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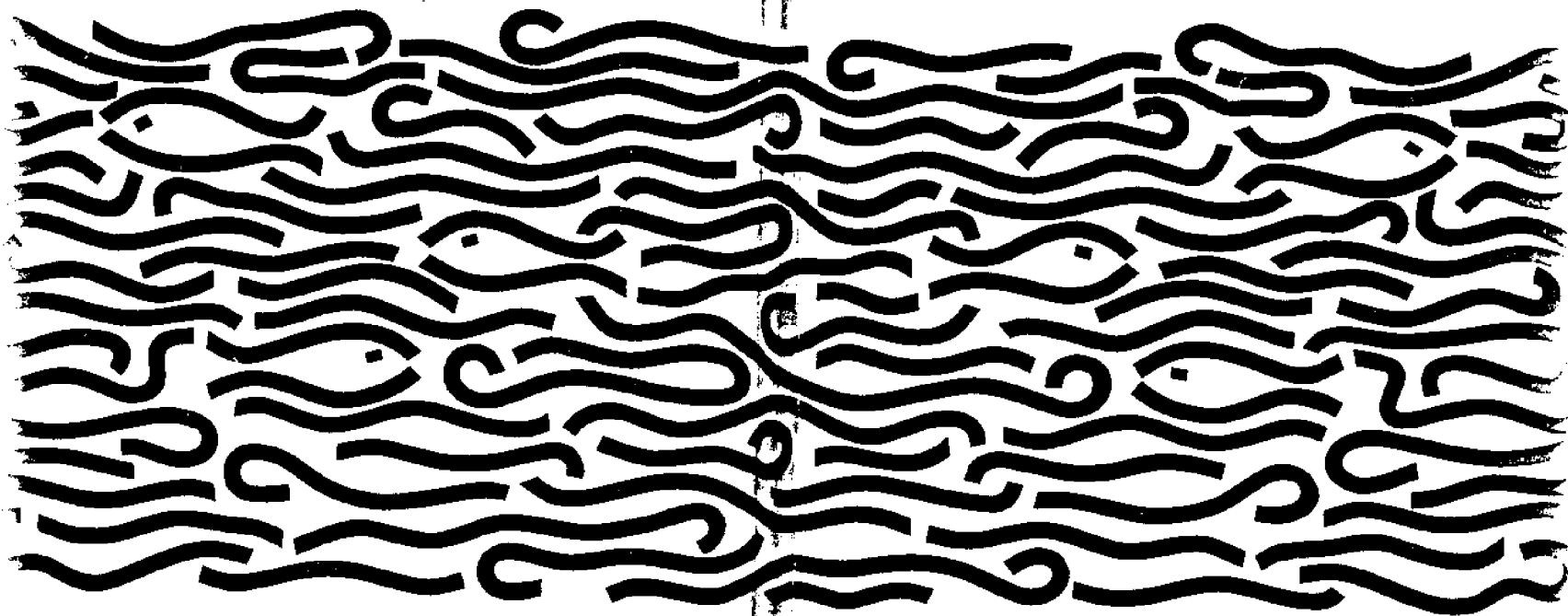
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FISH FOOD
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1ST PACIFIC NORTHWEST
TECHNICAL WORKSHOP



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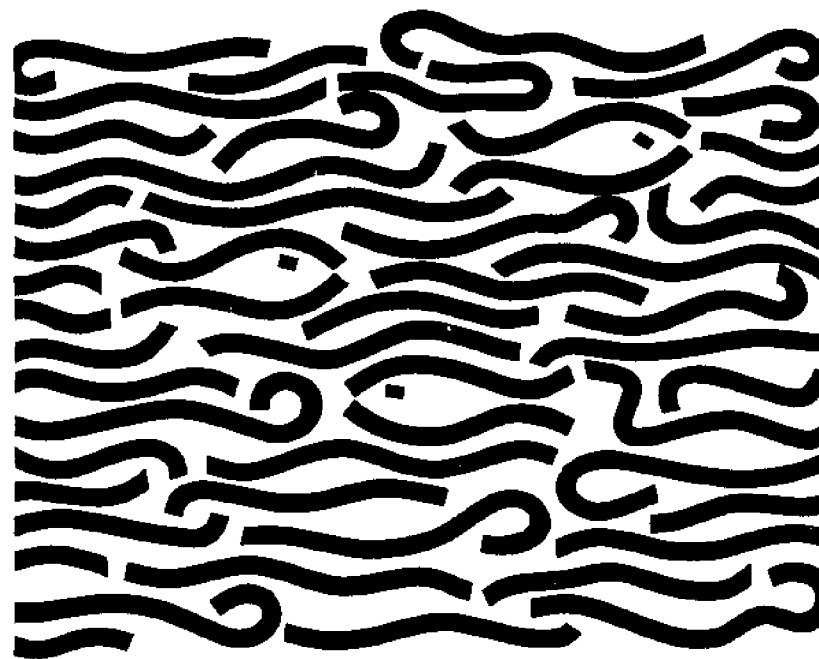
1ST PACIFIC NORTHWEST TECHNICAL WORKSHOP

WORKSHOP PROCEEDINGS

ASTORIA, OREGON

OCTOBER 13-15, 1976

WSG-WO 77-2



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This workshop would not have run smoothly, if at all, without the help of several people and agencies.

First, our thanks go to personnel of the Washington Sea Grant Program at the University of Washington, who prepared workshop flyers and other materials and served as the channel for our finances. Staff of the co-sponsors, the University of Washington's Fisheries Research Institute and the National Marine Fisheries Service Northwest and Alaska Fisheries Center, are to be thanked for assisting with the planning and programming.

Special thanks go to Washington Sea Grant Communications who coordinated the production of these proceedings, Joseph T. Durkin of the Hammond Laboratory, and National Marine Fisheries Service for cooperating with the co-chairmen in planning and providing much of the audio-visual equipment. Mary Lee Brown of the same laboratory provided invaluable assistance with registration, last minute details, and these proceedings. Also, Herb Jenicke, National Marine Fisheries Service at Auke Bay, kindly loaned us his tapes, which were exceptionally better than our own, of the discussion sessions.

Most of all, we wish to thank the participants for providing excellent presentations and stimulating discussions.

FOREWORD

Ideas for a workshop on Food Habits and Trophic Relationships of Pacific Northwest fish had been kicked around for several years. They coalesced during a professional meeting in March 1976, where regional food habits studies were addressed superficially. During that meeting, and during subsequent telephone conversations, we discussed the need for a workshop covering the present state of fish food habits studies.

As a result, the first Pacific Northwest Fish Food Habits Studies Workshop was designed to assemble West Coast biologists currently studying fish food habits for informal discussions on sampling design and techniques, analysis procedures, and current research. This type of research is sometimes nebulous--each investigator doing things just a little differently from everyone else. However, it seemed to us that the time had come to compare notes, to discuss the merits of various techniques, and in a forum for researchers with problems, to get the advice of regional experts in the field.

Flyers were sent to people who we thought might be interested in such a get-together. Originally we hoped to hold it at Hammond, Oregon, where the National Marine Fisheries Service maintains a field station in an old Coast Guard building. From the number of responses, it soon became evident that the field station could not comfortably hold the group; the original expectation was to host about 25-30, but registration eventually reached 50 people. So the workshop was expanded to 3 days and was moved to the Thunderbird Motel in Astoria, Oregon, where conference, room, and restaurant facilities were available. Despite its remoteness, we considered Astoria an appropriate setting both because of its scenic quality and because attendees would be less likely to wander off to more urban temptations as usually happens at meetings in big cities. We all came together, with a surprising minimum of late arrivals and no-shows, on October 15-17, 1976.

One of the most important results of the workshop was that researchers got to know each other and each other's work. Conversations extended into coffee and meal breaks and well into the night. This was the kind of

Interaction we had hoped for, and apparently achieved.

Other than a general limit on length, there was no particular format prescribed for workshop presentations. Thus, these proceedings represent a variety of subjects, rather loosely organized around the five session topics:

Purpose and sampling design

Sampling of benthic predators and prey: How different sampler and sampling techniques alter our impressions of the benthos

Laboratory procedures and identification

Data manipulation and presentation

Interpretation and results

Although they cover the presentations, the papers assembled here vary in length, format, and overall organization. Hopefully, future proceedings papers will be more uniform in format. The discussions (half of each session) proved to be so meaty and worthwhile that we have transcribed these from tape recordings and have included them here pretty much in their entirety.

Because this was the first "gathering of the minds", we planned to spend a great deal of time discussing methodology--and indeed we did. Unfortunately, even though the merits and disadvantages of various techniques were discussed at length, a standardized method (if there is one) was not derived. We still need to define the prey dimensions and weights, etc.--their pros and cons, and the appropriateness of each relative to the questions being asked. Therefore we strongly believe that one outcome of the next workshop should be a handbook on methodology of fish stomach analysis. Widespread use of such a handbook could mean that results of studies along the Pacific Coast of Canada and the United States, or anywhere else, might be more easily compared.

