to hatchery and wild coho during this period.

Similarity in stomach contents does, however, demonstrate that the potential for competition between hatchery and wild coho salmon in the estuary does exist. At some hypothetical level of high population density, food resources that were once abundant or limited resources that were once evident in similar proportions in the stomach contents might be diminished to the point that little similarity in the stomach contents of hatchery and wild coho salmon could be found.

With respect to life history strategies, wild coho salmon juveniles use the estuary for only a short period of time lasting from a few days to a few weeks (Reimers, 1978). Competition for available food resources in the estuary between hatchery and wild coho could be avoided, at least to some extent, by releasing hatchery coho after wild coho have migrated to the ocean. The only species of Pacific salmon known to make extensive utilization of the estuary as juveniles is fall chinook salmon (Rich, 1922; Snyder, 1931; Deschamps and Wright, 1971; Reimers, 1973; Sims, 1975). The importance of this period of extended residence in the estuary to the growth and survival of fall chinook salmon is demonstrated by the fact that over 90% of successful spawners returning to Sixes River, Oregon, had spend 3 months in the estuary before migrating to the ocean (Reimers, 1973). In view of this life history pattern, the potential for competition between cultured juvenile salmonids and wild populations of juvenile fall chinook salmon in the estuary is greater than with other species of wild salmon. As a part of my investigation, data on the stomach contents of over 3000 cultured juvenile salmonids (primarily zero age coho salmon) and wild fall chinook salmon captured in Yaquina Bay, Oregon, from July 1977 through October 1978 is currently being analysed to determine the degree of similarity in the stomach contents of these groups in the estuary.

Although similarity indices calculated for data taken over a short period of time can only be used to demonstrate whether the potential for competition between hatchery and wild fish does or does not exist, changes in the similarity of stomach contents along with changes in growth or relative abundances of hatchery and wild juvenile salmonids in the estuary examined over a number of years might be useful in determining the level of hatchery releases at which food resources become a limiting factor. In view of the large numbers of privately cultured salmonids that have already been approved for release in Oregon (54.8 million coho salmon, 62.0 million chinook salmon, and 120.5 million chum salmon), information of this type will be needed for management decisions. Although full scale ecological studies are needed to determine interactions between cultured and wild juvenile salmonids, as well as between them and other species of fish and their food organisms in the estuary, these types of studies may be too time consuming to be of immediate use in the management decisions which must be made.

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Competitive Interaction of Walleye Pollock And Pacific Ocean Perch In the Northern Gulf of Alaska (Abstract)

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ABSTRACT*

Since the early 1960's, a spectacular increase in the abundance of Walleye pollock (Theragra chalcogramma) has occurred throughout the northern Gulf of Alaska. Nearly synchronous with this change, the stocks of Pacific Ocean perch (Sebastes alutus) were severely reduced due to the activities of foreign trawlers. There are several lines of evidence which suggest that pollock are responding to a release from food competition with POP: 1) both species are found in roughly the same depth zone, 2) juveniles of both species make a nocturnal vertical migration to feed on planktonic crustaceans, 3) the euphausid, Thysanoessa spinifera, is the major prey item consumed by small adult pollock and by all mature POP, 4) pollock display density dependent growth and thus appear to be food limited. The predominant component of the diet of pollock changes from euphausids to fish with increasing fish size. POP eat euphausids over their entire adult size range. Consequently, competition is most intense between adult POP and the size range of pollock bounded by the size at which they first consume euphausids and the size at which they cease making diet vertical migrations. Compared to POP, pollock appear to be a classic r selected species as evinced by the attributes of rapid growth, early maturity, high fecundity, and low investment in parental care and predator defences, thus they are able to rapidly expand into the feeding niche previously monopolized by POP.

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*Manuscript in preparation.

Apparent Influence of Fluctuations in Physical Factors On Food Resource Partitioning

A Speculative Review

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Technical Paper No. 5050, Oregon Agricultural Experiment Station.

Abstract

Food resource partitioning is influenced by a combination of predator-prey effects and habitat disturbance by physical factors. A series of principal-prey partition plots of fish assemblages is examined with respect to fluctuation and disturbance in physical factors. Results indicated that greater disturbances seem linked with weakened prey partitioning among predators.

Introduction

Over the past thirty years a number of food-resource partitioning studies have been carried out with fish assemblages. Some authors have been able to relate degree of partitioning to biotic factors. In this study I will briefly review those relationships, present new data, and propose an interpretive extension to previous observations that may be helpful in understanding the effects of physical factor fluctuation on food-resource partitioning.

Interactive Segregation

Periods of diet overlap often represent transition phases in fishes. With time, the overlap disappears and food resource partitioning occurs (Kawanabe, H. 1959, Nilsson, N-A, 1960, Nilsson, N-A, 1964). Sometimes partitioning occurs because the two or more predator species diminish the prey density, and subsequently only the more efficient predator is able to capture the prey. It is also possible that none of the predators will continue to include the species as a principal prey after predation has lowered prey density. Prior to the introduction of red-side shiners (Richardsonius balteatus) in Paul Lake, British Columbia, small rainbow trout (Salmo gairdnerii) fed heavily on Gammarus (Johannes and Larkin, 1961). For a time after the introduction, both fishes fed on Gammarus. Its abundance was reduced due to the predation and then neither predator took Gammarus as a major food source.

After observing similar partitioning changes in salmonids and coregonids in Swedish lakes and reservoirs, Nilsson (1967) proposed the term "Interactive Segregation", and elucidated the concept that dietary partitioning strengthened (i.e., overlap decreased) when two or more predator species reduced the abundance of their common prey. He also reviewed enough cases to indicate that interactive segregation is a widespread phenomenon.

Food Resource Partitioning and Season

Several workers have published studies showing that partitioning becomes stronger when prey densities decrease due to factors extraneous to the effect of predators on prey. Keast (1965) studied food resource partitioning among fishes in Lake Opinicon, a eutrophic lake in Ontario, Canada. He found that partitioning was weaker when zooplankton abundances were high in August, as compared to May, shortly after the ice cover had melted, when zooplankton abundance was low. Chydorus was a principal prey of four feeding groups in May, but in August it was a principal prey of nine (Fig. 1). Increased partitioning in May followed by decreased partitioning in August was simply related to the annual productivity cycle, and the productivity lag following spring lake turnover.

Similarly, Zaret and Rand (1971) demonstrated weaker partitioning during the rainy season in a Panama stream as compared to the dry season (Fig. 1). These authors also showed that the weaker partitioning was due to an abundance of prey during the rains - a period of greater productivity.

Apparently fluctuating physical factors - temperature increase and water column overturn in Ontario; rains and flooding in Panama - could bring about a decrease in food resource partitioning. If one accepts that the tropical flooding, and accompanying increase in stream flow and turbidity, had a greater effect on prey abundance than did the Ontario lake turnover, then partitioning should have been weaker in Panama than in Ontario. To demonstrate this result, overlap was calculated among the principal prey in Fig. 1 as the acutal number of reoccurences of prey among predators divided by the maximum possible number of reoccurences. For example, in the tropical rainy season there were 9 reoccurences of principal prey and 35 reoccurrences possible, and so there was 9/35, or 26% overlap. In the Ontario lake there was only 10% overlap in August. The Ontario lake had stronger partitioning during the season of high productivity.

Arctic Food-Resource Partitioning

If fluctuation of physical factors brings about decreased partitioning, then an assemblage of fishes from a very constant environment, should have very strong partitioning. During August, 1969, I joined a group from the Arctic Biological Station (Canadian Fisheries and Marine Service) working in the western arctic on the Dease Strait near Cambridge Bay, Victoria Island, Northwest Territories. At this location the marine areas were covered with pack ice all year except for about a month in August. Temperature was constant the year-round at slightly

Lake Opinicon

May

	Labidesthes 61-81 mm	Notropis 40-70 mm	Pimephales 50-75 mm	Fundulus 65-85 mm	Lepomis 60-115 mm	Lepomis 130-170 mm	Pomoxis 75-115 mm	Ambloplites 45-70 mm	Ambloplites 75-115 mm	Micropterus 80-120 mm	Perca 60-110 mm
Chaoborus Pupae	+										
Diptera Adults	+	+									
Bosmina		+									
Chydorus		+	+	+	+						
Acroperus			+								
Bottom Ooze			+								
Chironomid Larvae				+	+	+	+	+			
Copepoda				+							+
Chironomid Pupae					+						+
Trichoptera						+					
Higher Plants						+					
Chaoborus Larvae							+				
Ephemeroptera Nymphs								+	+		
Anisoptera Nymphs									+	+	
Crayfish										+	
Fish										+	+
Zygoptera Nymphs											+

Lake Opinicon

August

	Labidesthes 61-81 mm	Pomoxis 75-115 mm	Notropis 40-70 mm	Ambloplites 45-70 mm	Ambloplites 75-115 mm	Lepomis 60-85 mm	Lepomis 86-115 mm	Lepomis 130-170 mm	Fundulus 65-85 mm	Perca 60-110 mm	Pimephales 50-75 mm	Micropterus 80-120 mm
Chydorus	+	+	+	+	+	+			+	+	+	
Polyphenus	+											
Daphnia	+											
Diptera Adults	+		+	+								
Chaoborus Larvae	+	+										
Chaoborus Pupae	+	+										
Copepoda		+										
Bosmina	+	+	+									
Chironomid Pupae				+								
Hymenoptera				+	+	+	+	+				
Trichoptera					+							
Ephemeroptera Nymphs					+							
Chironomid Larvae						+	+	+	+	+		
Fish							+					+
Odonata Nymphs							+	+				
Plant Seeds								+	+			
Pleurozis									+			
Sida										+		
Ostracoda										+		
Acroperus											+	
Bottom Ooze											+	
Higher Plants												+

Tropical Stream

Dry Season

	Gephyrocharax	*Roeboides*	*Eleotris*	*Aequidens*	*Gobiomorus*	*Neoheterandria*	*Piabucina*	*Astyanax*	*Poecilia*
Terrestrial Anthropods	+	+	+	+		+	+		
Coleoptera		+							
Ephemeroptera		+	+						
Odonata			+	+	+				
Chironomidae				+		+			
Diptera						+			
Prawns							+		
Fruit & Seeds							+	+	
Green algae								+	+

Tropical Stream

Wet Season

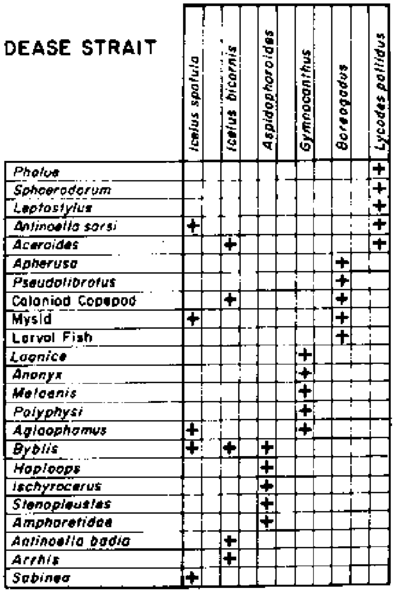
	Gephyrocharax	*Roebides*	*Eleotris*	*Aequidens*	*Neoheterandria*	*Astyanax*
Terrestrial Anthropods	+	+			+	+
Ephemeroptera	+	+	+	+		+
Miscellaneous Larvae		+				
Fish		+	+			
Plecoptera				+		
Trichoptera				+	+	
Fruit & Seeds						+

Figure 1. Principal-prey partition plots for fish in assemblages at two locations at two seasons. Lake Opinicon plots are interpreted from Keast (1965); Tropical stream plots for Zaret and Rand (1971).

below 0°C (J.R. Hunter, pers. comm.). Fishes were collected by otter trawl at a depth of 60 meters. The following number of stomachs were examined for the six fish species that were sufficiently abundant for analysis: Lycodes pallidus (129), Boreogadus saida (100), Gymnocanthus tricuspis (23), Icelus bicornis (60), Icelus spatula (64), Aspidophoroides olrikii (18). Prey items were weighed to 0.01 grams.

To deal with only those prey that contributed most to the fish energy budgets, we eliminated from the analysis prey that occurred in quantities of less than 10% by weight of all food eaten by a predator species. The remaining principal prey were largely amphipods and polychaetes as follows: amphipods: Apherusa glacialis, Ischrocerus megalops, Byblis gaimardi, Aceroides latipes, Pseudolibrotus sp., Anonyx nugax, Stenopleustes pulchella, Arrhis phyllonyx, Haploops laevis; polychaetes: Pholoe minuta, Sphaerodorum gracilis, Antinoella sarsi, Antinoella badia, Laonice cirrata, Melaenis loveni, Polyphysi crassa, Aglaophamus malmgreni, Ampharetidae unidentified; Cumacea: Leptostylus sp.; mysidacea unidentified; Decapoda: Sabinea septemcarinata.

A partition plot of the principal prey indicates strong resource partitioning (Fig. 2). In fact, there is only 6% overlap, which is supportive of the hypothesis that small fluctuations in physical factors and strong partitioning of food-resources are associated.



DEASE STRAIT	Icelus spatula	Icelus bicornis	Aspidophoroides	Gymnocanthus	Boreogadus	Lycodes pallidus
Pholue						+
Sphaerodorum						+
Leptostylus						+
Antinoella sarsi	+					+
Aceroides		+				+
Apherusa					+	
Pseudolibrotus					+	
Calaniod Copepod		+			+	
Mysid	+				+	
Larval Fish					+	
Laonice				+		
Anonyx				+		
Melaenis				+		
Polyphysi				+		
Aglaophamus	+			+		
Byblis	+	+	+			
Haploops			+			
Ischyrocerus			+			
Stenopleustes			+			
Ampharetidae			+			
Antinoella badia		+				
Arrhis		+				
Sabinea	+					

Figure 2. Principal-prey partition plot for an assemblage of marine Arctic fish.

Ranked Partition Studies

There are a few other diet partitioning studies where principal prey overlap could be calculated. These studies were conducted in the following places: the River Cam, England (Hartley 1948); the Irish Sea (Nagabhushanam 1965); the Passamaquoddy Bay, Canada (Tyler 1972); the Sea of Okhotsk (Skalkin 1959). It is not possible to evaluate objectively whether physical factor fluctuations, say, in Passamaquoddy Bay are "stronger" than physical factor fluctuations in Lake Opinicon. The situations, factors, and species are all different. However, all three marine studies are from boreal areas that are relatively moderate in their annual temperate fluctuations as compared to Long Island Sound or Chesapeake Bay (Tyler 1971). The River Cam, however, is an area that was disturbed by human activity, and might be considered highly perturbed. Hartley reported that there was a discharge from a nearby concrete plant a few years before the study.