Another area that received much attention, but that could not be sufficiently covered involved the statistics used in testing the significance of different prey compositions. Several of the best statistical analysts in this field attended and answered many questions; however, many more questions were posed in the process. The next meeting should include at least one entire session on the use of statistics as applied to fish prey compositions. Again, an important byproduct could be a handbook or at least a chapter in the previously mentioned handbook.

A third item for inclusion in such a handbook should be a list of useful sources, key, etc., categorized by taxonomic groups, used in identifying prey organisms.

After the workshop a survey sheet was mailed to attendees querying them about their opinions of the workshop and their desires for another one.

From the returned questionnaires, it appears that this workshop was a success and that there is a definite need to schedule similar workshops in the future. Several people suggested changes in format and new session topics. Others expressed the opinion that working groups rather than formal presentations would be useful. Still others indicated that this workshop was too short and that the next one should be extended to 4 or 5 days. Although the Astoria location was well received, the consensus was to move to another scenic location for the next meeting.

Because this type of research progresses slowly, new information is not generated fast enough to warrant an annual meeting. Therefore, most respondents indicated that we should meet every other year, which puts the next workshop in fall 1978. As co-chairmen for the first meeting, we have agreed to organize the 1978 session. However, we hope that by then the group will be well enough established that the chairmanship and editorship can be rotated among the various countries and states.

Finally, 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.

Charles A. Simenstad

Sandy J. Lipovsky

6 June 1977

INTRODUCTORY ADDRESS

Alonzo T. Pruter, Deputy Director
National Marine Fisheries Service
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I would like to welcome you to the first Pacific Northwest Fish Food Habits Studies Workshop. I think we obviously owe a real vote of thanks to the co-chairmen, Sandy Lipovsky and Si Simenstad. It looks as if they developed a really interesting, and useful agenda and gathered a good number of participants. I understand that you've come all the way from San Diego to Fairbanks; you could actually rename this workshop Pacific Coast Instead of Pacific Northwest with no problem. They even managed to produce some beautiful weather down here. I notice that Si and Sandy have such a busy schedule outlined for you that you are not going to have much time to take advantage of the nice weather and look around. That's a shame for those of you who haven't been to Astoria before because this city and the surroundings have a lot of interesting things to offer. This is the site of some important commercial fisheries, both in the Columbia River and nearby ocean waters.

The Columbia River has been used in many ways over the years; to produce fish; to produce sand and gravel for buildings; and as a deposit for pollutants. The expression "unique" is overworked today but I think that, in many ways, Astoria is unique and has some important lessons for everyone if they will look at the situation closely.

I'm always happy to return to Astoria. As Si mentioned, I started my career out here about 26 years ago with the Oregon Fish Commission; in fact, some of your agenda topics bring back memories. I guess my first exposure to food studies was while working for the Oregon Fish Commission in Astoria and I learned a few lessons. I recall that one of the things we were doing in those days was studying the distribution and life history of the black cod. I routinely used to ride a lot of the commercial trawlers out of Astoria that were fishing for Pacific Ocean perch; in those days the depth for trawling for them was generally from 100 to about 150 fathoms. The black cod were quite prevalent at the same depths and over the same substrate as the Pacific Ocean perch so the trawlers caught a lot of them with their perch catches. I used to look at and collect scales for age studies and examine a lot of stomachs so I thought I had a pretty good conception of the feeding

habits of black cod. However, a few years later a group of us returned with a different organization, on a contract with the Atomic Energy Commission to do some deep-water trawling off the mouth of the Columbia River in the Columbia River canyon. We found black cod commonly down to depths of 400 to 600 fathoms. Looking at the stomachs from black cod at those depths showed an entirely different feeding situation--cannibalism among other things being quite common. In the deep water one had a great simplification of the demersal community of black cod and Sebastolobus alascanus, scorpaenid rattails being the dominant forms. I suppose, because of that great simplification of community structure, the feeding habits of black cod were entirely different at those depths than in shallow water.

Even after this episode, in the mid-1960's, we did some of the first mid-water trawling with large mid-water trawls for hake off Astoria, Oregon and Washington, and we learned another lesson. The stomach contents of the hake were quite different when they were taken on the bottom or when they were taken in the water column; hake undergo diurnal migration. A researcher needs to have complete geographic coverage in his samples to really be able to generalize about the species in question. Otherwise, one had better confine his interpretation to the limited part of the range with which he is dealing.

There was another exciting discovery in terms of good studies, so controversial at the time that many people would not accept it. In the early 1950's, Dr. Fukuhara, with our laboratory in Seattle, was the first American scientist, to my knowledge, to go out with the Japanese mothership fishery in the North Pacific, Gulf of Alaska area. This is a gillnet fishery, as many of you know, and Dr. Fukuhara looked at a lot of sockeye salmon stomachs and found that they were feeding predominantly on fish and squid. Many people wouldn't believe that because sockeye salmon were known to be plankton eaters. But it was true that in that part of the Gulf of Alaska sockeye salmon do feed extensively on fish, smelt, myctophids, and squid. Again the lesson is pretty clear, either qualify your remarks in terms of the geographic coverage of the animal or be sure that you cover the entire range of the animal.

The same sorts of lessons emerge when one thinks about the sampling gear itself. You obviously need to know the selective characteristics of the gear you are using in order to properly interpret what you see. I see by your agenda that these kinds of topics are included and it is extremely fitting for a workshop of this sort. I notice also that your agenda includes a discussion of food chain dynamics or trophic relationships, or eco-system studies or whatever you want to call it. This, to me, is extremely important and gives the needed perspective to food habit studies.

I must confess that I probably feel this way so strongly right now because of a personal experience in which I've recently been involved, and am still, that has to do with passage of the Fishery Management

and Conservation Act by the U.S. Congress a couple of months ago. As you undoubtedly know, this extends the fishing limit of the United States out to 200 miles off the coast. The effective date of implementation of that 200 mile limit is March 1st of 1977 and to comply with terms of that Act it is necessary to develop management plans to govern all of the foreign fisheries that will be occurring within 200 miles of the U.S. after March 1 of 1977. Although the Act establishes regional councils around the country to develop management plans there was not enough time for these councils to be formed and develop the necessary detailed plans on such a short time frame so the Department of Commerce was assigned the task and it filtered down to the National Marine Fisheries Service--only for the foreign fisheries aspect. So now at the Northwest and Alaska Fisheries Center in Seattle we've been very busily engaged in developing these plans covering nine different fisheries extending all the way from the Bering Sea down to California, including a wide variety of species such as groundfish, shrimp, Tanner crab, king crab, snails (because Japan has a small snail fishery in the Bering Sea), and high seas salmon.

The key thing that we have to determine in relation to each of these plans is the maximum sustainable yield for each species and the equilibrium yield at current populations, densities, and levels. How in doing this--because of the lack of data--we had to look at each of these species and fisheries as if it existed in a vacuum and as if it was not a member of a community of organisms that interrelate to each other, competing for food and preying on each other. We basically ignored these factors, not out of ignorance but for a lack of understanding of the interrelationships, and that's not good. The result of that is to realize less food potential from the particular system you're looking at than you could realize if you understood the relationships between the different animals and organisms in the system. So, to me, that is one of the very relevant aspects of which you are going to be talking the rest of this week. The things you are doing now and in the future make you all potentially extremely valuable contributors to the whole management area.

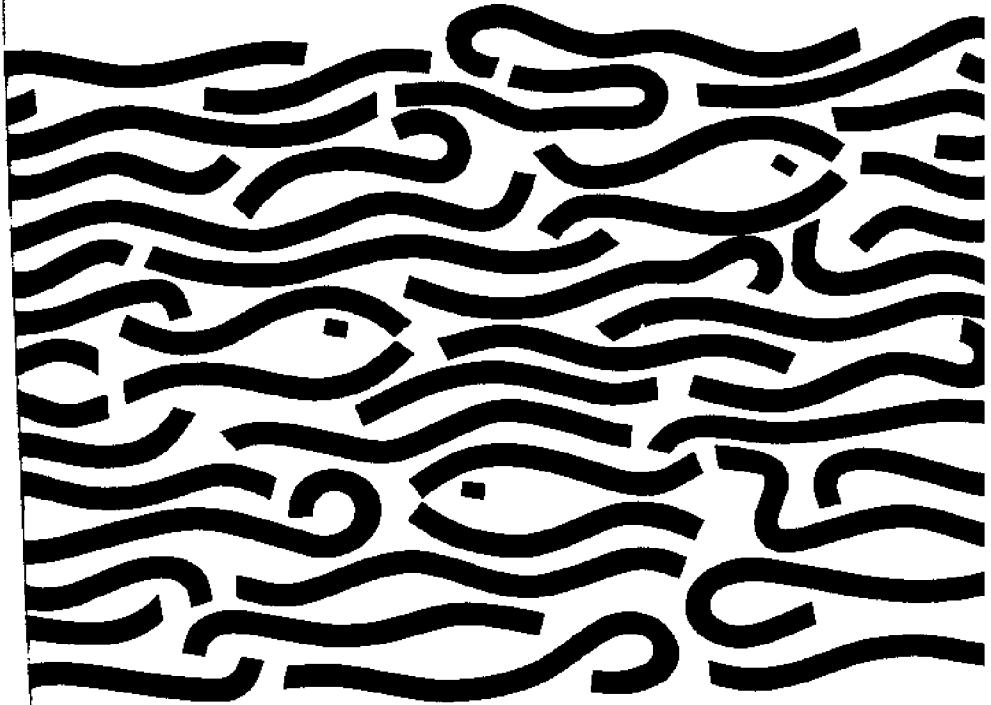
We need to know more than just what a particular species is eating at a particular time of point in space. We need to know the food habits at different sizes and ages, particularly at the larval stages, which probably are the critical stages for determining year class strength. One of the key features of good management is the ability to predict--and we can't do that very well now. It seems to me that food studies aimed at critical life stages, such as the larval stages, could help us understand the mechanisms behind year classes. In addition to year class strength, I think we need to know a lot more about rates of transfer of energy between trophic levels. We need to know the effect of selective fishing, or targeting on a particular species within a community, on the growth and survival of the non-targeted species, the competitors and predators in that system. We need to know the effects of the physical environment itself on the growth and survival of the elements in the community. When one begins to add up all the things we