Following these leads, I ranked the 10 prey partition plots roughly by amount of disturbance, the Arctic location and Lake Opinicon in May being least disturbed, the boreal marine studies somewhere in the middle, and the rainy season tropical and River Cam studies being the most disturbed. A preliminary plot of rank against percentage overlap showed increased overlap with increased disturbance. I then ranked the locations by percentage overlap and plotted overlap against rank (Fig. 3). There was one puzzling feature: why did St. Andrews winter rank among the studies with the most disturbed situation? Aside from that, the plot seems to support the theme of this paper--increased physical factor fluctuation increases diet overlap.

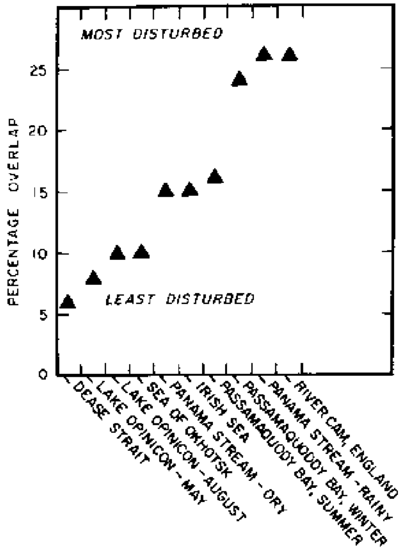


Figure 3. Percentage overlap in partition plots versus location ranked by percentage overlap. More disturbed situations tend to be to the right with high percentage overlap.

Conclusion

While the interpretations presented here are very preliminary, they are sufficiently suggestive to warrant some attention. The line of argument is weakened because prey taxa were sometimes coarsely identified in previously published studies. Also, the relative effects of physical factor perturbations on prey abundance and productivity could not be carefully assessed. Given these contingencies, the effect of both natural fluctuation and human disturbance is apparently to "weaken" food-resource partitioning. Possibly the disruption of partitioning occurs due to an increase in high turn-over, r-type (Gadgil and Solbrig 1972) species after the perturbation. Regularly repeated perturbation would allow persistence of r-type species in high abundance, accompanied by regular weakening of food-resource partitioning, and co-existence of predators that would otherwise not be possible.

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Competition Between California Reef Fishes

Niche Inclusion or Co-Extension?

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"Competition" occurs when animals inhibit each other's access to common resources that are actually or potentially limiting (see Birch, 1957). The ecological "niche", on the other hand, is an abstraction that has been variously defined (e.g., Elton, 1927; Hutchinson, 1957; MacArthur, 1968; Vandermeer, 1972). Unfortunately, operational definitions of the term have been conspicuously difficult to formulate, so relating niche theory to real biological systems has posed an important problem for ecologists. This is especially true when dealing with niche overlap between actively or potentially competing species. By discussing niches solely in terms of the primary dimensions of food and space, one can compute various overlap indices based on different measurements of what animals eat and where they occur (e.g., Cody, 1968; Schoener, 1968). Although such indices are useful in determining whether or not species are potential competitors, however, the most unequivocal test for interspecific competition involves experimental manipulations of the spatial distribution of animals and their resources (Connell, 1975).

Therefore, any practical definition of the niche must involve a spatial component subject to experimental investigation. This paper reports part of an experimental study of competitive interactions between the California reef fishes Embiotoca jacksoni and E. lateralis (Hixon, 1979). The "niche" of these fishes is thus operationally defined as the depth range each species occupies along a food density gradient extending from a relatively food-rich shallow zone to less productive deep reef microhabitats. Using this limited, but practical definition, an attempt will be made to relate current niche theory to experimental field data on this two-species system. Altering Hutchinson's (1957) original concepts, then, the "realized niche" will represent each species' bathymetric distribution in the presence of its competitor, while the "fundamental niche" will constitute each species' distribution after its competitor has been experimentally removed.

The Theory

In their review of experimental evidence for competition, Colwell and Fuentes (1975) distinguished and exemplified three types of fundamental niche relations among competing species: niche inclusion, reciprocal niche overlap, and coextensive niches. These model niche relations are depicted in figure 1. Since niche dimensions have lately been visualized as bell-shaped curves ("utilization functions") representing a species' resource utilization along some resource gradient (e.g., May, 1974), figure 1 has been similarly constructed. Relating these concepts to the above definition of the niche, this paper will discuss "resource utilization" in terms of numbers of individuals and the "resource gradient" in terms of depth of occurrence, parenthetically labelled in figure 1.

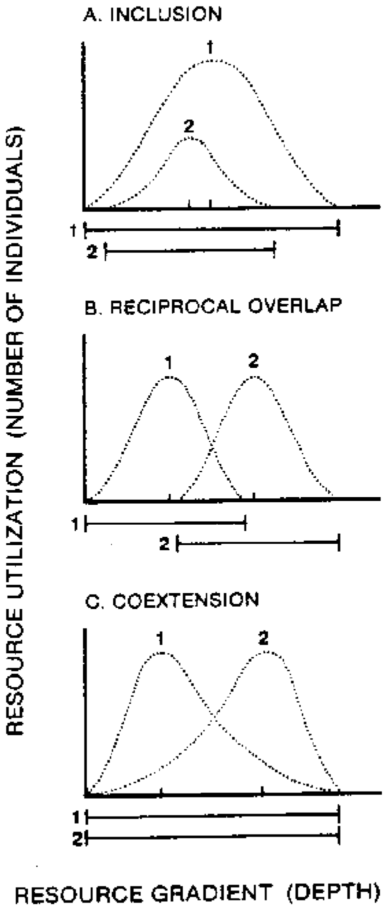


Figure 1. Model fundamental niche relations between two competing species. See text for further explanation.

"Niche inclusion", then, occurs when the fundamental niche of one species (a specialist) is a subregion of the niche of another (a generalist), as depicted in figure 1a (see also Miller, 1967). "Reciprocal niche overlap" occurs when the fundamental niches of two species overlap, but each contains an exclusive region in which the other cannot exist (fig. 1b). "Coextensive fundamental niches" overlap completely, although they may differ qualitatively, i.e., each species may be the dominant competitor in a different subregion of the same niche (fig. 1c). Where competition occurs in nature, of course, we observe realized niches, so an important problem in community ecology is to determine which of the three fundamental niche models prevails in any given system.

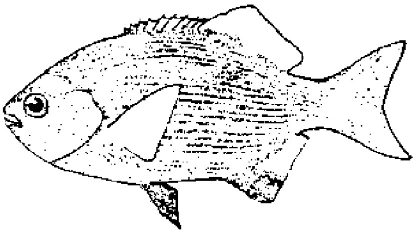
The System

The *Embiotoca* congeners are coastal fishes of the viviparous family Embiotocidae. The major zone of sympatry for these species is the Santa Barbara Channel, a marine ecotone off California separating a relatively cold-water biota north of Point Conception from warm-water communities to the south (Hedgpeth, 1957). *E. lateralis* rarely occurs south of this area, while *E. jacksoni* seldom occupies reefs north of Pt. Conception (D. J. Miller, pers. comm.; pers. obs.). Morphologically, these fishes are very similar (fig. 2). Each attains a maximum total length of about 35 cm (Miller and Lea, 1972). They are sexually monomorphic, and are nearly identical in mouth size and dentition (Tarp, 1952; DeMartini, 1969).

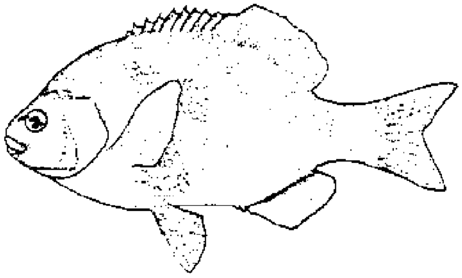
Within areas of reef and kelp off Santa Barbara, the Embiotoca congeners are numerically dominant members of a foraging guild of four yearround resident embiotocids (A. W. Ebeling and D. R. Laur, in prep.). Along with Rhacochilus toxotes and Damalichthys vacca, these fishes are generally observed swimming within a meter of the reef substrate and feeding on small benthic animals (Quast, 1968; Feder et al., 1974; Ebeling and Bray, 1976). Quantitative analyses of dietary overlaps within this guild have been completed by Ebeling (unpub. data), who sampled 30 individuals of each species. Fourteen categories of prey were distinguished on the basis of both taxonomic separation and relative size. The major categories included various small crustacea, polychaete worms, and ophiuroid brittle stars. An indication of proportional dietary overlap between each species pair was calculated using the similarity index of Colwell and Futuyma (1971), the value of which ranges from 0, when species share no prey types, to a maximum of 1, when species utilize common prey in identical proportions. With an index value exceeding 0.6, the Embiotoca congeners exhibit by far the greatest dietary overlap within their guild.

Ongoing investigations of the forage base of these fishes by D. Laur (U. C. Santa Barbara) indicate that the primary prey of the Embiotoca congeners, gammarid and caprellid amphipods, occur on basically two substrates. These prey are most densely distributed on medium-sized algae (especially Gelidium robustum) that dominate shallow reef areas, while in deeper areas they are found on benthic "turf", a low-laying matrix of small colonial animals and algae covering much of the reef bottom. Field observations indicate that E. lateralis picks its prey almost exclusively from shallow "algae", while E. jacksoni normally forages over deeper "turf" (Hixon, 1979; Ebeling and Laur, in prep.).

In summary, then, the Embiotoca congeners are very similar morphologically, overlap extensively in diet, yet forage over different substrates where they are sympatric. An experimental study of food substrate utilization and spatial relations between these fishes was thus undertaken to determine whether or not these species compete with each other and what relationship exists between their fundamental niches.



Embiotoca lateralis



Embiotoca jacksoni

Figure 2. The Embiotoca congeners. (Drawings by D. J. Miller, California Dept. Fish & Game.)

Methods

The competitive and niche relations of the Embiotoca congeners were studied in three ways: (1) a "natural experiment", comparing within-habitat distributions between areas of sympatry and near allopatry; (2) food substrate translocation experiments, comparing the utilization of shallow "algae" moved to deep reef areas and deep "turf" moved to shallow areas with normal foraging patterns; and (3) population removal experiments, comparing the within-habitat distributions of each species before and after its congener had been removed.

The within-habitat distributions of the fishes were documented at various locations by laying 30 m transect lines horizontally along 3 m depth contours from the shallowest to the deepest parts of a reef. As a SCUBA diver swam along each line at a constant pace, the number of individuals of each species occurring within 2 m of the line were tallied. As a "natural experiment", counts were made at similar reefs off Avila, north of Pt. Conception (where E. lateralis occurs nearly alone), Santa Cruz Island (within the major area of sympatry), and Anacapa Island (where E. jacksoni occurs nearly alone). (See Hixon, 1979, for exact locations and descriptions of these sites.)

To determine if each species would utilize the other's primary food substrate if that substrate was made readily available, shallow "algae" was translocated to deep water and deep "turf" was moved to shallow water at Santa Cruz Island. To control for this manipulation, both substrates were translocated simultaneously and placed side-by-side on meter-square plastic trays anchored to the bottom. Thus, algae and turf were offered together in both shallow and deep reef areas. Test substrates were selected from those over which fishes had been observed actively foraging. Each pair of trays was then observed on four separate occasions between Ocotber, 1977, and August, 1978, for a total of three hours. During these periods, the number of individuals of each species foraging over (i.e., vertically oriented toward) each tray, as well as the number of actual feeding bites, were tallied.

The most unequivocal evidence for competitive exclusion comes from controlled population removal experiments (Connell, 1975). The experimental design is straightforward. If one species expands its distribution into contiguous areas formerly occupied by an experimentally removed species, without expanding its range at a control site, then it is most likely that competition produced the original distributions. Such an experiment was run at Santa Cruz Island. Two permanent transect lines were established at each of three similar yet spatially isolated reefs. One line of each pair was set at a depth of 4 m, the apparent center of the bathymetric distribution of E. lateralis, and the other at a depth of 10 m, the approximate distributional center of E. jacksoni. Between March and July of 1977, ten sets of baseline population counts (described above) were made at each site. To control for any general variations in environmental factors, counts were made on the same days at all sites. Then, over a two day period in July, four SCUBA divers speared 130 E. jacksoni at one site and 56 E. lateralis at another, which constituted all the fish that could be found. The third site served as a control.

Following this manipulation, ten additional sets of population counts were made at each site, with the experiment ending in October of 1977. After each set of experimental counts, any new or remaining individuals of the "removed" species were speared. Eventually, 63 additional

E. jacksoni and 45 additional E. lateralis were removed. Within six months of the completion of these experiments, the population density of each removed species had returned to baseline levels, presumably due to immigration from nearby reefs.

For reasons discussed below, a similar removal experiment was run during the summer of 1978. This time, however, algal food substrates were removed from the shallow zone of one reef, as well as all E. jacksoni. Some 20 diver-hours were required to effectively defoliate a reef area measuring approximately 70 m by 9 m using knives and hedge shears. A total of 118 E. jacksoni were removed during this experiment.

Results

This section qualitatively summarizes the results of the above experiments. Hixon (1979) details these results with numerical data and analyses.

The "natural experiment" compared bathymetric distributions of the Embiotoca congeners between areas of sympatry and near allopatry. Where either species occurred nearly alone, it occupied all reef microhabitats, extending from shallow water to the reef base at depths of about 18 m. In sympatry, however, E. lateralis numerically dominated only shallow areas to a depth of about 6 m; E. jacksoni dominated all deeper areas. Moreover, the two species exhibited surprisingly little overlap in their bathymetric distributions. The species' sympatric distributions are apparently not influenced by physical factors such as water temperature, nor by biological factors such as differential predation (Hixon, 1979). Also, their allopatric distributions resemble those reported from other such areas off northern and southern California (Miller and Geibel, 1973; Haldorson, 1978; E. S. Hobson, pers. comm.).

The food substrate translocation experiments compared the two species' forage "preferences". When algae and turf were offered side-by-side in shallow water, E. lateralis still foraged almost exclusively over the tray containing algae, a result consistent with previous field observations. When presented both food substrates in deep water, on the other hand, E. jacksoni readily fed from both. There was, in fact, no significant difference between the number of bites taken from the two substrates. This experimental result contrasts sharply with previous observational data, which indicate that E. jacksoni normally forages over turf, and only rarely enters shallow water and feeds off algae. In areas where either species occurred nearly alone, individuals were commonly observed feeding from both substrates.

The population removal experiments constituted direct tests for interspecific competition. During the initial experiment, there were no significant changes in the bathymetric distribution of either species at the control site. Also, where E. jacksoni was removed, the distribution of E. lateralis remained unchanged; E. lateralis did not move into deep areas formerly occupied by E. jacksoni. Where E. lateralis was removed, on the other hand, the distribution of E. jacksoni changed rather dramatically. The density of E. jacksoni not only increased significantly in shallow water, but also decreased significantly in deep water, indicating a net movement of resident fish into areas formerly dominated by E. lateralis.

The second removal experiment was run to determine why the bathymetric distribution of *E. lateralis* did not change after its competitor had been removed. This experiment was designed to test the idea that food is not limiting for *E. lateralis* in the area of sympatry. This seemed reasonable because the density of this species is relatively low here at the southern margin of its range. Algal food substrates were thus removed from reef areas dominated by *E. lateralis* to increase the "economic density" (sensu Elton, 1958) of that species, thus "forcing" it to utilize deeper microhabitats formerly occupied by *E. jacksoni*. However, while population densities did not change significantly at the control site, almost all *E. lateralis* left the test site rather than forage over deeper reef areas. These fish presumably crossed some 100 m of open water swimming to the nearest neighboring reef.

Discussion

The results clearly suggest that the *Embiotoca* congeners actively compete with each other. The "natural experiment" and field observations indicate that where these species cooccur, they segregate spatially and utilize different food substrates. Where either species occurs nearly alone, however, it utilizes the full range of reef microhabitats and forages over both food substrates. These data suggest that the two species have coextensive fundamental niches (fig. 1c).

However, translocation and removal experiments in the area of sympatry suggest different niche relations. *E. jacksoni* can utilize all microhabitats and both food substrates. Yet *E. lateralis* will not descend to deeper reef areas nor forage over turf, even if forced to abandon its "preferred" shallow zone by removing its algal food substrates. Thus, the fundamental niche of *E. lateralis* appears to be included within that of the more generalized *E. jacksoni* (fig. 1a).

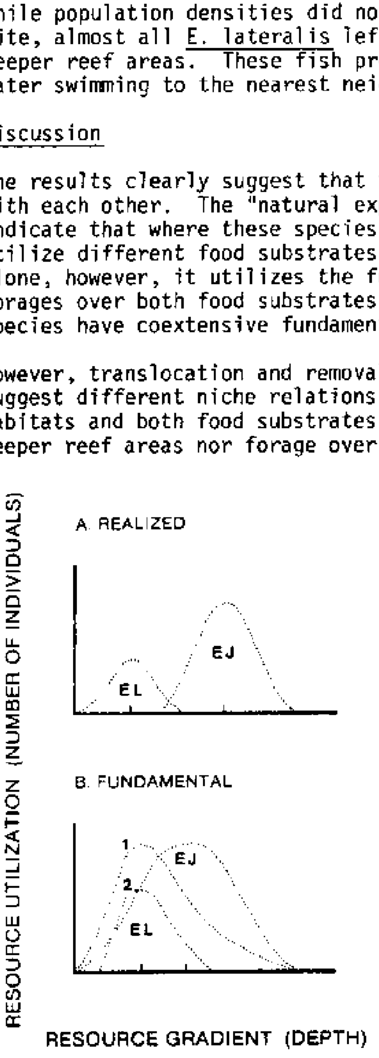


Figure 3. Hypothetical niche relations between *Embiotoca jacksoni* (EJ) and *Embiotoca lateralis* (EL). See text for further explanation.

How can these alternative conclusions be reconciled? I suggest that the relatively low population density of *E. lateralis* in the area of sympatry may account for apparent niche inclusion. The density of *E. lateralis* north of Pt. Conception, where this species occurs nearly alone, is considerably greater at all reef depths than at the southern margin of its range, where it cooccurs with *E. jacksoni* (Hixon, 1979). Individuals in these relatively dense populations also forage over both food substrates, which may account for increased dietary breadth in this species north of Pt. Conception (Haldorson, 1978). Hence, while *E. lateralis* populations may be at or near carrying capacity north of Pt. Conception, marginal populations in the area of sympatry with *E. jacksoni* may be well below carrying capacity. What limits the marginal population densities of E. lateralis is unknown, but warmer water may be a factor. This would explain why E. lateralis feeds almost exclusively from algae and does not competitively exclude E. jacksoni from all reef microhabitats where the two species cooccur; E. lateralis is simply occupying the richest part of the reef--the relatively productive shallow zone--and is under no intraspecific competitive pressure to exploit deeper areas. Thus, even if forced to abandon the shallow zone when its algal food substrates are removed, E. lateralis "prefers" to find another shallow reef rather than forage over less productive deeper areas at the defoliated reef.

This population density hypothesis is illustrated in figure 3. The realized niche relations (fig. 3a) represent the observed bathymetric distributions of the Embiotoca congeners in the area of sympatry. The fundamental niche relations (fig. 3b) show E. jacksoni occupying all reef microhabitats, as it does in the absence of its competitor. The fundamental niche of E. lateralis, however, is represented by two curves. The upper curve (1) represents the niche of this species at relatively high population densities, where E. lateralis occupies most reef areas yet is most abundant in the food-rich shallow zone. This resembles the situation where this species occurs nearly alone north of Pt. Conception. Combining this curve with that representing E. jacksoni, we observe niche coextension (cf. fig. 1c). The lower curve (2) in figure 3b represents the niche of E. lateralis at relatively low population densities, where this species occupies only its "preferred" shallow zone. This resembles the situation south of Pt. Conception, in the area of sympatry with E. jacksoni, where the fundamental niche of E. lateralis appears to be included within that of its congener (cf. fig. 1a). In this situation, E. jacksoni occupies a competitive refuge in deeper microhabitats that E. lateralis will not utilize. This condition apparently maintains the continued coexistence of these species within the same California reef habitat.

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Note added in proof:

Subsequent to the writing of this paper, *E. lateralis* not only returned to the reef where shallow algal food substrates and all *E. jacksoni* had been removed, but also occupied deep microhabitats exclusively, thus providing more positive support for the population density hypothesis.

Food Resource Partitioning by Demersal Fishes from the Vicinity of Kodiak Island, Alaska

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Introduction and methods

In July 1977, the author was given the opportunity to board a vessel chartered by the International Pacific Halibut Commission (IPHC). The stomachs of 1077 demersal fish were collected from 45 trawls taken in the vicinity of Kodiak Island, Alaska. Thirty-five of these trawls were from offshore sites, and ten from the nearshore zone. All samples were collected from predetermined sites used annually by the IPHC to assess halibut stocks. From the perspective of feeding analysis, the sampling technique resulted in some unassessable variability in dietary composition and fullness due to depth, location and time of day. The stomachs were preserved for later laboratory analysis. The data were analyized for the partitioning of food resources between species with respect to both prey type and prey size.

The biomass proportions (wet weight) of 14 prey categories were computed for the diets of six demersal fish species and three size groups of Pacific halibut (table 1). Some of these prey categories represented taxonomic groups. For the non- decapod crustaceans, two habitat categories were used, specifically 'small pelagic crustaceans' which comprised of euphausids, mysids and hyperiids, and 'small epibenthic crustaceans' which comprised of gammarids, isopods and cumaceans. The fish prey were grouped into three morphological categories, 'flatfish','roundfish' and 'longfish'. Prey size measurements were recorded for shrimps, crabs and the three fish categories, except when advanced digestion made this impossible. Other prey categories were not measured, either because of their restricted size range, infrequent occurence or they were only encountered as parts (e.g. polychaetes and siphons).

The distribution of the prey sizes for each combination of prey category and predator was assumed to be log-normal for two reasons. First, if a predator foraged on a particular type of prey without discrimination with respect to size,the prey size distribution would still be strongly skewed, because a stomach can hold many more small prey than large prey. Secondly, a normal distribution assumes the existence of negative and zero prey sizes, whereas the log-normal distribution does not. In fact, some of the crab and shrimp prey distributions with large samples did resemble the log-normal distribution (e.g. fig.1a, 1d). The fish prey distributions were notably irregular, because of small sample sizes and the dominance of certain age groups of common species, most notably sand lance (*Ammodytes hexapterus*) and pollock (Theragra chalcogramma). The mean and standard deviations of the log of the prey sizes are listed with the appropriate prey categories in table 1.

Measurement of resource utilization overlap. Many different indexes of feeding overlap have been utilized by fisheries biologists. Cailliet (1976) listed four different methods, of which Morisita's Index of overlap appeared to be the most widely used. Zebold (1970) used still another index. All of these indexes exhibit the same value range, from zero (no overlap) to one (identical diets).

In theoretical ecology, the standard measure of resource and habitat utilization overlaps is α, which originated from MacArthur and Levins (1967). Several problems encountered with MacArthur and Levins's original equation resulted in a few modified versions. Robert May (1975) reviewed these modifications and determined the properties of an equation by Pianka (1973) most desirable. If a discrete resource dimension is being examined for overlap, the α equation is;

$$\alpha_{ij} = [\overset{a}{\Sigma} p_{ia} p_{ja}] / [\overset{a}{\Sigma} p_{ia}^2 \cdot \overset{a}{\Sigma} p_{ja}^2]^{1/2} \qquad \text{eq. 1}$$

The values p_{ia} and p_{ja} are the proportions of the resource category (i.e. prey type) 'a' in the diets of predators 'i' and 'j' respectively. If a resource is continuously distributed and its utilization by the competing predators can be described by the resource utilization functions $U_i(R)$ and $U_j(R)$, then equation 1 can be modified to:

$$\alpha_{ij} = [\int U_i(R) \cdot U_j(R) dR] / [(\int U_i(R) dR)^2 \cdot (\int U_j(R) dR)^2]^{1/2} \qquad \text{eq. 2}$$

If the utilization functions are normally distributed, then the solution to eq. 2 is (May 1974, eq. 3.2):

$$\alpha_{ij} = [2\sigma_i \sigma_j / (\sigma_i^2 + \sigma_i^2)]^{1/2} \cdot \text{EXP}\ [-(\mu_i - \mu_j)^2 / 2(\sigma_i^2 + \sigma_j^2)] \qquad \text{eq. 3}$$

Where μ_i and σ_i are the mean and standard deviation of $U_i(R)$.

An advantage of the α coefficient over the other competition indexes is that it can be modified to handle more than one resource dimension, provided that the observations are recorded for all dimensions simultaneously (see discussion). May (1975) constructed an α equation for two dimensions, which can be modified to handle one discrete and one continuous dimension that is normally distributed:

$$\alpha_{ij} = \frac{\overset{a}{\Sigma} p_{ia} p_{ja} [2\sigma_{ia}\sigma_{ja} / (\sigma_{ia}^2 + \sigma_{ja}^2)]^{1/2} \cdot \text{EXP}\ [-(\mu_{ia} - \mu_{ja})^2 / 2(\sigma_{ia}^2 + \sigma_{ja}^2)]}{[\overset{a}{\Sigma} p_{ia}^2 \cdot \overset{a}{\Sigma} p_{ja}^2]^{1/2}} \qquad \text{eq. 4}$$

Results

The resulting overlaps between interspecific predator pairs, derived by the application of equation 4 to the data in table 1, are shown in table 2. High overlaps occurred between the rock sole and the butter sole. and between the halibut size groups and several of the non-halibut predators. The rock and butter soles were apparent epibenthophagous 'snippers', biting off the siphons and polychaetes exposed near the surface, and taking the small crustaceans that were available. Their depth and geographical distributions were almost identical. However, Smith (1936) suggested that the butter sole preferred silt and mud bottoms, whereas the rock sole preferred gravel or rocky bottoms.

The overlap between the smallest size class of halibut and the flathead sole was easy to account for: The small halibuts were restricted to depths above 50 meters, while the flathead sole not common above 50 meters. The high overlaps between the two larger size classes of halibuts, and the Pacific cod and arrowtooth flounder cannot be explained on the basis of any known habitat dimension. It should be noted that the halibut studied herein were largely juveniles, while the other species were adults. Perhaps the juveniles of a species do not fully occupy their own niche space.

Discussion

As it is often the case in fisheries feeding studies, there were almost as many problems as there were answers. First of all, the digestion rate of different prey organisms were different. Fish and cephalopods usually underwent faster digestion than crustaceans, which had chitonous exoskeletons. As a result, the proportions of the biomass of fish and cephalopods were underestimated, and prey size measurements for the fish were harder to acquire. While a laboratory study on the digestion rates of different prey items could be useful in estimating unbiased biomass proportions, the type of digestion in the predator must also be considered. Epibenthophagous and benthophagous fish generally have a small stomach which serves as a storage organ for food that is digested in the intestine. Piscivores and large crustaceans eaters digest their prey beyond recognition while in the stomach (Karpevitch and Bokoff 1937, deGroot 1971, pers. obs.).

Competitive dietary comparisons of two or more predators should be based on the nutritive proportions of the prey categories in the diet of each predator. There are at least four ways of estimating the nutritive value of a prey; wet weight (as used herein), volumetric displacement, dry weight and caloric determination. The first two methods are the easiest to use, but may be biased by the fraction of water in the tissues of different types of prey. Dry weight techniques eliminates this source of bias, but may lend to another. Shell fragments, other inorganic particles, and heavy prey parts (bones, chiton),which maybe undigestible or partially digestible, will carry considerably more weight when dried and may result in a greater source of bias.

Caloric determination of each prey item is certainly the best method, but could be very time consuming. Perhaps the ultimate solution is the creation of a catalog listing the caloric values for a range of sizes of representive species in each basic prey taxon or morphology. This could be put together from data from past studies, and future investigators can fill in the gaps according to their need. The advantages of such a catalog would be economy and would provide an alternative to crude estimates based on weight or volumetric displacement. For an example, if the length of a partially digested flatfish prey can be determined, the caloric value could be estimated by consulting the catalog for a listing of caloric values of a prey species with a similar morphology (i.e., another flatfish), and extrapolating for the caloric value of a prey the same length. This would bypass the problems of bias in weight because of digestion.