SESSION 1

**PURPOSE
AND SAMPLING
DESIGN**

need to know it becomes pretty obvious that the only way to achieve that knowledge is through a real multi-disciplinary approach, coordinating the efforts of many researchers. It's an awesome task but it can be done and I think we have the tools with which to do it. One of the biggest helps is the field of eco-system dynamics and modeling that is just getting started. I think that's fair to say. This field has a great potential by being able to help us--in the area of food studies, for example--to identify some of the critical species or elements in the different systems. I think enough is known about modeling at the present time to at least point us in directions that will save us a lot of time by filling in the gaps of knowledge for those particular species or elements of communities that appear to have the greatest impact or driving force within the systems. I'm glad to see you are going to have some discussion of this in your workshop.

So again I certainly commend all of you for coming to this workshop. I know that when you leave here you will be happy with the things you discussed. You may not go away all agreeing to use the same identical methods in your studies but I bet you will go away knowing what everybody else is doing up and down the coast and their rationale and it seems to me with that kind of start it's only a matter of time until you come to common agreement on techniques and methods, making the results up and down the coast comparable to each other.



SESSION LEADER:
Howard Horton

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SEVERAL APPROACHES TO THE FEEDING ECOLOGY OF FISHES

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The investigation of fish food habits is becoming very popular among researchers in such fields as ecology, ichthyology, and fisheries biology. It is not the intention of this short paper to review this rapidly growing field, but rather to briefly present several approaches to studying fish feeding ecology that we have utilized in studying fishes from three distinct habitats: the deep-sea basins off Santa Barbara, California, in which the midwater fishes Leuroglossus stibilus (family Bathylagidae) and Stenobrachius leucopsarus (family Myctophidae) were studied (Cailliet 1972a,b); the Monterey Submarine Canyon, where we have investigated the sablefish (Anoplopoma fimbria) population as it related to the local trap fishery (Osada and Cailliet 1975); and Elkhorn Slough, a shallow coastal embayment in central California, which harbors a rich and interesting fish fauna (Cailliet et al. 1975).

In each of these three habitats, different questions have been asked regarding the feeding habits of resident fishes, but the basic information gathered was similar. That is, prey items taken from stomachs and intestinal tracts were identified to the lowest possible taxa so that prey composition information would be as accurate as possible. Three measures of abundance were used: number, volume, and frequency of occurrence of each prey item. These three measures of prey abundance tell the investigator different things about the feeding habits of a fish. For example, the numerical importance (usually expressed as percent by number, %N) and frequency of occurrence (that proportion of stomachs containing a specific prey item, %FO) reflect the process of selection used by the fish in its feeding behavior by pointing out how many prey and how often a certain type of prey was selected, but little about the amount of nutrition (or energy content) the fish gained from that item. Whereas, the volumetric importance (percent by volume or weight, %V) of a prey item indicates more about the nutritional value of the prey item. In order to combine these three measures of "importance" of prey, a single index was derived (Pinkas et al. 1971) that proves useful in ranking prey items, but still allows %N, %V, and %FO to be presented and evaluated separately. This "Index of Relative Importance" (I.R.I.) is calculated by adding the %N and %V, then multiplying the result by %FO, thus calculating the area of a rectangle produced by plotting a three-way graph, in which %N and %V are plotted vertically and %FO horizontally (see Fig. 7). These three measures of prey abundance can also be presented in tabular form (see Tables 1-3).

In all three of our studies, we have calculated I.R.I. values to rank the prey items, but they have been used to answer different kinds of questions about the feeding ecology of fish predators. These feeding studies fall into five general categories, and serve to demonstrate the diversity of approaches that can be taken in fish feeding analyses.

affected by the intensity of exploitation. Thus, in attempting to manage that resource, information on "interspecies relationships of a type that can be important in regulating population productivity: predation" is useful (Watt 1968, p. 133). During a trap fishery project on the Monterey Bay sablefish population (Osada and Cailliet 1975), we examined stomach contents to determine the kinds of prey they consumed. Sablefish from traps set in water deeper than 400 fathoms ate mostly large crustaceans (decapod shrimp and crabs), squid, and other fishes (Table 3). Thus, changing the intensity of the sablefish fishery in Monterey Bay might affect the trophic role they play in the submarine canyon, both in terms of their prey utilization and that of their trophic equivalents or potential competitors, such as the rattails (family Macrouridae), which also consume these kinds of prey (Pearcy and Ambler 1974).

An Ecological Approach using Trophic Diversity and Resource Overlap

In many cases, studies of fish resource utilization are simply started out of scientific curiosity, with little or no practical reason other than to utilize ecological concepts to understand the trophic interrelationships of a population or community of fishes. Much of the literature dealing with trophic ecology has not concerned fish as subjects, but most of the concepts discussed, such as trophic diversity or resource breadth (Hurtubia 1973) and food overlap (Horn 1966), are equally applicable to fish studies. Recently, researchers have been applying such concepts to varied groups like microcarnivorous "picker-type" fishes from kelp beds (Bray and Ebeling 1975), killifishes from coastal waters (Fritz 1974), deep-sea rattails (Pearcy and Ambler 1974), and demersal skates from the Atlantic coast (McEachren et al. 1976). In this final section, I will briefly present an ecological approach to the feeding of flatfishes in Elkhorn Slough, California. Many of the observations already made regarding spatial and temporal differences in feeding are also evident from this study, but will not be discussed further. Rather, I will stress the various ecological tools we have used to describe trends in the feeding habits of four species of flatfish: Platichthys stellatus, Parophrys vetulus, Citharichthys stigmæus, and Psettichthys melanostictus.

First, in order to fully describe the trophic composition and diversity of a predator, a sufficient number of fish guts must be examined. One way to determine sample sufficiency is to plot the cumulative number of prey categories observed against the randomly pooled number of guts examined (Hurtubia 1973). The minimum number of fish guts necessary is estimated as the point at which the curve levels, and once this level is reached, the prey composition can be described with less fear that some important food source has been overlooked due to insufficient sampling. Such curves for flatfish at the bridge station indicate that an adequate number of guts would be between 60 and 80 (Fig. 3). At the ocean station, however, insufficient samples of all fish but Citharichthys were obtained to adequately describe trophic composition. Once sufficient numbers of guts have been examined, the resource breadth can be described in a variety of ways, including the Index H

derived by Brillouin, and used to estimate trophic diversity by Hurtubia (1973) because of its relevance to gut content analysis. Once H values have been calculated for a series of individual fish, the frequency distribution of H values among individuals should be observed to see if the mean trophic diversity will be representative of the predator population as a whole (Hurtubia 1973). Mean H values for these flatfish appear representative for both locations studied, excepting perhaps Platichthys at the ocean station (Fig. 4).

Since diversity indices such as H are influenced both by a richness component (the number of species) and an evenness component (J, the apportionment of individuals among species) (Pielou 1975), the component which influences the trophic diversity values most should be assessed. One way to evaluate this is to plot both mean J and mean H for each species at a location (see Fig. 5). The higher H for Parophrys and Citharichthys at the bridge station was influenced by relatively high evenness among prey species, while both size classes of Platichthys had lower overall trophic diversity values, despite high evenness. At the ocean station, where Psettichthys appears for the first time, and has a low trophic diversity, the trends were a bit different, with Parophrys exhibiting the highest diversity but relatively low evenness.

Prey composition for these flatfish can be presented by major groupings (Fig. 6) or by I.R.I. diagrams, relating the numerical, volumetric, and frequency importance of more specific prey taxa (Fig. 7). Generally, most individuals fed upon polychaetes in both locations, while Citharichthys appeared to switch to amphipods and decapods at the ocean station (Fig. 6). Although it is beyond the scope of this paper to discuss specific prey taxa, it is interesting to note that the differences found in mean diversity and evenness (Fig. 5) are also apparent in the shapes of the I.R.I. diagrams, especially when Parophrys and Citharichthys are compared at the ocean station (Fig. 7).