Diet composition is just one aspect of competition. Other resource and habitat dimensions must be taken into consideration if the full scope of competition is to be measured. Other dimensions which may be important are time of foraging activity, depth distribution, habitat and microhabitat preferences, temperature and bottom sediment type. Measuring overlap along more than one dimension is possible, but only if observations are recorded in every dimension simultaneously (May 1975). Thus, for every dimension added to the plan of a study, the scope of the project increases geometrically, rather than linearly. For an example, if a feeding ecologist decides to study the feeding overlap between two species of fish by collecting thirty stomachs of each from one trawl, the scope of the project would be small, but not very informative: The degree of competition may change with respect to the time of day, season, depth, abundance of food resources, and the type of food resources available. But if he tries to examine the competitive overlap by examining five different depths, five periods during the day and five periods during the year, the study would require 125 trawls, and 7500 stomachs. Furthermore, as more dimensions are added, the analysis and interpretation of the data becomes increasingly difficult.

A basic difference exists between the terrestial communities, from which competition theory has developed, and the marine fish communities like the one studied herein. Most terrestial animals stop growing as they approach maturity, and many species receive extensive parential care as juveniles. Marine fish grow continuously until death, and must forage on their own from hatching. In fish populations, the greatest contribution to niche width, or variability in resource utilization, is the size distribution. Christensen and Fenchel (1977, eq. 3.91) described niche width as a sum of three factors; The within phenotype component (i.e. variability in resource utilization by the species as a whole), the between phenotype component (i.e. the degree of specialization by individuals within a population) and the age structure component or, in the case of fish populations, the size distribution component. The first two components have been throughly investigated in both theory and in the field. The latter component has been treated in some studies (e.g. Schoener 1968, Zebold 1970), however the analysis and implications of this component as it exists in fish communities has not been fully investigated.

Figure 2 shows two models of niche space utilization, which the author has termed as the 'anthill' and 'ridge' models. The anthill model applies to the typical terrestial community in which resource utilization by each species occurs in a relatively restricted size range. The ridge model is best concieved as continuous rows of anthills representing the different sizes of each species in the community. It describes the community structure of marine fishes. The ridge model suggests some rather difficult analytical problems. How can the overlap between two species, which both utilize a wide range of resources as they grow, be measured? Overlaps may be high between certain size classes, and low between others. Determining the overall overlap between two species would not have much pracitcal significence. By partitioning each species into several size classes and evaluating the overlap between each size class, an investigator can determine which size class is experiencing the most competition and who that competitor is.

Conclusions

An examination of a subartic demersal fish community suggests that food resources are partitioned with respect to prey type and prey size. A method for measuring overlap in resource utilization along two dimensions is shown. High overlaps exist between some of the predators, and a few of these could be attributed to habitat partitioning. However, overlaps

Table 1. The biomass proportions of 14 prey categories in the diet of 9 predator groups. The means (μ) and standard deviations (σ) of the LOG_{10} of the prey lengths for five prey categories are shown.

	PREDATOR								
PREY CATEGORY	Pacific cod	Great sculpin	Arrowtooth flounder	Flathead sole	Butter sole	Rock sole	Pacific halibut less than 300 mm	Pacific halibut 300 to 599 mm	Pacific halibut greater than 599 mm
Polychaeta	0.004	0.000	0.000	0.006	0.185	0.309	0.001	0.001	0.008
Gastropoda	0.007	0.008	0.000	0.000	0.092	0.000	0.000	0.002	0.000
Bivalvia siphons	0.000	0.000	0.000	0.000	0.256	0.106	0.000	0.001	0.000
Bivalvia-whole	0.002	0.000	0.000	0.000	0.099	0.104	0.000	0.000	0.000
Cephalopoda	0.008	0.000	0.007	0.000	0.009	0.000	0.000	0.000	0.035
Small pelagic crustaceans	0.013	0.000	0.005	0.201	0.000	0.007	0.001	0.000	0.000
Small epibenthic Crustaceans	0.002	0.000	0.000	0.004	0.031	0.112	0.004	0.000	0.000
Natantia	0.296	0.002	0.002	0.551	0.017	0.026	0.451	0.037	0.010
μ	0.927	-	-	0.595	-	-	0.505	1.119	1.286
σ	0.293	-	-	0.193	-	-	0.352	0.169	0.094
Paguridae	0.008	0.001	0.000	0.001	0.004	0.003	0.033	0.053	0.004
Brachyura	0.098	0.729	0.000	0.031	0.282	0.050	0.088	0.089	0.066
μ	1.213	1.463	-	0.701	-	0.897	0.682	1.128	1.417
σ	0.181	0.219	-	0.167	-	0.129	0.253	0.224	0.096
Ophiuroida	0.000	0.000	0.000	0.140	0.021	0.048	0.000	0.000	0.001
Flatfish	0.128	0.152	0.002	0.007	0.000	0.044	0.057	0.109	0.109
μ	2.018	-	-	-	-	-	1.349	1.911	2.082
σ	0.251	-	-	-	-	-	0.045	0.129	0.130
Roundfish	0.253	0.108	0.972	0.007	0.001	0.192	0.044	0.468	0.621
μ	2.000	2.061	2.171	-	-	1.291	1.301	2.012	2.082
σ	0.216	0.232	0.100*	-	-	0.167	0.203	0.249	0.130
Longfish	0.182	0.001	0.012	0.045	0.001	0.002	0.322	0.241	0.145
μ	2.134	-	-	-	-	1.894	1.876	1.967	2.009
σ	0.101	-	-	-	-	0.693	0.255	0.142	0.280

Table 2. A summary of the predator feeding habits and the interspecific overlap in food resources consumed by these predators. High overlaps are underlined.

predator number	predator species i	feeding habits	sample size	predator species j							
				2	3	4	5	6	7	8	9
1	Pacific cod Gadus macrocephalus	Generalist; crustaceans and fish	139	0.275	0.378	0.409	0.170	0.097	0.464	0.689	0.591
2	great sculpin Myoxocephalus polyacanthocephalus	Specialist on large crabs	46		0.112	0.008	0.065	0.032	0.034	0.251	0.243
3	arrowtooth flounder Atheresthes stomias	Specialist on large fish, particularly pollock	41			0.161	0.002	0.001	0.009	0.601	0.812
4	flathead sole Hippoglossoides elassodon	small shrimp, euphausids and ophluroids	69				0.090	0.112	0.701	0.055	0.030
5	butter sole Isopsetta isolepis	epibenthophagus 'snipper' polychaetes and siphons	49					0.610	0.132	0.111	0.073
6	rock sole Lepidopsetta bilineata	epibenthophagus 'snipper' polychaetes, siphons and amphipods	134						0.114	0.062	0.029
7	Pacific halibut less than 300 mm Hippoglossus stenolepis	shrimps, small fish and crabs	105								
8	Pacific halibut 300 to 599 mm Hippoglossus stenolepis	fish and some crabs	175								
9	Pacific halibut greater than 599 mm Hippoglossus stenolepis	large fish	55								

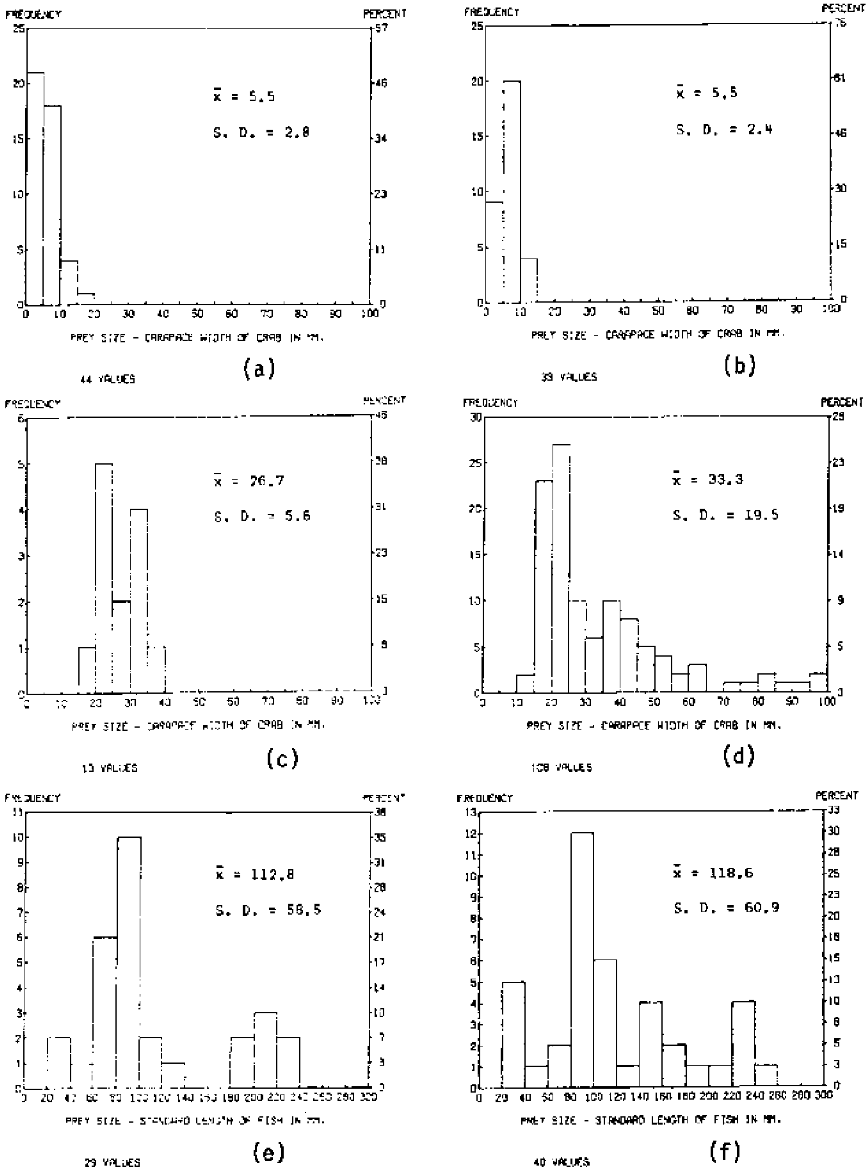
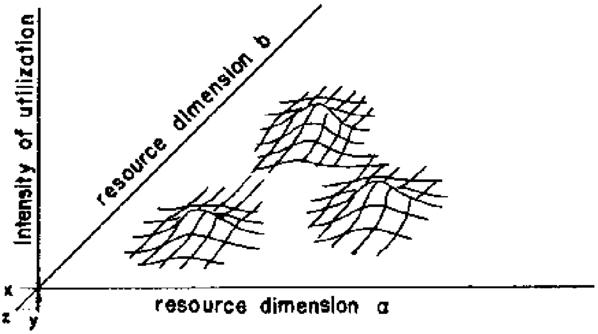
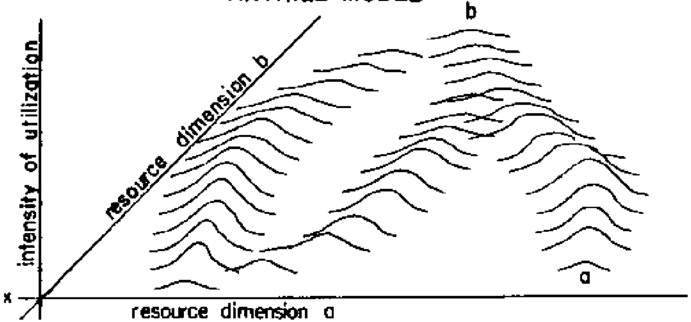


Figure 1. Six graphs showing the disribution of prey sizes by certain predators. Graphs (a) through (d) shows the selection for increasingly larger crabs by flathead sole, small halibut, large halibut and great sculpin. Graphs (e) and (f) shows the size of roundfish consumed by cod and medium-sized halibut. The irregular distributions in graphs (e) and (f) were typical of the fish prey.



ANTHILL MODEL



RIDGE MODEL

Figure 2. Two conceptual models representing alternate hypothesizes of how resources are partitioned along two dimensions. The 'anthill' model describes the resource utilization by a community in which each species is relatively uniform in size. The 'ridge model' is more applicable to fish communities. Fish forage on their own from hatching, and their resource utilization shifts from 'a' towards 'b' as they grow.

between the Pacific halibut and two other predators were high and could not be accounted for. A method for measuring the overlap along two resource dimensions is shown. A discussion of some of the problems in methodology and competition theory is presented.

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SESSION 4 Competition
DISCUSSION

Myers replied to a question regarding the size of the fish she sampled that the hatchery coho ranged from about 10 cm to 35 cm and the wild fish were all around 8 to 12 cm. Hunter then posed the question that the hatchery fish might be using the food resources of the wild fish. Word did not understand how a person distinguished between a hatchery fish and a wild fish; Myers replied that she used several techniques, among them scale analysis. Cailliet wondered how the hatchery fish were fed; Myers responded that they received a diet similar to the Oregon Moist Pellet. Simenstad noticed from Myers' small sample size that she might have had trouble catching a lot of fish and asked her if she had any idea of the proportion of the fish that immediately left the estuary. Myers suggested that the coho move right through and was interested in how long the hatchery fish remained in the bay after they had been planted; the data from 1978 showed that the hatchery fish were staying around about three weeks.

To a question about the size of the natural run Myers indicated that a good population estimate for wild salmonids does not exist at this time. Levy noticed that when she had a high catch of hatchery fish there was a low catch of wild fish and vice versa. Myers admitted that the plant occurred a couple of days before the first sample and the migration of wild fish peaked about May 13 so there were not too many to catch after that. Levy suggested that she might take the two groups of fish and seclude them in a tank for observation, an idea Myers thought interesting.

Koski wondered what sort of numbers of fish Weyhaeuser intended to release in the next few years. Myers explained that Weyhaeuser has permits to release 9.5 million coho, 10.6 million chinook, and 20 million chum. They also have permits for similar releases in Coos Bay. Koski then asked if there was any estimate of the population abundance of chinook in the bay; Myers replied that she wished she did. Horton then responded to Koski's question by saying that the population of fall chinook is sufficiently large that the Oregon Department of Fish and Wildlife allowed Weyerhauser Corporation to take a portion of the run to develop stock for their own release program so that the fall chinook Weyerhaeuser is releasing are probably an extension of the natural run from the bay but there have not been good monitors on the run size.

Caillet had two questions regarding Tyler's presentation. The first was if the measure of overlap accurately measured differences relative to the number of categories set up. Tyler said that it was a proportion. Cailliet clarified his question by suggesting that if Tyler made finer divisions between categories an observed trend may not actually be there and suggested to Tyler that he statistically test the validity of the divisions he utilized.

Cailliet asked Hixon if he cared to make a statement about the relative degree to which the two species E. jacksoni and E. lateralis could be considered territorial. Hixon said that territoriality is a difficult item to study. However, he considered male Embiotica jacksoni to be an inferior competitor. Cailliet wondered what would happen if, in addition to removing the food, Hixon also removed the feeding site. Hixon said that he had expected the E. lateralis to remain in their accustomed areas even without the food and become thinner but was surprised that they left fairly soon. He suggested that it indicated that the fish took some decisive action. Hunter interjected that his impression of territorial fish is that they establish a home range and protect it as long as the food resource is in some area near the home range. If the food resource is saturated because of a school of fish or a swarm of something like crustaceans then the home range structure tends to break down and there is no need for it at that point in time. Hixon agreed that by altering the food supply one can alter the size of a fish's territory.

Chess remarked to Hunter that perhaps even delineation of size classes is improper since changes may occur at uneven intervals. Hunter explained that sometimes fish were not available in each size class. Cailliet noted that there are two alternatives with the alpha ij measure, one is the effect of j on i and the other is the effect of i on j; it seemed to him that Hunter had just performed a one-way competition coefficient. Hunter replied that there were other problems which dictated the use of that particular equation.

Feller asked a question of our collective vocabulary, remarking that overlap and competition were not the same thing! Sibert encouraged even more concern about the two dimensions of overlap. He suggested that speaking of two resources that are seldom if every independent can create complications. He went on to clarify a comment by Bledsoe that, while the occurrence or the abundance of the resources may be correlated, their utilizations are independent and what you are trying to calculate is the utilization of the resource rather than the abundance of the resource. Hunter explained that he interpreted the formula to take both into consideration.

Sibert suggested several points for discussion:

1. High diet overlap indicates "competition" (eg. Somerton)
2. High diet overlap does not indicate "competition" (eg. Tyler)
3. What indicates "competition"?
    a. stunted growth
    b. resource depletion
    c. decreased stomach fullness
    d. behavior

4. Multiple resource overlap
5. Declare moratorium on word "competition" (i.e., deposit in a word bank for future withdrawl....and accumulated interest?)

Sibert challenged anybody to define the difference bewteen the first two positions. Crow accepted with the answer that high diet overlap was indicative of a transient state whereas Tyler was pointing out that when you let that system go through a period of adjustment that you wound up with a low diet overlap. So if anyone does observe competition it will not last that long.

Tyler took issue with Somerton's interpretation by saying that one conclusion from the dietary overlap documented by Somerton was that there are so many euphausiids out there that anyone can get them and so that is why pollock got the way they are now. He went on to say that overlap in the diet means that there is no density-dependent phenomenon occurring at that particular life stage but you have to qualify that in terms of the species of euphausiids. Sibert agreed that point was not clear to him either, saying that one cannot say too much about the interpretation of diet overlaps without knowing something about the condition of the food resource or other information and that would fall under Item 3 above. He also suggested that you could measure stomach fullness under conditions of high or low diet overlap; if fish were not getting their full ration then perhaps you would have evidence for competition. Word suggested actually getting in the water and observing the fish to see whether they compete for food. Hunter suggested that another way would be to remove one of the predators. Hixon astutely observed that that would be called an experiment. Hunter suggested behavioral interaction.

Bledsoe related back to Word's comment and said that you might want to distinguish between two basic types of the "unusuable word;" on one hand you could have active competition involving antagonistic behavior that occurs in the presence of another fish species which does not occur in its absence. On the other hand you could have passive competition where fish are feeding in the same area on the same item and the feeding rate of one animal is superior to the other. If the resource is depressed, such as due to herbivores, the animal with the lower feeding rate will be at a disadvantage and eventually will not show up. He insisted that it is an important distinction to make.

Hixon theorized that in any system you have a mixture of exploitative and interference mechanisms operating. For example, in his study E. lateralis was much more adept at aggressively excluding E. jacksoni during the time of day when both fish were feeding together. However, he observed the feeding mode of E. lateralis to be much more adept at picking prey off algae than E. jacksoni and when he did see E. jacksoni feeding off algae, they were more sloppy and their gut contents reflected that. Word cautioned that especially in the rocky intertidal habitat that most of the antagonistic behavior is intraspecific--a species driving off members of its own species. Hixon concurred.

Chess commented that he has studied two types of rockfish--blue and black--that at certain times had considerable diet overlap, but only during certain periods, e.g., during the absence of oceanic upwelling. Normally blue rockfish take smaller prey and black rockfish take larger prey. This is a disturbed situation yet it happens half the year. He suggested that although it was diet overlap perhaps it wasn't true competition. Tyler noted that we were talking about equilibrium models and nonequilibrium models in a sense. An equilibrium situation should have one species eliminating the other and the species together should be displaying strong partitioning. It appears to him that when there was overlap it indicated a nonequilibrium state and conversely, a nonequilibrium state could be a competitive one. Simenstad brought up the point that we were implying different time scales in our discussion; in one case we were talking about short-term interaction and in another we were describing long-term interaction, which might cross several generations.

Sibert suggested that we should look for competition in different life history stanzas. He gave larval stages as examples, whose behavior was radically different from an adult and might just as well be considered a different predator species. Hunter took issue with this, saying that they were not truly independent since the feeding strategies were evolving even at an early stage. He went on to suggest that one might expect a higher competition in juveniles of most species for the reason that selection acts on the morphology of fish that achieve adult size and thus we might look for a higher competition or overlap at the younger stages. Hunter further commented that the genetic component of the smaller fish must allow for a competitive advantage in the adult fish because juveniles suffered the highest mortality, thus that is when the selection occurs. Cailliet said that competition is not necessarily higher; according to Margalef overlap is just higher. Cailliet went on to point out that Lasker's work with larval engraulids showed that the phytoplankton on which they feed is patchy; if the larval engraulids ended up in a bare patch they were in trouble and contrarily, if they were in a good patch they were fine.

Chess suggested that perhaps a more meaningful way to look at this question involves looking at how a resource is used. In his studies he has observed pile perch and kelp greenling living together and feeding on generally different things most of the year; but this spring (1978) a big batch of caprellid amphipods appeared and both species started feeding on caprellids. And, when the caprellids dwindled, the fish returned to their usual partitioning of food resources.

We returned to a heated argument regarding the use of the word competition. Some defended its use while others were opposed to its use. Bledsoe intervened with the suggestion that it is okay to use the word if one first defines an operational definition prior to using it; otherwise we confuse our colleagues. Once again the point was made and emphasized that we tend to become too casual and inconsistent with our use of technical terms.

SESSION 5
Modeling and Summation

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Implications of Optimal Foraging Theory For Food Web Studies

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The hypothesis that an animal is able to modify its foraging behavior to achieve maximum benefit from its foraging behavior has intuitive appeal, especially in the face of the extreme plasticity of the diets of some organisms. This paper will attempt to synthesize several approaches to optimal foraging theory into a hierarchical model of foraging activity. At each level of the model the decision rule for optimal foraging and its implications will be discussed. An attempt is made to bridge the gap between theory and data. Unfortunately, the range of predicted behaviors is so broad and the field situation so complex that little more can be done than argue for why the animals do not appear to obey the optimal foraging models.

Definitions

Optimization is the attempt to minimize or maximize some quantity. This paper will concern itself only with short term optimization, and uses the maximization of energy intake per unit foraging time (E) as the goal. This results in similar predictions to minimizing the time spent foraging (T). The net energy gain from an individual of the i^{th} species is:

$$E_i = p(\text{assimulatin efficiency} \times \text{energy content} - \text{handling costs}) - \text{pursuit costs}$$

where p is the probability of successful capture. E is the expected energy intake rate which is an instantaneous rate and may change during the foraging interval (i.e., dE/dt is nonzero, E is a function of the time spent foraging). $\overline{E}$ is the observed average energy intake rate over the entire foraging interval. If dE/dt = 0, then E is constant and is equal to $\overline{E}$. The foraging interval (T) is the summation of time spent searching for prey (T_s) and time spent handling prey (T_h). Handling time includes the pursuit and handling of prey regardless of whether they were captured. t_h is the handling time of an individual prey item.

Hierarchical Decision Model of Foraging Activity

Four decisions define the foraging activity of an animal:
(1) When do I forage?
(2) Where do I forage?
(3) How do I forage?
(4) What prey do I pursue?
Question (1) is asked the least and is hypothesized to be the most important and the least flexible. Question (4) is asked the most. Errors in its answer are the least costly, and, as such, probably the least critically optimized. This paper will stress the importance of questions (2) and (3) as the key decisions the animal makes concerning optimal foraging. Each of these decisions is now investigated in turn.

When do I forage?

This question appears to be the most constrained and hence the least flexible. Usually time presents the greatest differences in environmental conditions such as temperature, light, and wind which determine the activity of animals. Even if a predator is unaffected by these conditions, its prey or its predators may be affected (e.g., most planktivorous fish are visual predators and most zooplankton species stop foraging and migrate into deeper water during the day, confining fish to eating only at dawn and dusk (Werner and Hall, 1974)).

However, the duration of foraging activity can be optimized. Schoener (1971) presented a cost benefit model to predict the time spent in foraging activity. Schoener assumed that the accumulation of energy represents a benefit to the animal but since the animal is limited in its ability to process food into future benefits the more the animal ate the less valuable each additional unit of food became. Thus, d(benefit)/dt is a decreasing function of time spent foraging. This would be especially true of K-selected species (MacArthur and Wilson, 1967) whose reproductive effort is constant, independent of energy consumed, whereas r-selected species would tend to have indeterminate growth and variable reproductive effort through which excess consumption can be put to use. The costs of foraging include the unfavorable thermoregulation environment, predation risk, and competing time demands of mating and territorial defense. These costs tend to increase as the time spent foraging increases, i.e., d(cost)/dt is an increasing function of time spent foraging. The animal should then stop foraging when

$$\frac{d(\text{benefit})}{dt} = \frac{d(\text{cost})}{dt} \quad .$$

This model would predict that efficient foragers (E high) should spend less time foraging than inefficient foragers. That animals with determinate growth and fixed reproduction should be time minimizers and spend less time foraging than animals with indeterminate growth and variable reproduction which should be energy maximizers. This model would also predict that during times of high costs (e.g., setting up territories, mating, or bad weather conditions) that an animal may not forage at all.

Where do I forage?

This question assumes that the animal is constrained to or has already chosen a habitat which is patchy and the question concerns which patches the animal visits and how long it stays in each patch. The model assumes that the animal can only search in one patch at a time. Charnov (1973) and Charnov et al. (1976) show that this question is only relevant when there is resource depression. Resource depression occurs when the rate of energy accumulation by the animal decreases as long as it stays in the same patch (i.e., dE/dt is decreasing). Charnov cites three reasons for resource depression: (1) numerical response - as the predator removes prey the number left in the patch is decreased; (2) frequency response - the predator removes the most desirable and the most easily caught prey first and the longer the predator stays in the area, the more difficult and the less desirable the remaining prey; and (3) behavioral response - the longer the predator remains in the patch, the more prey recognize its presence and change their behavior to reduce their chance of being eaten. If resource depression did not occur (i.e., E constant), then the optimal forager would pick the patch with the largest E and stay there. Most sessil or immobile organisms fall into this category (e.g., barnacles). However, temporary territorial behavior may also be a result of a lack of resource depression (e.g., when blackbirds prey on emerging insects there is no resource depression and the birds are highly territorial, and trout feeding on the insect drift in a stream do not experience resource depression and are territorial). When resource depression exists, a predator may visit several patches during a foraging interval. The decision rule for which patch to visit assumes a mean rate of energy accumulation

$$\overline{E} = \frac{1}{T}\int_0^T E(t)dt \quad .$$

An animal will forage in patch A only if the rate of energy intake (E) while in patch A is greater than $\overline{E}$. With resource depression, dE/dt is negative and the animal will leave patch A when $E = \overline{E}$. The animal will use the same criteria for all patches and this criteria can be expressed as giving up time, the critical time between prey encounters after which a predator will leave a patch. Since $\overline{E}$ includes the travel time between patches the more mobile the predator and the closer together the patches the more patch switching will be exhibited by the predator. This model leads to the following predictions: (1) as energy demand increases a time minimizer will spend more time foraging and will visit more patches, broadening its diet; (2) in a more productive environment, a time minimizer will spend less time foraging and visit fewer patches, whereas an energy maximizer will be unaffected; (3) as the best patches increase in prey abundance relative to the others, predators will visit fewer patches; (4) as patches not currently visited increase in prey abundance they will be visited by predators; and (5) the ultimate in resource depression occurs in flocking predators which rapidly depress the prey in a patch and tend to be highly mobile, visiting lots of patches.

How do I forage?

A predator can only use one search method at a time. If a predator has more than one search method, one will be chosen. A search method will favor some types of prey over others, with corresponding changes in the relative encounter rates. Alternate search methods exist when training is present (i.e., by specializing on one prey species the predator experiences an increase in the encounter rate, the probability of successful capture, or the digestion efficiency, or a decrease in handling time or digestion time). The decision rule for selecting search modes is the same as selecting patches and the results are the same. The search mode is also assumed to be affected by resource depression. However, if the prey abundance of all species is reduced enough, the predator will stop using specialized search methods and will only use its most general search methods.

What prey do I pursue?