It is possible to more quantitatively evaluate differences in prey species composition among fish predators. Several ways to do this have been derived, such as similarity indices (McEachren et al. 1976), Kendall or Spearman rank correlation methods (Bray and Ebeling 1975, Fritz 1974), and Morisita's Index of overlap (Horn 1966, Pearcy and Ambler 1974, Bray and Ebeling 1975). We calculated Morisita's Index of overlap for Elkhorn Slough flatfish and noticed that Psettichthys at the ocean station had very low values when compared with all other species except Citharichthys, in which case both species had been feeding heavily upon one species of Acanthomyxis (D. Ambrose, unpubl. data). Also, the overlap values among the other flatfishes tended to be low, ranging from 0.03 to 0.11. At the bridge station, however, overlap was generally much higher among the three species, ranging up to 0.95. A general conclusion, based on all of the information used thus far (Figs. 3-7), is that Citharichthys and Parophrys are more generalized feeders, while Psettichthys, which lives only in the ocean and consumes mostly fish prey, is more specialized and therefore had the lowest trophic diversity.

Finally, one must also evaluate whether the feeding habits of fish are variable due to preference of the predator for certain prey or simply to differences in the availability in the environment sampled. Since our study in Elkhorn Slough was concurrent with a benthic survey of invertebrates (see Nybakken *et al.* 1975), we were able to estimate the relative availability of prey items (%P) and compare this with the actual proportion each item comprised in the diet (%R). Then, we calculated an electivity index (Ivlev 1961), which reflects the food preference of the individual flatfish species. Again, discussing individual prey taxa is impossible in this paper, but it can be noted that several prey items were consumed in direct proportion to their availability, while many others were either not well represented in the diet (the fish did not take them, even though they were available) or were not captured in the benthic samples (thus, the cores did not adequately sample some items).

This combination of approaches is one way of attempting to cover the many ways fish feeding habits can be studied. It is hoped that the above discussion will be useful to researchers dealing in such studies.

Acknowledgements

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Table 1. Major food items of Leuroglossus stilbius and Stenobranchius leucopsarus off Santa Barbara, California*

	%N	%V	%FO	I.R.I.
Santa Barbara Basin				
<u>Leuroglossus stilbius</u> (n = 256)				
<u>Oikopleura</u>	51.0	20.2	27.0	1920.4
salps	18.8	31.6	38.1	1920.4
ostracods	13.7	15.9	23.0	600.8
copepods (1-2 mm)	5.3	4.6	9.8	97.0
crustacean debris	----	3.9	7.8	30.4
zoa larvae	0.4	1.6	10.3	20.6
<u>Euphausia pacifica</u>	0.9	3.3	4.8	20.2
miscellaneous (7 types)	7.9	18.9	33.3	35.0
<u>Stenobranchius leucopsarus</u> (n = 349)				
ostracods	20.7	18.2	36.8	1431.5
<u>Euphausia pacifica</u>	11.3	21.5	28.1	921.7
copepods (1-2 mm)	18.3	11.4	29.2	867.2
copepods (2-3 mm)	14.9	10.8	25.2	647.6
crustacean debris	----	15.5	32.5	503.8
fish scales	14.9	2.0	26.5	447.9
copepods (3 mm +)	3.0	4.6	7.6	57.8
miscellaneous (10 types)	16.9	16.0	23.5	70.6
Santa Cruz Basin				
<u>Leuroglossus stilbius</u> (n = 129)				
<u>Oikopleura</u>	59.6	25.1	42.4	3591.3
salps	0.8	17.6	27.9	1071.4
copepods (1-2 mm)	8.0	5.6	13.5	183.6
zoa larvae	3.3	7.9	14.5	162.4
copepods (less than 1 mm)	5.3	1.5	14.2	96.6
crustacean debris	----	4.9	8.8	43.1
<u>Euphausia pacifica</u>	3.2	2.6	5.7	33.1
miscellaneous (9 types)	19.8	39.0	68.6	134.0
<u>Stenobranchius leucopsarus</u> (n = 145)				
<u>Euphausia pacifica</u>	24.9	32.5	44.7	2565.8
copepods (3 mm +)	17.3	20.1	28.6	1067.6
copepods (1-2 mm)	17.9	7.7	27.7	709.1
copepods (2-3 mm)	6.9	5.0	16.4	195.2
ostracods	8.6	5.2	15.2	194.6
<u>Nematocelis difficilis</u>	4.6	8.6	10.1	133.3
crustacean debris	----	6.3	19.0	119.0
miscellaneous (10 types)	19.8	14.6	34.0	163.3

* Adapted from original table in Cailliet (1972a).

Table 2. Major food items of Leuroglossus stilbius during two oceanographic periods off Santa Barbara, California*

Fish were taken from Santa Cruz Basin

UPWELLING PERIOD (May to July, n = 39)

prey	%N	%V	%FO	I.R.I.
<u>Oikopleura</u>	56.7	37.9	46.8	4427.3
salps	14.5	22.3	28.7	1056.2
copepods (1-2 mm)	11.5	12.9	20.4	497.8
unidentified	----	8.2	9.7	79.5
<u>Euphausia pacifica</u>	0.3	6.0	9.2	58.0
ostracods	1.8	4.2	4.2	25.2
zoa larvae	0.2	2.4	3.7	9.6

THERMAL STRATIFICATION PERIOD (August to December, n = 34)

prey	%N	%V	%FO	I.R.I.
copepods (less than 1 mm)	5.2	34.9	47.8	1916.8
copepods (1-2 mm)	22.6	6.5	45.8	1332.8
copepods (2-3 mm)	21.9	9.6	37.7	1187.0
zoa larvae	11.0	10.2	47.7	1011.2
<u>Oikopleura</u>	29.0	9.0	23.0	828.0
unidentified	----	16.2	22.0	356.4
salps	3.3	10.9	16.8	238.6

* Adapted from original table in Cailliet (1972a).

Table 3. Major food items of sablefish (Anoplopoma fimbria) from traps set deeper than 400 fathoms in Monterey Canyon**

prey	%N	%V	%FO	I.R.I.
fish remains	27.5	27.1	41.1	2241.8
decapod shrimp	12.0	11.1	16.8	388.6
squid	10.5	12.3	15.7	356.5
unidentified material	9.5	11.1	14.7	303.3
decapod crabs	6.0	6.0	11.6	138.7
<u>Merluccius productus</u>	5.5	6.2	7.4	86.7
amphipods	3.9	3.4	5.3	38.7
cnidaria (jellyfish)	1.9	2.7	4.2	19.4
crustacean remains	2.2	1.7	3.2	12.2
euphausiids	1.6	0.9	4.2	10.7
bivalves	2.1	1.3	3.2	10.6
<u>Squalus acanthias</u>	1.6	2.1	2.1	7.6
unidentified flatfish	1.6	1.9	2.1	7.4
miscellaneous (13 types)	14.1	12.2	19.2	42.1

** Adapted from unpublished manuscript by E. Osada.

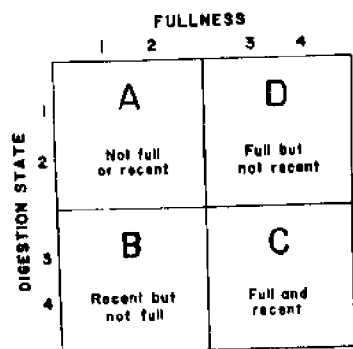


Figure 1. Four categories of feeding states to determine recency and intensity of feeding (Adapted from Cailliet 1972a).

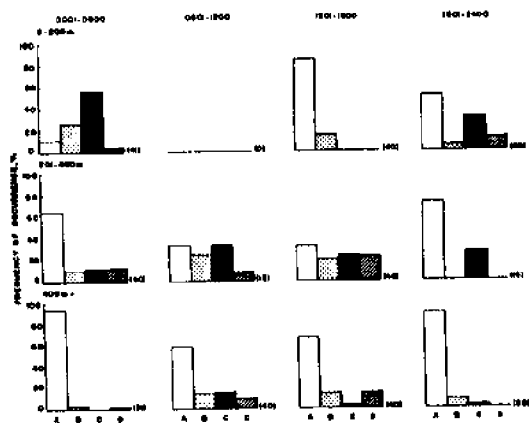


Figure 2. Fullness and recency-of-feeding histograms for *Leuroglossus stibbus* in the Santa Barbara Basin pooled over all months among four time and three depth intervals. The vertical axis measures the percent frequency of occurrence by time-depth category for fullness-recency states A-D (see Fig. 1; adapted from Cailliet 1972a).

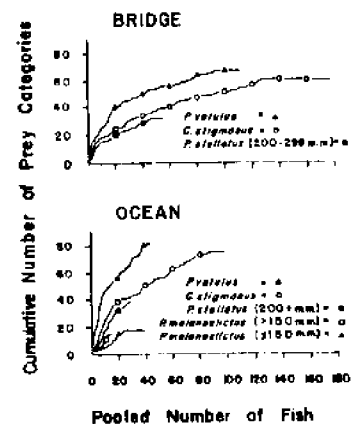


Figure 3. Curves of cumulative number of prey categories versus pooled number of fish examined from four flatfish species near Elkhorn Slough (from an unpublished manuscript by D. Ambrose).

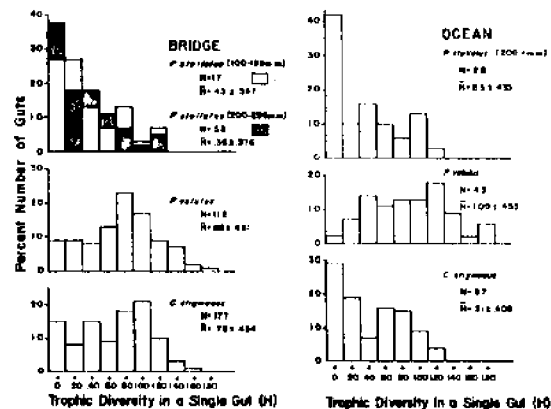


Figure 4. Frequency distribution of the trophic diversity in single guts for three species of flatfish from two stations near Elkhorn Slough (from an unpublished manuscript by D. Ambrose).

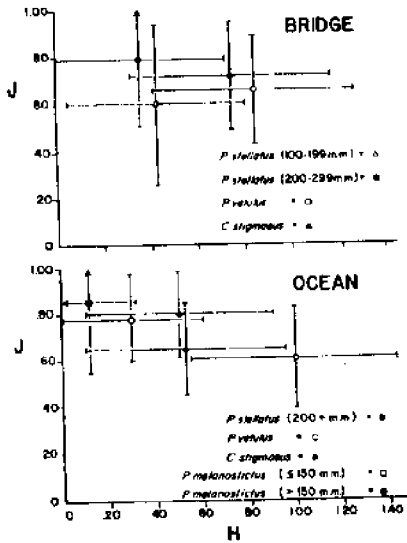


Figure 5. Mean (and Std.Dev.) H and J values for prey of four species of flatfish from two stations near Elkhorn Slough (from an unpublished manuscript by D. Ambrose).

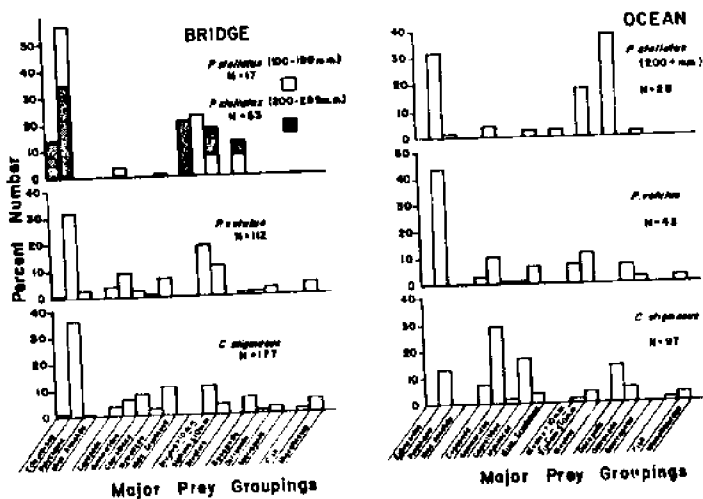


Figure 6. Percent frequency of the major prey groups found in three species of flatfish from two locations near Elkhorn Slough (from an unpublished manuscript by D. Ambrose).

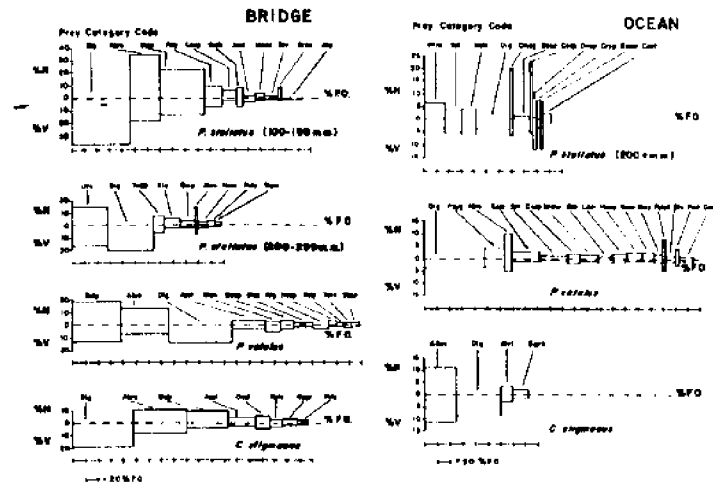


Figure 7. I.R.I. diagrams for the more common prey items of three species of flatfish at two locations near Elkhorn Slough (from an unpublished manuscript by D. Ambrose). Prey codes are not explained due to lack of space, but are available from the author.

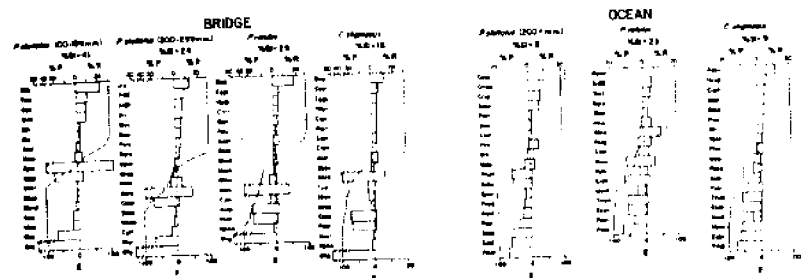


Figure 8. Percent by number (%P) of available prey taxa, proportion in diet (%R) of these taxa, and electivity Indices (E) showing the ratio of %R to %P in three species of flatfish from two locations near Elkhorn Slough (from an unpublished manuscript by D. Ambrose).

NERITIC REEF FISH COMMUNITIES--SOME PROBLEMS AND A POSSIBLE SOLUTION

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Extensive diversity among the neritic fishes of the northeastern Pacific Ocean is characteristic and apparently unique to rocky reef habitats (Miller and Gelbel, 1973). Much is still unknown about the biology of individual fish species inhabiting these reefs and about the interactions between these species. The purpose of this paper is to explain how food habitat studies can be used to help understand the community ecology of neritic reef fishes. In my presentation I will attempt to develop a conceptual framework for studying the feeding ecology of these fishes and to briefly explain how we are using such a framework to study neritic reef fish communities adjacent to Depoe Bay, Oregon.

The Community Concept

The fundamental basis of the community concept in ecology is that coextensive populations interact with each other and with their environments through the transfer of energy and materials.

In some ways it is difficult and in other ways it is very useful to consider neritic reef fishes as constituents of a neritic reef community. The difficulties are mainly in considering these organisms as constituting some sort of discrete community which can be considered separately from other such communities. Such a consideration would entail much more information than is now available on the territoriality and movement patterns of the constituent species. This, however, is not within the scope of the present discussion. The utility of the community concept to the discussion here is that, because of the complexity of neritic reef food webs, an adequate explanation of the feeding relationships of these fish populations is probably best approached from the perspective of an interacting fish community (Vinogradov 1971).

Trophic Complexity

Neritic reef food webs are good examples of extremely complex trophic interactions. Trophic interactions between neritic reef fishes can be conceptually organized into successive degrees of interaction depending on how direct the interaction is. The only direct, or first degree trophic interactions are predator/prey relationships in which food energy is actually transferred from one organism to another. In this complex food web each predator/prey interaction represents an indirect, or lower degree, interaction at least to some extent with every other organism in the community. This trophic complexity obviously leads to very difficult conceptual and methodological problems for those who seek to understand these communities.

These difficulties are further compounded when the dynamics of trophic interactions are considered. Neritic reef food webs are probably based mainly on exogenous organic material--that which has its origin elsewhere. Planktonic organisms (i.e. ctenophores, fish larvae, and invertebrate larvae) and small pelagic fishes (i.e. herring [*Clupea harengus*] and smelt [*Thaleichthys pacificus*]) probably constitute the majority of this exogenous organic production. The fluctuation of the quantity and quality of this energy source is partly responsible for the dynamic nature of neritic reef food webs. In this sense, the dynamics of these food webs are determined by factors extrinsic to the community. There are also factors intrinsic to the community which partly determine its dynamic trophic structure, one of the most evident being that food habits of fishes change as they grow older.

Community Stability

This dynamic trophic structure has direct relevance to discussions of community stability. Systems are stable, that is, they persist through their capacity to change. This concept of system stability clearly encompasses other meanings of stability such as environmental predictability and system response to external perturbations. Because community stability ultimately determines the productivity of a neritic reef community, those persons responsible for managing this resource should orient their interests toward understanding what regulates the stability of these communities.

Trophic structure and composition of these communities change on several scales of time and space and therefore notions of system stability must be placed in some context of time and space. What regulates community stability on an evolutionary time scale cannot possibly be perceived on daily, seasonal, or annual time scales. Similarly, stability regulation of these shorter time scales cannot possibly be perceived in an evolutionary perspective.