This is the question most often discussed in the optimal foraging literature (e.g., Emlen, 66; MacArthur and Pianka, 66; Schoener, 71; MacArthur, 72; Timin, 73; Pulliam, 74; Charnov, 76; and Pearson, 76). This question assumes that after the animal has selected a patch and search method that several classes of prey are available to it and all are searched for simultaneously. The term prey classes is used in place of prey species because different individuals of the same species may have different E_i/t_{hi}. Individual values of E_i/t_{hi} will vary as a function of size, distance from predator, and physical condition of prey. Charnov (1976) demonstrated the importance of distance from the predator and Werner and Hall (1974) showed the importance of size. The decision rule for this question is independent of resource depression. Each class of prey is ranked by E_i/t_{hi}. Since all prey are searched for simultaneously, the ranking of a prey is independent of its abundance and encounter rate. E is calculated (note: this is E the instantaneous rate not $\bar{E}$ the average over the entire foraging interval). The current rate is used since there is no cost involved in adding or subtracting a prey from the diet, whereas a traveling or training cost is involved in changing patches or search methods. This also assumes that there is no time involved in making a decision of whether to pursue a prey (see Pearson, 1976). The i^{th} class of prey is included in the diet if $E_i/t_{hi} > E$. The inclusion of a species in the diet is determined by the absolute abundance of what is in the diet, independent of the abundance of what is not in the diet. An item not in the diet cannot "work its way into the diet" by becoming abundant and the diet is adjusted by adding to and deleting items from the bottom of the list. The top rated item is always taken, and as the top rated items increase in abundance, the lower rated items are removed from the diet.

Effect of Prey Size

The energy return from a prey is proportional to its size but its handling time increases exponentially with a lower threshold at small sizes and the slope increases towards infinity at an upper threshold (Werner, 1974). Hence, as prey size increases, E_i/t_{hi} assumes the form of a parabola, steep at the extremes and broad in the intermediate sizes. This would indicate the size selection is sharp at the extremes but is not important for prey of intermediate sizes. Predators which consume either very small prey or very large prey should be very size selective but predators eating prey of intermediate sizes where handling time is proportional to prey size should be less size selective.

Switching Model

Murdoch (69, 73, and 75) has proposed a switching model applicable to the questions of where and how. Murdoch performed laboratory studies of animals' preference when the prey were at equal abundances. He developed a model to predict if the prey would switch if the relative abundances were changed from 50-50 to 20-80. If the animal displayed a strong preference at 50-50, then no switch occurred at the altered abundances since one of the prey was far more desirable than the other. However, it is likely that the predator would switch if the prey were altered to a greater extent. If the predator showed weak preference then a switch would not occur since the prey were rated very similar and were in the same patch-search method. However, if the animals show individual variation with some animals preferring one and some preferring the other, a switch will occur if the relative abundances are altered. The individual variation indicates that the prey species are in different patches or search methods and the prey are equally rated at their current abundances. When the relative abundances are changed then the different patches or search methods assume different values and all animals switch to the preferred patch-search method. Murdoch has verified the predictions of the model with ladybird beetles not switching (Murdoch, 1973), with fish switching patches (Murdoch, 1975), with snails switching digestion modes (Murdoch, 1969), with birds switching search images (Murdoch and Oaten, 1975), and evidence for switching due to handling time changes has been found in pollination ecology.

Murdoch's switching model may be applied to field studies by observing electivities. If the animals exhibit a strong preference, or if all animals exhibit a weak preference the animals are not near a patch or search mode switch. However, if the animals show individual differences the animals are near a switch as the different individuals are foraging in different patches and/or search methods which are rated equally at the current point in time. But as the prey abundances change one of the patches or search method will become more favored and all the animals will forage in that patch-search method combination.

Summary

In a patchy environment or in a predator-prey combination where predator training can affect the E_i/t_{hi} of the prey, the where-how decisions of the predator should have the largest effect on the diet. In this case, the predator will drop any item from its diet, the absolute and relative abundances of all prey determine the optimal diet allowing a prey to work its way into the diet by becoming abundant. In a homogeneous environment without predator training the what question will determine the diet. In this case, the predator will base its decisions on the absolute abundance of the prey in the diet and the top rated prey will never be dropped from the diet and prey not in the diet will not be included if they increase in abundance (table 1).

Within a where-how decision the amount of individual variability may help to locate times when a switch is occurring. Unfortunately, the precise nature of the feeding decisions in a field situation will always be difficult to ascertain because of a variety of confounding factors: (1) since animals experience resource depression they will use more than one patch and/or search method, which will broaden and complicate the diets of individual fish; (2) spatial variability will present different conditions to different individuals in the population resulting in variability between fish; (3) within each patch-search method the animals are faced with "what?" decisions, blurring the diet selection pattern between where-how questions and what questions; (4) each prey species will be placed into several classes of prey, thus the predators are not responding to prey species but to prey classes, where a prey class may be composed of some individuals from several different species on the basis of size, swimming ability, and distance from the predator when sighted; and (5) animals have neither perfect knowledge nor perfect judgment and will make errors in decisions. The above complications probably make any application of optimal foraging theory to field data extremely difficult except for folklore generalizations such as, "predators will specialize in a productive environment."

	Where How	What
Habitat	Patchy	Homogeneous
Training	Yes	No
Restricted Search	Yes	No
Decision Rule	$E = \overline{E}$	$E_i/t_{hi} = E$
Needs Encounter `Rate For Individual Prey	Yes	No
Switch Off Best Prey	Yes	No

Table 1. Comparison of Where-How and What Questions.

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Mechanisms of Population-Energetics Linkages in Age-Structured Food Web Models

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Mathematical Description of Population Processes

A major objective of research in fisheries management is to be able to predict the future yield of a fish population given a measure of the amount of harvest effort which is to be employed. One of the most commonly used approaches for this purpose employs a differential equation model of population growth known as the stock production model (general case of the Shafer model). The rationale of this approach is that the mathematical equations reflect at some level of resolution the mechanisms which are occurring in the animal population such as growth, mortality, and reproduction. The stock production model, however, makes only the most limited use of an analogy between actual biological mechanisms and mathematical equivalents thereof. Most notably omitted from the equation is the age structure of the population, a predominant characteristic of all living populations, plants or animals. Various population dynamics formulations have been proposed to consider the age structure of a population. These are variously known as Leslie matrix models or, in fisheries literature, as Beverton-Holt or yield per recruit models. These formulations, while employing a basic age structure, utilize the approximation that ages of animals occur in discrete groups as opposed to the concept that an animal can have an age which is represented by any positive real number. There are also a number of other important characteristics of living populations for example, a dependence of mortality, growth and reproduction on food consumption, which are mimicked by neither of the above two classes of management models. These are the only two classes of models which are widely used for fisheries management purposes. The objective of this paper is to explore the development of a model which will go beyond the above mentioned factors in a mathematical structure which more closely mimics the mechanisms of actual populations yet still is simple enough in its structure to be utilized for management purposes, i.e., prediction of the expected yield of a harvested population.

Mechanistic vs. empirical models.

First it is necessary to distinguish between 1) the mechanisms in a real population which are basic to its functioning and which are the causes of 2) observed phenomena which I will term emergent behavior of the population and hence of the mathematical model. A mechanistic population model is one in which the mathematics are analogous to the causal mechanisms occurring in the population. Such a model is used to predict and study emergent behavior. By contrast, an empirical model contains mathematics derived by fitting arbitrary methematical forms to empirically observed emergent behavior. These latter models can also be used for predictive purposes but in a much more limited sense. They cannot be used to test whether or not a given causal mechanism is capable of producing a type of emergent behavior.

An example of confusion of the concepts numbered 1) and 2) above is provided by the treatment in population models of a type of emergent behavior of populations known as density-dependent mortality. This type of mortality is observed in a population if the mortality rate coefficient (dimensional units of time^{-1}) is dependent on the population size or, in more directly observable terms, if the populations' overall mortality rate (units of animals/time) is other than linearly related to population size. An empirical model would reflect density-dependent mortality by including a term for population loss of the form $-K \cdot f(N)$ where N is population size, K is a positive parameter and $f(N)$ is a non-linear function of N (frequently a quadratic). The common types of models for fish yield contain density-dependent mortality terms and thus are empirical, not mechanistic models in that regard. They have nothing to say about the origin in population mechanisms of the emergent phenomenon of density-dependent mortality. Such models do not have the necessary mechanistic resolution to "see" the underlying causes of population mortality. Frequently, however, density-dependent mortality is incorrectly referenced as a "mechanism" of a population model.

It should be clear from the above that the mechanism-empiricism dichotomy of models is not a discrete but a continuous categorization. A model is "more mechanistic" than another or "more empirical"; it is not either mechanistic or empirical. Further, a model may have some points which are highly mechanistic in their formulation and others which are purely empirical. For example, a mechanistic reproduction function incorporating dependence on animal energetics and an empirical density-dependent mortality term. Alternatively a model may have several mortality formulations, some of them mechanistic and some empirical in origin.

Mechanistic formulations have their origin in deductive logic and, at least when first stated, constitute hypotheses to be demonstrated or contradicted or, alternatively, form the axiomatic basis for any results of study of the model. Empirical formulations have their basis in inductive logic. Finally, all mechanistic formulations and models lead to an empirical component at a finer level of resolution. Consider the statement "Population rate of change is equal to the difference of birth rate (B) and death rate (D)." Such a hypothesis is deductive in origin, is based on certain assumptions (such as zero net migration) and leads to a mechanistic formulation such as equation 1).

$$\dot{N} = B - D \tag{1)}$$

The next step in model development might be to substitute empirically observed functions for B and D such as in 2):

$$B = bN \tag{2a)}$$

$$D = mN^n \tag{2b)}$$

This (m, b and n are parameters) gives a form of the stock production model when substituted back into 1). Thus mechanistic concepts have contributed to the basic overall structure of the model and empirical methods have contributed the fine details. A population model completely mechanistic in formulation would include metabolic pathways, the quantum dynamics of organic molecules, the atomic structure of the carbon atom and more as yet unknown to science. This is impossible, impractical and (fortunately) not needed. What is needed and practical in population biology is further use of deductive methods in model development than that illustrated in eqs. 1) and 2) before resorting to empirical substitution.

One of the principal failings of the currently fashionable classes of model for analysis of managed populations is their failure to predict certain types of emergent behavior of real populations, notably their variability in time. The stock production model, for example, predicts smooth, gradual changes in population size as a function of changes in amount of harvesting effort. The simpler age structure models can predict either the same type of smooth change or they can predict simple oscillations in response to an assumption made about the reproductive characteristics of the population. Real populations, however, are known to behave erratically at times. Outbreaks, in which a population will maintain itself at very low numbers, then periodically increase drastically and then decrease again back to a background level are common. Another important characteristic of real populations is what I shall term pseudo-periodicity in which the population will vary between limits with a period which changes in a stochastic or random manner. This is in contrast to the periodic functions of mathematics in which the period of variation is basically constant, hence the term pseudo-periodic. One objective of the model development below is statement of a set of basic mechanisms concerning the operation of a population and its interaction with other populations which can predict such known emergent behavior as population outbreak and pseudo-periodicity.

Emergent behavior due to age structure in a population model.

Recent studies of the basic continuous variable differential equations for age structured population models (known as the Von Foerster equations, Von Foerster, 1959) have been carried out by George Oster and various of his associates (Oster and Takahashi, 1974, Auslander *et al*, 1974, May and Oster, 1976). One of the important results of their research is that age structured population models can exhibit behavior under certain conditions in which the dependent variable of the model, total population size, undergoes erratic non-transient behavior which while bounded above and below is nonconstant and yet is not periodic. Oster has termed behavior of this type "chaotic."

In a recent paper, May and Oster give an example of a very simple non-age structured discrete type model which illustrates this type of behavior. This model, $N_{t+1} = N_t\exp[r(1-N_t)]$, gives the size of a population at a time t+1 as a function of size at time t. Fisheries biologists will recognize this equation as being fundamental to the spawner-recruit relation utilized by Ricker (Ricker, 1975). Figure 1 graphs the population size at time t+1 as a function of the current population size. For values of the parameter r which are large, there are infinitely many roots of this system, i.e., values of the population at time t which will be transformed, after a certain number of generations, back into the same population size. For a value of r=5, this will result in a population size versus time graph similar to that which appears in Figure 2A. This type of behavior is what I have referenced above as population outbreaks. Note that there is no constant periodicity to these population outbreaks but they seem to occur at more or less random time intervals, although there is a certain near constancy to these periods (pseudo-periodic behavior).

An important consequence for our ability to predict the size of a future population using such models is illustrated by Figure 2B in which the same model is graphed for a parameter value r=5.1. Notice that the same qualitative characteristics of the population size occur, however, the times at which the outbreaks occur differ slightly and the general shape of the detailed outbreak curves are slightly different, so the detailed quantitative characteristics, i.e., population size, are quite different. In attempting to predict population size at some future time t, the error in going from one value of r to the other might be several hundred or thousand per cent although the change in the parameter value was only two per cent. Thus, the detailed quantitative size of the population is extremely sensitive to the value of the model parameter r.

I conclude from this result that it will be impractical to utilize models with such characteristics for prediction of the detailed size of a population at some future time. However, it is not at all impossible to predict the qualitative characteristics of the size of the population. In particular, the population could be characterized stochastically. The upper and lower bounds of the population size could be determined and two important techniques could be utilized to study either the size of a population as predicted by a model or the size of a real population as determined by field studies or catch and effort data. These two approaches are 1) spectral analysis--largely a method of engineering mathematics which includes such techniques as Fourier analysis and the development of autocorrelation functions for time series data; and 2) the development of statistical density functions for population size. In its simplest form, this latter technique means simply the estimation of means, variances, and perhaps higher moments of the model's dependent variable, or in a more comprehensive approach, the estimation of complete density function of the population size variable. Notice that though we are dealing with a purely deterministic model, we are treating its dependent variable as if it were a random variable as has been done in analysis of empirical populations for many years.