Several mechanisms have been proposed to be individually responsible for the stability of a community. Some authors consider trophic-web complexity to increase community stability (MacArthur 1955; Elton 1958), while others consider trophic complexity to reduce or have little effect on community stability (Turnbull and Chant 1961; Debach 1964; Paine 1969; May 1971; Steele 1974). Others have suggested that parameters such as time-lag (Wangersky and Cunningham 1957), threshold feeding responses (Holling 1965; Steele 1974), life history pattern (Murphy 1968), and spatial heterogeneity (Simberloff and

Wilson 1969) are the major determinants of community stability. Within this framework it becomes very confusing to discuss what is responsible for the stability of neritic reef communities.

An Approach to Conceptualizing Neritic Reef Fish Communities

Many problems in conceptualizing neritic reef fish communities exist because successive degrees of trophic interactions operate simultaneously and vary temporally and spatially. Data collected on the food habits of neritic reef fishes can lead inductively only to very partial generalizations concerning their spatially and temporally variant relationships. Indeed, even if data could be collected which represent all possible states of every component of this complex system, the conceptual problems in interpretation would be almost impossible to deal with. However, a fundamental challenge for science is to explain the phenomena of complex systems in all of their dynamic states. Albert Einstein (1940) suggested that what is necessary to explain such diverse phenomena is a "logically uniform system of thought" in which individual phenomena must be correlated with theoretic structure. The explanation and functional significance of natural phenomena can probably best be understood in the context of a generally applicable theory. This notion is supported by Carl Hempel (1966), a contemporary philosopher of science, who wrote:

... If science were to limit itself to the study of observable phenomena, it would hardly be able to formulate any precise and general explanatory laws at all, whereas quantitatively precise and comprehensive explanatory laws can be formulated in terms of underlying principles.

One generally applicable theory, formulated by Booty and Warren (n.d.) to explain the dynamics of resource utilization in biological systems, represents a possible approach to understanding these complex communities. Their theory of resource utilization employs complex sets of non-linear isoclines projected on successive phase planes as a time-invariant, general explanation of the continuous flux of interdependent variables. There is great utility of such a theoretical framework in which to consider systems such as neritic reef fish communities. This theoretical framework eliminates conceptual difficulties such as deciding whether a population is regulated by density-dependent or density-independent processes, or deciding whether community stability is achieved by mechanisms intrinsic or extrinsic to the species involved. In a very general way, it subsumes the temporally and spatially variant phenomena which characterize neritic reef fish systems.

Application of Theory

We are now in the process of collecting data on these spatially and temporally variant food relationships among fishes inhabiting neritic reefs adjacent to Depoe Bay, Oregon. Analysis of these data should provide a preliminary base for understanding the productivity and resource utilization within these communities by helping us see what food resources are being utilized by which fishes. We are also collecting otoliths, scales, lengths,

and weights which can be used to back calculate relative growth rates of fish species which, within the context of a fish community, can lead to empirical generalizations concerning interactions between these populations. A more adequate explanation of the productivity and resource utilization within these communities will come from accurate determinations of stock densities, their fluctuations, and how these fluctuations are correlated with environment parameters. It will probably be many years before we can obtain such information, but this will be a necessary task if we are to successfully manage this resource. The utility of Booty and Warren's isocline theory is that, within this framework, these relationships will become much more visual and usable to us.

Conclusion

One of the most important attributes of such a theoretical approach is that it should, for its domain, help us see the fundamental problems most demanding explanation and it should suggest the most promising approaches to their explanation. Thus, within a framework such as that provided by Booty and Warren's isocline theory, we can adequately assess what questions are worth answering with regard to neritic reef fish communities. It is clearly seen within this framework that spatial and temporal variation of trophic relationships among these fish populations is essential in our understanding of how these systems might respond to external parameters such as upwelling, fishing pressure, and marine pollution.

Finally, it is dangerous to believe that we can ever perceive a system precisely as it is and so we must remain open to new and creative thought and approaches to science. Einstein (1940), being the theoretician that he was, admitted that, at best, theoretical knowledge was "hypothetical, never completely final, and always subject to question and doubt".

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A STUDY OF FISH FOOD HABITS AS RELATED TO THE BIOLOGICAL ENRICHMENT OF AN AREA

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Since 1966, the VANTUNA Research Group of Occidental College has been examining the fish fauna of King Harbor, Redondo Beach, California. In 1974, Southern California Edison Company began sponsoring this research as a part of their research and development program in thermal effects. Edison discharges warm effluent from their steam electrical generating plant into the outer portion of this harbor.

Utilizing quantitative diver isobathic transects run monthly at prescribed stations and depths within and adjacent to the harbor and at comparative sites on the Palos Verdes Peninsula, Catalina Island, and in Santa Monica Bay, we have demonstrated that both numbers of fish as well as numbers of species are significantly higher at King Harbor than at the adjacent habitats studied (Figs. 1 and 2, Table 1).

Since 1974, we have attempted to analyze factors that could contribute to this observed biological enrichment. A number of factors would appear to represent probable sources of enrichment: thermal discharge; upwelling from the adjacent submarine canyon; the artificial reef qualities of the harbor breakwater and its protection of inshore waters, and possibly enriched food resources. The first two factors, which result in considerable thermal diversity, have been demonstrated to affect fish community diversity (Terry and Stephens 1976). Comparative studies in adjacent harbors (Los Angeles, Santa Monica, Newport, etc.) indicate that the artificial reef quality of a breakwater does enhance fish numbers and that protected waters (Stephens et al. 1974) do support large populations, especially of juvenile and subadult fish. However, as none of the above comparative localities support populations of comparable size or diversity to that of King Harbor, either thermal or food resource enhancement or a combination of these factors appear to be important in sustaining the observed ichthyological enrichment.

With this in mind, in 1975 we began a study of food habits of King Harbor fishes in order to resolve the role food resources might play in the ichthyofaunal enrichment observed at the study habitat. Preliminary

studies had been conducted by C. Terry (unpubl.) utilizing surfperch populations within the harbor. Her emphasis was placed on the function of food specialization in resource division. This emphasis is maintained in our current design but has been supplemented by additional approaches which are more specifically directed towards the total enrichment picture. Resource separation certainly can enhance diversity and perhaps allows more effective resource utilization, therefore the maintenance of more dense fish populations. Observations of resource separation through stomach content analysis and fish feeding observations alone, however, cannot satisfactorily resolve these possible effects though they may demonstrate conclusively that resource separation exists.

In 1975, we began a multifaceted approach to food resource problems in King Harbor based on Cathy Terry's original work with the Emblotocidae. The first phase involved expansion of her gut content studies to all collectable ichthyofaunal elements, in order to place her original observations within the total framework of the "harbor community".

Specimens were collected for stomach content analysis with gill nets, spears, and traps. Fish feeding habits were analyzed by diver observation and underwater cinephotography. Approximately 30 of 45 common resident species are included within these analyses. At present we have developed a preliminary classification of King Harbor fishes using four basic categories: epifaunal grazers, piscivores, planktivores, and herbivores (Table 2). We are now subjecting these data to discriminant analysis utilizing Occidental's IBM 376 computer.

Dietary preference data will also be run against Edlson's data collected on invertebrate distributions within the harbor. In addition, our divers are seasonally sampling the epifauna to give us a qualitative index of changes in invertebrate community structure. Previously determined fish distributional data - depth, temperature, habitat, season, etc. - can be correlated with food resource distributions; a high concordance of these data would appear to reflect an interdependence of distributions.

Periodicity of feeding activity has been investigated by both diurnal and nocturnal diving surveys. Levels of epifaunal grazing, the dominant feeding in King Harbor, are being investigated by fish exclusion experiments. The effects of fish exclusion cages on unmodified epifaunal growth as well as epifaunal establishment (succession) are being examined at several depths and localities within the harbor. Our fish cage experiments are supplemented by regular diver observations and detailed stomach examinations of species observed as important grazers in the area of the cages.

Analysis of the caloric content of major epifaunal dietary elements began in 1975. These bomb calorimetric studies will continue seasonally and as adequate quantities of food items are collected.

Levels of food intake, assimilation, food conversion, and growth are being

examined by a variety of means. Basic growth characteristics for each important species are being estimated by otolith examination. Otoliths and fecundity are examined on all specimens collected for stomach content analysis. Juveniles of selected groups of ecologically important species are being maintained in our laboratories and will be used during the next year's food conversion studies. These studies will be carried out at three temperatures representing the thermal variation within the harbor. Estimates of food utilization (using prepared standardized foods) will be developed. During Year I of this study, Ehrlich restricted his efforts to grunion and top smelt because of ease of raising these fish from egg to adult. He was able to show a strong correlation between preferred temperatures and assimilation efficiency (Ehrlich, pers. comm.). Estimates of food conversion can then ultimately be correlated with feeding observations (i.e. bites/minute), grazing observations (epifaunal growth with and without grazers), fish growth, estimates of biomass of harbor fish populations, and estimates of reproductive energy drain and fish recruitment.

The aim of this study is not only to determine the role that food resources in King Harbor might play in the ichthyofaunal enrichment of the area, but to ultimately develop an ichthyocommunity resource model along the lines developed by Parrish (1975) which will define the role, if any, that thermal effluent plays in this system.

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Figure 1. Average number of fish observed per transect at King Harbor and Palos Verdes.

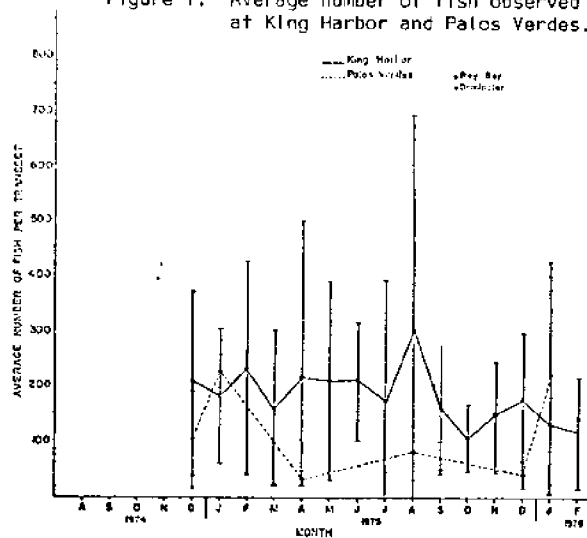


Figure 2. Number of fish species observed per transect at King Harbor and Palos Verdes.

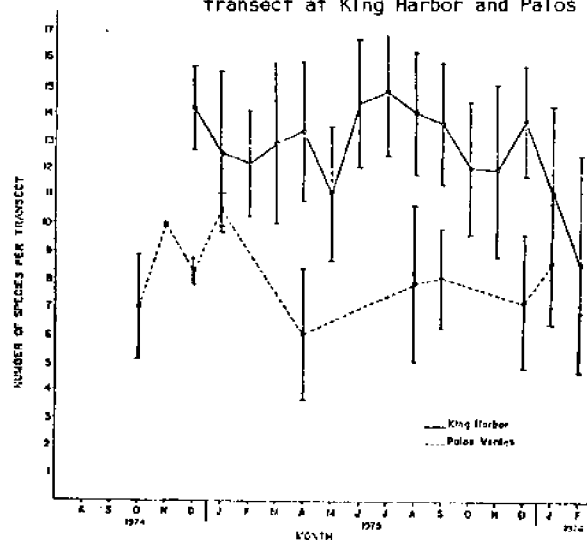


Table 1. Number of species and mean abundance at King Harbor compared to Palos Verdes and Catalina Island

	Species					
	mean/station		mean/transect			
	mean	var.	mean	var.	number/ station	number/ transect
King Harbor	19.1	30.8	12.4	20.6		
Palos Verdes	13.4	7.8	8.4	1.4		
Catalina Island	14.7	6.5	10.6	2.6		

	Individuals					
	mean/station		mean/transect			
	mean	var.	mean	var.	number/ station	number/ transect
King Harbor	834.4	206116	245.0	28497.6	72	198
Palos Verdes	308.5	71001.4	108.9	9384.9	6	21
Catalina Island	572.4	43059.7	157.2	4898.6	22	100

Table 2. Trophic categories of fish from King Harbor (using preliminary dietary analysis data)

<u>Secondary Carnivores, etc.</u>			
Herbivores	Planktonotrophs	Grazers (general)	Predators
<i>Hermosilla</i>	<i>Engraulis</i>	<i>Rhacochilus</i>	<i>Paralabrax</i>
<i>Girella</i> (A)	<i>Chromis</i>	<i>toxotes</i>	<i>clathratus*</i>
<i>Medialuna</i> (A)	<i>Seriphus</i>	<i>Phanerodon</i>	<i>Paralabrax</i>
<i>Hypsoblennius</i> :	<i>Sebastes</i>	<i>furcatus</i>	<i>nebulifer</i> Q, T
<i>gilberti</i>	<i>mystinus</i> (J)	<i>Hypsurus</i>	<i>Paralabrax</i>
	<i>Sebastes</i>	<i>caryi</i>	<i>maculatofasciatus*</i>
<u>Primary Carnivores</u>	<i>serranoideus</i> (J)	<i>Enbiotoca</i>	<i>Sarda</i>
	<i>Neoclinus</i>	<i>jacksoni</i>	<i>chiliensis</i>
<i>Clinocottus</i>	<i>stephensae</i> JS	<i>Micrometrus</i>	<i>Sebastes</i>
<i>analis*</i> JS	<i>Hypsoblennius</i>	<i>minimum</i>	<i>paucispinis</i>
<i>Hypsoblennius</i>	<i>jenkinsi</i> JS	<i>Hyperprosopon</i>	<i>Reterostichus</i>
<i>gilberti*</i> JS	<i>Cymatogaster</i> (J)	<i>argentum</i>	<i>rostratus*</i>
<i>Gibbonsia</i>	<i>Atherinops</i>	<i>Caulolatilus</i>	<i>Scorpaenichthys</i>
<i>elegans*</i> JS	<i>affinis*</i> Q	<i>princeps</i>	<i>marmoratus*</i> JS
<i>Rhacochilus</i>	<i>Rathbunella</i> sp.	<i>Gibbonsia</i>	<i>Scorpaena</i>
<i>vacca*</i>		<i>metzi</i>	<i>guttata</i> T, JS
		<i>Gibbonsia</i>	<i>Paralichthys</i>
		<i>elegans*</i>	<i>ocelliformis</i> Q
		<i>Clinocottus</i>	<i>Sebastes</i>
		<i>analis*</i>	<i>auriculatus</i> Q
		<i>Scorpaenichthys</i>	<i>Sebastes</i>
		<i>marmoratus*</i>	<i>carinatus</i> Q
		<i>Coryphopterus</i>	<i>Sebastes</i>
		<i>nicholsii</i>	<i>serranoideus</i> (A), T
		<i>Anisotremus</i>	
		<i>dauidsoni</i>	
		<i>Oxylebius</i>	
		<i>picta</i>	
		<i>Cheilotrema</i>	
		<i>eatumum</i>	
		<i>Menticirrhus</i>	
		<i>undulatus</i>	
		<i>Citharichthys</i>	
		<i>stigaeus</i>	
		<i>Atherinops</i>	
		<i>affinis</i>	
		<i>Hypsypops</i>	
		<i>rubicunda</i> Q	
		<i>Halichoeres</i>	
		<i>semicinatus</i> Q	
		<i>Oxyjulis</i>	
		<i>californica</i>	
		<i>Pimelometopon</i>	
		<i>pulchrum</i> Q	
			Grazers (general)
			continued:
			<i>Hexagrammos</i>
			<i>decagrammus</i> T

* = facultative
 JS = Stephens (unpubl. data)
 Q = Quast
 T = Turner

SAMPLING CONSIDERATIONS IN THE ANALYSIS OF FOOD WEB RELATIONSHIPS

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One of the first steps in any sampling survey is a clear statement of objectives. In analyses of food or feeding relationships, it is important that the sampling design and data to be collected be selected based upon their relevance to the study's overall goals. Three common inter-related objectives in feeding studies are:

- (1) To identify predator feeding roles and activity patterns;
- (2) To determine predator food composition and feeding rates; and
- (3) To evaluate characteristics of prey selection, with comparisons between predators.

These objectives can perhaps best be approached by a combination of behavioral and morphological observations, laboratory determinations, and analytical studies of results.

Identification of Feeding Roles and Activity Patterns

The advantage of classifying predators into general feeding roles ("nocturnal planktivore", "diurnal epifaunal picker", etc.) is that the functional descriptions may have wide applicability throughout each predator's zoogeographic range, even though prey composition may vary. As a result, the identification of general patterns of feeding behavior provides a basis for evaluating the functional structure of communities (Allen, 1974, 1975).

A starting point for any study of feeding behavior is a critical examination of the predator morphologies. In many cases, the approximate feeding behavior of fish predators and types of prey they feed upon can be inferred by examination of predator body size and shape, orientation and

size of the eyes, and the structure and size of teeth, jaws, and gill rakers (De Groot, 1969; Yazdani, 1969; Gosline, 1971; Ebeling and Cailliet, 1974; Hobson, 1974).

Behavioral observations in the field and laboratory can also provide key information for the classification of feeding roles: how is food obtained, and what are the activity cycles of predators and prey? Is the predator an active searcher, or does it sit and wait? Are prey selected visually, or by tactile perception? Is feeding off- or on-bottom?

If sampling is to be conducted examining food composition and/or feeding rates, then an important behavioral observation is the determination of predator activity patterns: does feeding follow a diel cycle, or is it continuous? Numerous field observations have documented striking differences in the feeding behavior of shallow-water fishes between day and night, during twilight hours, and between morning and afternoon (Keast and Welsh, 1968; Hobson, 1965, 1974; Hobson and Chess, 1976). Clearly, the timing of sampling for food analysis needs to be related to the timing of predator feeding periods for at least two reasons: (1) If feeding is markedly periodic, then food composition is most accurately determined by sampling just following the end of the feeding period, before digestion (Windell, 1968); and (2) for evaluation of estimates of feeding and digestion rates.