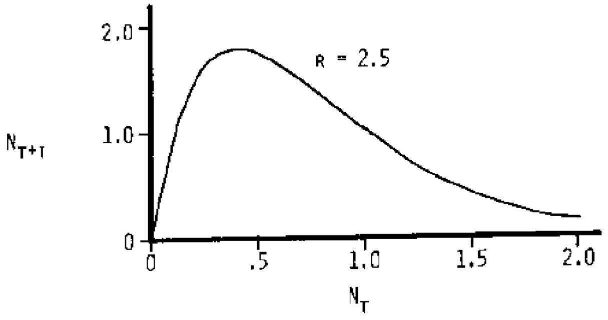

Fig. 1. Recursive generating function for the model of May and Oster (1976) which exhibits "chaotic" behavior for values of r greater than ~2.69+

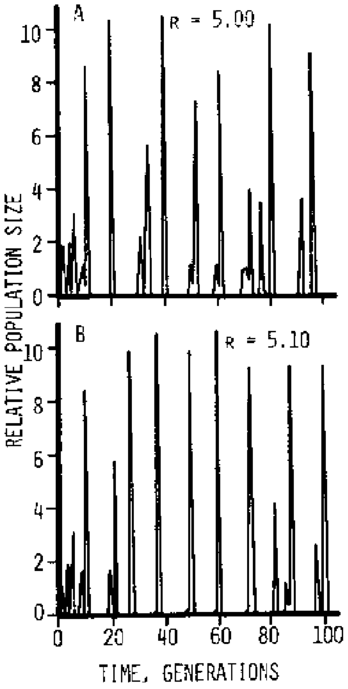

Fig. 2. Population size, N_t, over time for May and Oster's (1976) "chaotic" model. Part A and B illustrate the effect of a 2% change in parameter r: quantitative population sizes at any time are totally different though the general qualitative shape of the curve is the same.

Model Development

I propose, in the following development, a model which extends the use of deductive logic to develop a much more complex mechanistic population structure before resorting to empirical approaches to fill in the final details. In particular, I want to include the following mechanisms in the model:

1) Age and size structure--the distribution of ages and sizes of animals comprising the population is explicitly predicted by the model. The equations are a discrete approximation to the partial differential population formulation of Von Foerster (1959) in which the age step may be made small independent of the time step, in contrast to Leslie models.

2) A food web structure in which a series of population nodes, each representing different animal species, are allowed to feed upon each other and in which predation by one group will appear as a mortality in its prey population.

3) A realistic relationship between quantity of food consumed and change in size of animals in each population node.

4) A mechanism to link rate of consumption to mortality in the case of an animal which does not get enough to eat, and

5) A mechanism to relate size of an animal to fecundity or reproductive ability.

This model goes much deeper into the mechanisms which structure the functioning of a biological population than do standard, age-structured population dynamics models. In particular, I will incorporate the intuitive concepts that growth of a population is dependent upon its relationship to other animals in the ecosystem, that reproduction of the organism is dependent upon its energy status in terms of trophic relationships, and that mortality in a population is basically due to processes such as disease, starvation, predation, perhaps even old age. However, we should throw out the concept as a postulated mechanism that animals die of density-dependent (or density-independent) mortality. These are rather regarded as emergent behavior whose role is to be predicted (or not) by analysis of the model.

In order to incorporate these admittedly complex mechanisms and yet maintain as simple a model as possible, we will first develop a model for a single population which is assumed to be cannibalistic. The mechanisms for the cannibalism will allow development of a complete set of multispecies trophic relationships when combined with a diet quality model, also to be postulated. We will ignore the question of the degree of spatial resolution of the model though this is admittedly an important aspect of interpretation of a theoretical model in terms of any real population size. Problems in terms of the appropriate degree of spatial abstraction of a model are beyond the concerns of this paper. Finally, we will want to explore the emergent behavior of the set of population mechanisms developed and also explore the likelihood that it would be possible to gather the appropriate empirical data to estimate the characteristics of the deductively justified mechanisms. Alternatively, the deductive mechanisms may be seen as hypotheses to be verified or refuted accordingly as emergent behavior of the model agrees or not with the observed behavior of a real population. It should be emphasized, as pointed out above, that comparison between the size of a model population and the size of a real population should be not in terms of absolute numbers over time. Instead, comparisons in terms of spectral and statistical characteristics, as explained above, are the appropriate criteria for comparison.

Energetics sub-model.

Let w, N be the average weight and population density time functions for an age class of animals. (We will omit subscripts for the age class until later in the development when they are needed.) We will develop an ordinary differential equation for rate of change of these two variables. Age classes will change instantaneously at time points $t_i = t_0 + i \cdot \Delta\tau$ with reproduction accumulated over the interval $t_{i-1} - t_i$ making up the new first age class.

To conform with Von Bertalanffy empirical growth we must have

$$w(t) = w_\infty(1 - e^{-k(t-t_0)})^3 \qquad (3)$$

or, in differential form,

$$\dot{w} = 3k(w^{2/3} w_\infty^{1/3} - w). \qquad (4)$$

In contrast, a mechanistic equation for weight change would explicitly identify intermediate system variables representing gross energy (ge, rate of consumption), heat increment (hi), methane and urine production (em,eu), respiration and its dependence on activity (af, activity factor relative to basal metabolism) and miscellaneous energy losses (ms).

$$\dot{w} = ae \cdot ge - hi - em - eu - p_1\, af\, w^{p_2} - ms \qquad (5)$$

where ae is assimilation efficiency; p_1 and p_2 are parameters. Since the first four terms in eq. 5 are all proportional to ge, this can be reduced to

$$\dot{w} = p_3\, ge - p_1 w^{p_2} \qquad (6)$$

with three parameters and one exogenous variable, ge. Equating (2) and (4) and solving for ge*, the rate of consumption required for

Von Bertalanffy growth, we get

$$ge^* = \frac{1}{p_3}\left[3k\, w_\infty^{1/3}\, w^{2/3} - 3k\, w + p_1\, w^{p_2}\right] \tag{7}$$

Feeding response mechanism.

Assume that the rate of consumption, rc, is a function of the amount of food in the environment, fd, given by a Holling disk equation with a refuge as shown in Fig. 3.

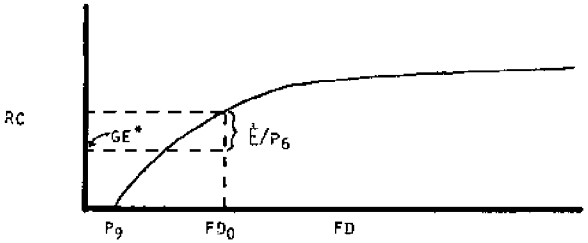

Figure 3. Rate of consumption of food (rc) in relation to food available (fd) and the Von Bertalanffy gross energy requirement ge*.

$$rc = \begin{cases} L \cdot p_7\,(fd - p_9)\;/\;(p_8 + fd - p_9) & \text{if } fd > p_9 \\ 0 \quad \text{if } fd \leq p_9 \end{cases} \tag{8}$$

where L = body dimension, p_9 is the food refuge density parameter, p_7 & p_8 are asymptote and shape parameters for the relation.

For a given amount of food available at some point in time, say $fd = fd_0$, the rate of consumption will be either above or below the Von Bertalanffy rate, ge*. We can formulate the weight equation and gross energy as follows:

Let

$$\dot{w} = \begin{cases} 3k(w^{2/3}\, w_\infty^{1/3} - w) & \text{if } ge^* < rc(fd) \quad (9) \\ p_3\, ge - p_1\, w^{p_2} & \text{if } ge^* > rc(fd) \end{cases}$$

$$ge = rc(fd) \tag{10}$$

Mortality due to predation.

In order to allow development of a single-species model, assume that we have a cannibalistic species except for the very smallest cohorts which will consume an exogenous food supply given by a driving function. We will also introduce an age class subscript here: $N_i(t)$, $w_i(t)$.

Let $L_i = p_4 w_i^{1/3}$ be the average length of animals in age class i; assume that an animal in class i can be eaten by another which is in a size range given by $q_1 L_i - q_2 L_i$. Then the continuous variable part of the population dynamics will describe the mortality process as follows:

$$\dot{N}_i = - \sum_{j \epsilon A_i} mt_{ij} \tag{11)*}$$

where mt_{ij} is the rate of consumption of animals in age class i by age class j and A_i is an indexing set which contains the age class indices of those classes with lengths $L_j \ \epsilon\ [q_1 L_i, q_2 L_i]$.

If we assume that this mortality is proportional to the number of predators given by class A_i, then we can formulate the feeding function for age class i as

$$fd_i = p_5 \Big(\sum_{j \epsilon B_i} N_j w_j + d_i \Big) \tag{12}$$

where p_5 is a parameter, B_i is the indexing set giving class nos. j such that $i \ \epsilon\ A_j$, and d_i is the exogenous food supply function. The formulation of mt_{ij} then will be:

$$mt_{ij} = N_j \, rc_j \, \frac{N_i}{\sum_{k \epsilon A_j} N_k w_k + d_j} \tag{13}$$

---

* This equation is modified in the next section to include mortality due to inadequate food supply.

Mortality due to inadequate weight.

The average weight of an age class which consistently gets an inadequate food supply will drop below the Von Bertalanffy curve for its age. If this weight loss is sufficiently serious, the probability of mortality will increase. If mortality due to starvation of an individual in the age class is a Poisson process (as defined in Parzen, 1962, equal probability of death in a unit time interval) then the average rate of loss for the age class as a whole will be given by a linear instantaneous loss rate with a rate constant increasing infinitely as the probability becomes certain. A term added to eq. 8 of the form $-f_i N_i$, when f_i is the starvation mortality rate variable, is appropriate under these assumptions. The rate variable f_i should be a decreasing function of the average weight w_i* of the ith age class expressed as a fraction of the Von Bertalanffy weight $w_{vB}(\tau)$ age τ. This can be given by the following relations.

$$f_i = \begin{cases} 0 & \text{if } w_i^* > p_{12}/p_{13} \\ (p_{12}/w_i^*) - p_{13} & \text{if } w_i^* \leq p_{12}/p_{13} \end{cases}$$

$$w_i^* = w_i/w_{vB}(\tau_i) \tag{14}$$

This functional relationship is graphed in Fig. 4 as a hyperbola intersecting the horizontal axis at some fraction of the maximum value of w_i* = 1.0.

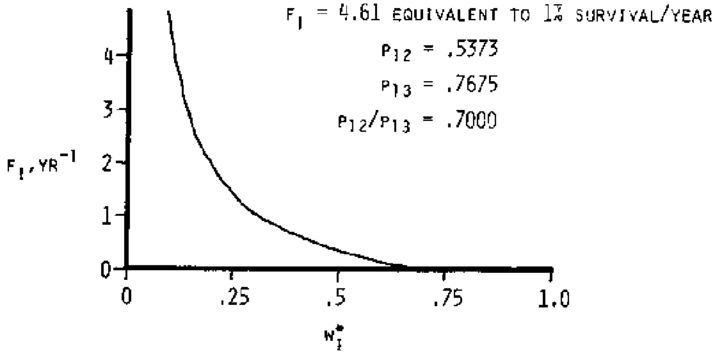

Figure 4. Starvation mortality rate parameter, f_i, Yr^{-1}, as a function of weight, w_i*, as a fraction of Von Bertalanffy weight (as given by equation (11).

The parameters used to generate the graph of Fig. 4 assume 1%/year survival for weight of 10% of maximum and that animals whose weight exceeds 70% of maximum suffer no starvation mortality.

Equation (8) can be modified to include both predation and starvation terms as follows.

$$\dot{N}_i = -\sum_{j\varepsilon A_i} mt_{ij} - f_i N_i \tag{15}$$

Reproduction

There are several plausible ways that reproduction could be made a function of weight and/or food supply; we will choose the following as an example of a species which can convert a large food supply directly into reproductive value. Let E be the number of eggs produced as a function of time, then let

$$\dot{E} = \begin{cases} 0 & \text{if } w_i < p_{10} w_i^* \\ p_6 \sum_i [\max(0., rc(fd_i) - ge_i^*) N_i] & \text{if } w_i \geq p_{10} w_i^* \end{cases} \tag{16}$$

In Fig. 3 preceding eq. (8) the quantity indicated as $\dot{E}/p_6$ is an available consumption rate, over that which is necessary to grow at a Von Bertalanffy rate, and the resulting energy is converted to new animals with an efficiency p_6.

The reproduction is incorporated in age class 1 and age classes are aged in discrete steps by defining the following events which modify the otherwise continuous variable model.

$$N_i(t_k^+) = N_{i-1}(t_k^-) \qquad i = 2\ldots.. \tag{17}$$

$$\left.\begin{aligned} N_1(t_k^+) &= E(t_k^-) \\ E(t_k^+) &= 0 \end{aligned}\right\} \quad i = 1 \tag{18}$$

$$\left.\begin{aligned} w_i(t_k^+) &= w_{i-1}(t_k^-) \\ w_1(t_k^+) &= w_0 \end{aligned}\right\} \quad i = 1,2\ldots \tag{19}$$

where $t_k = t_0 + k\cdot\Delta t$ defines a set of discrete times at which "graduation" and "birth" events take place.

Comparison with Existing Models

There have been several models proposed in the fisheries literature containing mechanisms similar to these described. Parrish (1975) describes a multi-species trophic interaction model in which each node (species) in a food web is represented by an age-structured array of weight (w_i) and population density (N_i) variables. The approach to animal energetics (i.e., use of a Von Bertalanffy growth equation in differential form and replacement by a mechanistic equation where food is insufficient) is identical to that taken here. Reproduction is modelled by Parrish using the empirical formulation of Beverton and Holt (1957) however. Parrish's (1975) model then cannot be used to determine whether recruitment to a population as a function of density of the adult population has a functional form following that of Beverton and Holt (1957), that of Ricker (1954) or some other form. Conversely, the model proposed above can be used to project the form of a recruitment curve as an emergent phenomenon resulting form the basic mechanisms hypothesized. This projection might be particularly interesting since cannibalism of adults on their own young is a hypothesis which has been proposed to account for the shape of the Ricker curve.

Mortality resulting from starvation was modelled by Parrish using the empirical result of Ivlev's (1961) starvation experiments in which fish mortality was studied under very limited feeding regimes. The result of Ivlev's experiments were not applicable to the situation in which a fish was simply chronically underweight rather than chronically underfed. The approach taken above will allow the possibility of prediction of the survival curves of Ivlev (or contradiction of them) as a consequence of the mechanistic assumption of starvation mortality as a Poisson process parameterized on relative weight of an average individual.

The trophic model of Kremer and Nixon (1978) is aimed primarily at zooplankton and lower trophic levels rather than fish and is designed to explicitly consider environmental driving functions, especially temperature, on biomass dynamics. The feeding response curve used for zooplankton is the Ivlev relation which is similar in form to the Holling disk equation used above. Reproduction of zooplankton is assumed to be proportional to the difference in respiration energy and assimilated food. Assimilated food is calculated from the feeding response curve mentioned above. Thus, the reproduction mechanism is basically similar to that used here, however energetics are not constrained to conform to an a priori curve as above. The model of Kremer and Nixon is, additionally, far too complex to be used for the objective of this study.

The detailed trophic model of Andersen and Ursin (1977) comes closest, at least in the fish biomass submodel, to the approach used above. Andersen and Ursin, however, use a Beverton and Holt reproduction mechanism in the "reduced" form of their model making it subject to the same criticism as that of Parrish. The full model assumes egg production to be proportional to the average weight of an age group and does not have any detailed mechanism to relate reproduction to energetic status of the adult. Feeding response is modelled using the disk equation. These are then distinct mechanistic differences between the Andersen and Ursin model and the model described above. In addition the model of Andersen and Ursin is also far too complex to meet the objective of this study.

Results and Discussion

Results presented here will be limited to the qualitative shape of biomass versus time curves for comparison with the qualities of other similar models as discussed in the introduction. Fig. 5 shows the behavior of total biomass of the population for three levels of an extraneous density-independent mortality of age 1 larvae of 99%/yr, 95%/yr and 63%/yr. Simulations were done for 30 generation times in a model with up to thirty age classes (though usually no more than twelve were present at any one time).

The simulations were performed first with cannibalistic mechanisms switched off, an extraneous non-depleting food source (similar to Parrish, 1975) and an extraneous density independent mortality schedule on all age classes. Table 1 contains the appropriate parameter values and initial conditions. Physiological parameters were chosen to be similar to those for Pacific halibut, however the absence of a complete food source and food web make this study appropriate only to a hypothetical species. The population was allowed to come to a stable equilibrium and then the cannibalistic mechanism was switched on and extraneous food supply removed for all but pre-reproductive age classes. Fig. 5 shows the result for 40 generations following the onset of the cannibalistic mechanism. The population, for the two higher mortality levels, begins to fluctuate in a complex pseudo-periodic wave form but is not particularly erratic. For the lower mortality level, the population increases exponentially in a series of cyclic jumps where wavelength is eight generations, exactly twice the minimum age for reproduction (four years).

TABLE 1. PARAMETER VALUES USED FOR THE SIMULATION RESULTS DEPICTED IN FIGURE 5.*

W_∞ = 1000. LBS.
K = .0350 YRS.$^{-1}$
T_0 = -.6217 YRS.
P_1 = 14.6 LB./LB.$^{3/4}$·YR.
P_2 = .75
P_3 = .1
P_4** = .921 FT. LB.$^{1/3}$
P_7 = 876. LB./YR.·FT.
P_8 = 650. LB.

P_9 = 0. LB.
P_5 = 1.0
Q_1 = .05
Q_2 = .40
P_{12} = .5373 YRS.$^{-1}$
P_{13} = .7675 YRS.$^{-1}$
P_6 = 10. (# OF EGGS/LB.)
D_I = 650. LB. (I = 1,2,...,4)

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*TO PARAMETRIZE THIS MODEL TO AN ACTUAL ECOSYSTEM IT IS NECESSARY TO EXPRESS N_I AS NO. OF ANIMALS/(UNIT AREA) AND TO DESIGNATE AN AREA FOR WHICH THE MODEL IS REPRESENTATIVE. SINCE THIS INVESTIGATION CONSIDERS ONLY THE ABSTRACT PROPERTIES OF THE MODEL, NO SUCH AREA HAS BEEN DESIGNATED AND THE UNITS OF N_I ARE SIMPLY NO. OF ANIMALS.

**THIS PARAMETER, P_4, IS USED TO CONVERT ANIMAL WEIGHT IN LBS. TO A BODY DIMENSION (LENGTH, L) IN FEET USING THE RELATION $L = P_4 \cdot W^{1/3}$.

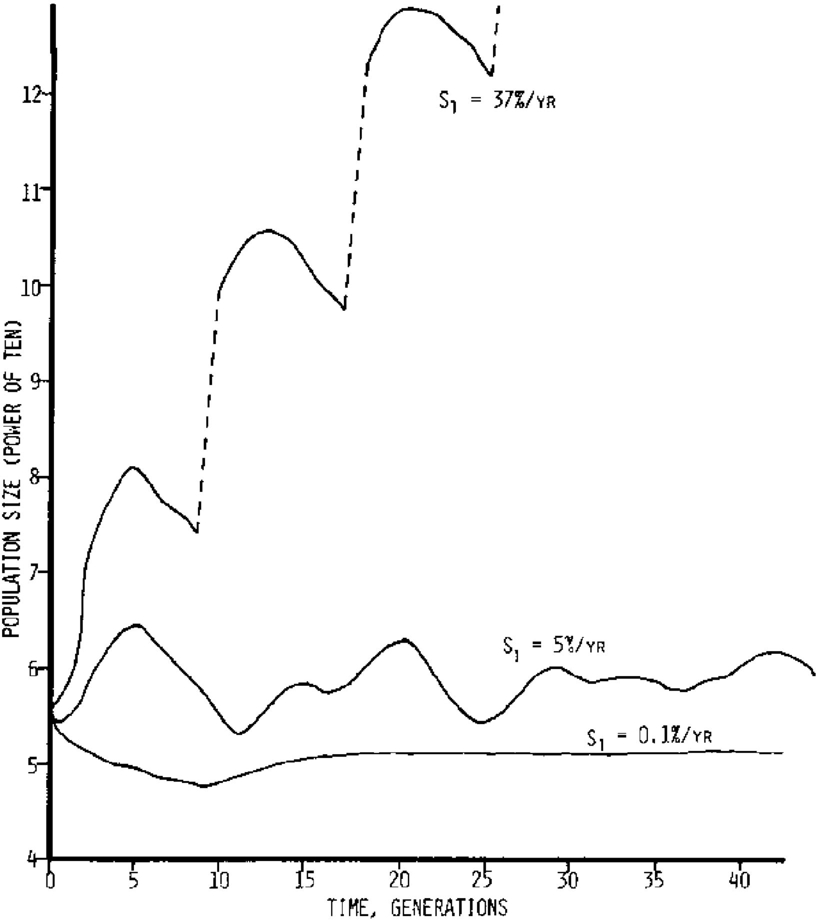

Fig. 5. Population size over time since beginning of cannibalistic predation for three different levels of survival from external mortality of age 1 animals (S_1, total yearly mortality). The graph illustrates a range of behavior from simple re-equilibrium (S_1 = .1%) through a bounded pseudo-periodic regime (S_1 = 5%) to an exponentiating cyclic increase (S_1 = 37%).

The study thus far conforms to the expectations expressed in the introduction: population biomass shows a non-transient, non-constant pseudo-periodic equilibrium. Future studies of the charactistics (emergent phenomena) of this model will be directed at determination of density dependence of survival, growth and reproduction of the population under a variety of extraneous mortality and food supply conditions. Attempts will be made to calibrate the model against commercially fished marine species, notably walleye pollock, Pacific halibut and Pacific Ocean perch. Further approaches to model development will extend the framework to a true multi-species form by addition of hypotheses concerning modes of diet selection. Finally, the model will be utilized in an attempt to simulate historical abundances of trawl-caught species in regions of the eastern North Pacific.

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SESSION 5
Paraphrased Panel Discussion

PANEL MEMBERS
Lewis J. Bledsoe
Douglas M. Eggers
Gary Smith

QUESTION POSED TO PANEL: What is the significance of theoretical studies for applied ecology, particularly management of fish populations?

EGGERS: In my view theoretical endeavors are simply a method of generating predictions from hypotheses and if you can do this you have a more powerful approach to a particular management problem. Everybody has a different idea on how biological systems operate. The question of theoretical ecology versus applied ecology is a difficult problem as indicated by some of the discussion about competition yesterday. What is usually looked at are exploited ecosystems with the intent to try to predict consequences of various processes, e.g. competition, predation, resource fluctuation, etc. But it is very difficult to take the theory and somehow abstract a practical model that is going to tell you how a system is going to respond to a perturbation. What you have to do is design a model to predict the outcome of a perturbation, then design a monitoring system to test the model.

BLEDSOE: So models strengthen a hypothesis?

SMITH: Perhaps the best example of this process is trying to maximize catches from fish stocks and yet preserving the stock. (Makes graph on blackboard) We can use models to provide long term predictions and also short term projections of the condition of a stock and consequences of certain management decisions.

BLEDSOE: How do you decide on a model?

SIBERT: What you're asking then is, What is the danger in using a multiple regression prediction of a stock as compared to a long-based understanding of population dynamics?

BLEDSOE: Such questions as--Which of two possible modes of feeding occur?--for example.

BLEDSOE: But sometimes it is difficult to predict cause and effect from a particular situation or model.

CROW: If you're interested in switching, for example, under a theoretical model you can predict under what conditions a switch will occur. Then this can be measured, e.g. when the fish are switching are these conditions in effect? Such models can be tested.

BLEDSOE: That would establish that the consequences of assuming switching are certain diet patterns. But you still don't settle or lend credence to the theory that the switching might account for its behavior but to establish that switching actually occurs you would have to do something more to prove it, e.g. make sure there isn't some other behavior responsible.

EGGERS: Maybe you should use your model to tell you what the conditions are under which you'd expect certain concrete observations.

BLEDSOE: We as scientists would all like to someday think that we proved something about the environment. The truth is that, given the plasticity of the environment and the plasticity of organisms, all we can really do is to accumulate evidence to lead you to believe one thing or another and you always have to state your conclusions based on some assumptions. If the data I collected last year on a group of fish is assumed to be the way they behave this year then we can conclude thus and so. We can seldom make very many absolute statements.

CROW: That is one use of models, i.e. to test a hypothesis and to help you falsify it. Models are good at showing us where we're wrong.

BLEDSOE: There is one question that I would very much like to discuss: When you do a food habits study the end product that you come up with may be a set of indices of overlap or it may be a set of I.R.I.'s. I would like to know in what way that I.R.I. or indice of overlap might be coupled with deductive-inductive theoretical approaches to aid in answering questions like what kind of interactions will occur between Pacific Ocean perch and pollock?

SIMENSTAD: I suggest that, to begin with, you'd require some measure of prey availability relative to the occurrence of food in the stomachs. If it was available at a certain level in stomachs of one fish and available at a different level in another fish then you'd have an indication of differential availability or, theoretically, selection.

BLEDSOE: So long as you assume the null hypothesis that animals eat in proportion to what is available, then the I.R.I. is really an availability index. But if the fish are selective, you are stuck at that point.

SMITH: It is also important to remember the power of the analysis is dependent on the time and space scales of the two populations of fish.

BLEDSOE: Models can answer questions only within the context and framework of the model, e.g. it is capable of answering questions such as, What is the yield of this thing? However, you cannot answer a food habits study! We know something of a real world occurrence--at this time that animal ate that prey. Someone has to close this gap with theory. The lacking of the I.R.I. and overlap is that there they are dead ends as far as plugging into other hypotheses; what we do need are data that do plug into other analyses. For example, the selection coefficient I proposed. If you could somehow estimate a selection coefficient which has the basic properties that are required for that particular model, then you could probably figure out a way to generate predictions. For instance, given a set of food data, what is the best value of the selection coefficient for amphipods when the predator is sole?

HUNTER: Is the size of the predator and the prey necessary for the model?

BLEDSOE: Well, you certainly could use the data. I think it is a mistake to assume that all the detailed data necessary for a complex model must be measured precisely; the information can always be used to some level. What degree of sensitivity is required to answer your specific question? I think some models can demand too much information.

SIBERT: Don't you think that by increasing the number of assumptions and decreasing the number of empirically derived parameters you increase the analytical attractability of a model.

BLEDSOE: Well, I don't think you'd increase the attractability.

CROW: I have got the impression that we have got to come to grips with the fact that there's a limit to what you can do analytically! We are surely limited in our analytical ability to analyze many things at once.

BLEDSOE: But we can also oversimplify the models in order to make them work.

SIBERT: There are hidden assumptions in every measurement. There are so many things you assume that you don't even think about them when you make the measurement!

BLEDSOE: You can almost say that in any study it's almost impossible to write down all the assumptions that you make. For example, whoever writes down the assumption that the rate of population change is birth rate minus death rate? That's intuitively obvious.

SIBERT: In terms of diet analysis, the bias in your gear is huge, e.g. you get different diets if you sample the same fish with different gear.

TYLER: One difference that seems to be emerging is that non-modelling efforts seem to be asking, for example, is how a resource is partitioned and what are things eating. Modelling studies ask how this variable changes when the other variable changes. Very few of the studies that are ever reported in trophic sessions such as this ever ask those questions. To get an empirical basis for functional relationships is very difficult. At this rate field work and modelers will never get together and things will become static. We need to gather the data that dynamic models need.

BLEDSOE: This context is interesting. In some cases we take a risk to get defined data. Of course we could fish at high levels of effort to see what would happen but we run the risk of destroying the population in the process. We must balance empirical data and reasonable assumptions.

TYLER: Since most models have a density-dependent component as a continuous variable, one or more studies start out trying to look at that variable in terms of any response that a trophic biologist wants to study, e.g. just look at that species of organism where they exist in different densities and go on from there.

SMITH: Part of the problem is the lack of ability of a lot of researchers to see how their data might be able to fit into a model. Of course, there aren't that many large trophic models in existence anyway.

BLEDSOE: The complexity of the tool itself prevents many people from using it. We don't have the proper tools to match the data.

CROW: My basic theory is that some people are more trusting of traditional data analysis than of models.

BLEDSOE: That's putting the cart before the horse. You have to have a model before you can do the data analysis; that is, you have to have a hypothesis before you can verify or refute it.

GABRIEL: How about the people who would be perfectly amenable to gather that data to support somebody else's model if they knew what models people were building. If people would publicize what information they need and in what form maybe more cooperative studies could be presented. People could swap back and forth more than they do now.

BLEDSOE: There is an increasing amount of teamwork required. Each researcher is a specialist and can't be expected to be able to know and do all aspects. There are field biologists, stomach analysists, modellers, etc.

ELLISON: It seems that when I read a journal article written by a theoritician that they develop a program and select data from here and there about different organisms. Now I work with one species and try to use the model and much of it just doesn't fit. It would appear that field biologists are specialists and theoreticians tend to be gross generalists.

HIXON: That's the primary gap I see although not so much in applied ecology. Some of the models are too far beyond reality and they sometimes generate no testable hypothesis. I think that the gap is widening. You have to either generate testable hypothesis or generate modellers and empirical data gatherers simultaneously.

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