Determinations of Food Composition and Feeding Rates

1. Listing of Food Items: What is eaten?

In the simplest analysis, feeding relationships can be described as the list of prey species found within predator stomachs examined. A measure of the fidelity of each connection is the food item's frequency (or proportion) of occurrence within stomach samples.

If meaningful results are to be obtained, careful attention must be given to survey design (Cochran, 1963). A specific target population must be identified, and related to variations of predator and prey in both time and space. The distribution of sampling, and sampling effort (number and size of samples), must be related to overall research objectives. Randomization should be incorporated so that each individual fish in the target population (and samples) has an equal chance of selection. As opposed to the collection of large single samples, the use of smaller interpenetrating subsamples enables assessment of variance within sampling periods.

Since the qualitative composition of food ingested is frequently related to predator size (Tyler, 1971, 1972; Daan, 1973; Jones, 1975), it is often desirable to subdivide the sampled predator population on the basis of size class intervals. The size of the sample taken from each interval should then be proportional to the number of individuals within each size-

Interval.

The method of sampling must be evaluated as a potential source of bias. Specimens collected in towed net samplers (plankton nets or trawls) may feed on unusual prey with the net, or have unusual items forced into their guts (Judkins and Fleming, 1972). Sampling method and differential effects of sampling depth must also be considered in assessing the occurrences of empty stomachs.

The selection of sample size for determinations of proportions of prey occurrences can be based upon a relation of sampling theory and survey objectives for precision of estimates (Cochran, 1963). The frequency of occurrences/non-occurrences of a prey species within stomach samples would be expected to follow a binomial probability distribution. As a result, confidence limits for sample proportions can be readily determined graphically (Tate and Clelland, 1959).

2. Relative Food Composition: Principal prey

Many, if not most, studies of feeding result in a description of each predator's relative food composition as an approach to identifying principal prey. In subsequent analyses of the division and use of food resources, comparisons of food composition are often made between predators (Dragovich and Pottoff, 1972; Tyler, 1972; Jones, 1975). Descriptions of relative composition (expressed as percent contribution, or average weight of individual food categories per stomach) should be recognized as distinctly different from estimates of feeding rates.

The choice of the units of measure (numbers, volumes, wet weights, dry weights, elemental weights, or energy equivalents) must be based upon a relation of research objectives and cost. It is important to recognize that different types of measurements may give markedly different results (Holden and Raitt, 1974).

Biases in the determination of relative food composition include: (1) readily digested prey may be underestimated; (2) problems in the enumeration and measurement of fragmental and amorphous materials (mucus, detritus, chitin, bivalve siphons, etc.); and (3) the potential influences of discontinuous feeding patterns must be considered.

3. Feeding Rates: How much is eaten?

Although the implied objectives of most feeding studies are to determine feeding rates (energy or material flux t^{-1} , or prey mortality t^{-1}) and the relative contributions of individual food sources to these rates, few studies of marine fishes have convincingly estimated natural rates of food ingestion or predation (Lasker, 1970; Trevaillon ETAL., 1970; Daan, 1973).

Food consumption rates can be estimated by three principal approaches:

(1) direct measurements of prey abundance before and after predator addition/exclusion (lab or field); (2) measurements of digestion rates by laboratory feeding followed by sequential assay (lab), uptake of radioactive isotope-labelled prey (lab), or following the digestion of stomach contents of strongly diel-feeding predators (field); and (3) by determination of the predator's energy or material budgets (Windell, 1968; Davis and Warren, 1968; Southwood, 1975).

A number of important factors and potential sources of bias must be considered. An attempt must be made to quantitatively assess occurrences of empty stomachs, and to evaluate the percentages representing stomach eversion, food regurgitation, or true lack of contents (Daan, 1973; Pearcy and Ambler, 1974). Temperature can be expected to strongly influence feeding and digestion, with changes in rates of approximately 7-11 % per 1 °C change (Wieser, 1968).

Evaluation of Characteristics of Prey Selection

The terms "specialist" and "generalist" have frequently been used to compare the feeding characteristics of different predators. Within-surveys, these descriptions have meaningful applications (with definition) for comparing the number of prey species, distribution of amounts of each prey, and range in prey sizes observed among different foragers.

Meaningful use of the terms "selectivity" or "food preferences" must be assessed in the context of relative prey availabilities. Relative prey availabilities may, or may not, be related to prey abundances. If comparisons are to be made of food resource use and division between predators, stomach analyses should be restricted to individuals co-occurring within samples (Jones, 1975).

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INTERACTIONS BETWEEN JUVENILE SALMON AND BENTHIC INVERTEBRATES IN THE SKAGIT SALT MARSH

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Objectives, Sampling Design, and Preliminary Results

This past spring and summer we conducted preliminary sampling of fish and benthic invertebrates in the salt-mudflat system of the lower Skagit River in Puget Sound, Washington. During the spring and summer months, the numerous small tidal streams that dissect the surface of the delta in this area supported very high populations of starry flounders (*Platichthys stellatus*), staghorn sculpins (*Leptocottus armatus*), three-spine sticklebacks (*Gasterosteus aculeatus*), and the juveniles of chum (*Oncorhynchus keta*), chinook (*O. tshawytscha*), and pink (*O. gorbuscha*) salmon. The purpose of our sampling was two-fold. First, we wanted to obtain a general picture of utilization of the delta area by fish and to assess the impact of their predation on populations of the benthic invertebrates which comprise a large proportion of their diet. Second, the study allowed us to evaluate various approaches to sampling which may be useful for future research. In this preliminary work we have concentrated our efforts on juvenile chum and chinook salmon.

Fish sampling techniques

After experimenting with traps and with a 25-m beach seine, we found that a 7-m wide by 2-m deep beach seine with 1/8-inch mesh was both effective and practical. It was light enough to carry on foot, and suitably sized for sampling 5-to 10-m wide tidal streams.

Most of our sampling was done in Index Slough, near the South Fork of the Skagit River. We established 6 stations at 80-m intervals along its length and made 10-m hauls during low tide periods. The effective spread of the 7-m seine was about 5 meters. Fish were identified and counted in the field. Selected samples were subsampled; the subsamples were preserved and returned to the lab for diet analysis and length-frequency measurements.

Results

Large numbers of chum and chinook were present in the tidal streams in late April and early May. There was a sharp decline in early May (Figure 1); the peak outmigration may have preceded our initial sampling.

Our preliminary diet analysis of chum salmon indicated active feeding in the tidal streams. The values for percent fullness of stomachs, shown in Table 1 are generally quite high, although the fish at station 5 had not fed as much as those at the other 2 stations. Since station 5 had the highest fish density, it is tempting at this time to speculate that this difference may reflect intraspecific competition.

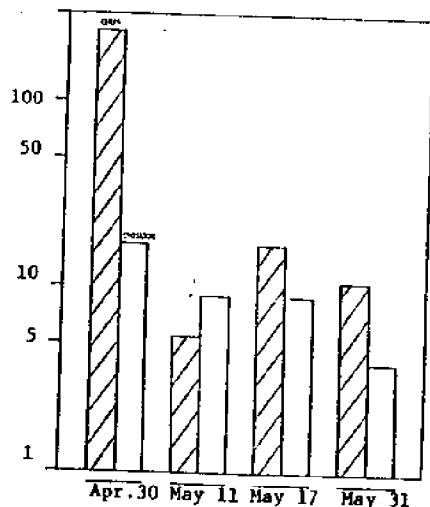


Figure 1. Estimated density of juvenile chum and chinook salmon in Index Slough, Spring, 1976. Fish per 100m².

maintaining tidal stream invertebrate populations?

Planned future work

To answer these questions, basic life history information is required for the prey species concerned. We are obtaining this data from two sources: first, studies on the community structure of salt marsh benthic invertebrates;* second, benthic sampling conducted concurrently with our fish sampling.

Table 1. Foregut contents (dry weight as percent dry body weight) of chum salmon collected from 3 Index Slough Stations on April 30, 1976

STATION	N	\bar{x}	S.D.	RANGE
1	10	3.88	-	-
3	10	5.18	1.96	2.46 - 7.71
5	10	2.04	1.62	0.18 - 5.04

*Ph.D. Thesis research of J.E. Smith

Most of the diet items fell into three categories:

1. *Corophium salmonia*, a tube dwelling amphipod abundant in the delta.
2. Harpacticoid copepods, which were important numerically in the stomachs, but accounted for less than 5% of the total dry weight of the diet.
3. Adults, larvae, and pupae of insects.

Our spring sampling has led to many specific questions about the effects of fish predation may have on the invertebrate populations. For example: What is the intensity of predation and what is its effect on the abundance and size distribution of prey organisms, both in tidal streams and on the adjacent marsh? Can the invertebrates in tidal streams support this predation pressure through reproduction alone, or does immigration from the flats play a role in

At several fish sampling stations we have established 4 "transects" along each of which we are taking 5 benthic cores at monthly to bimonthly intervals. Two of these transects are located within the stream in areas of presumably high predation pressure, and the other 2 are placed on the adjacent marsh, where predation pressure is assumed to be relatively low. Fish sampling in tidal streams will continue to be by seining at low tide, with additional trawling or collecting by other methods on the adjacent marsh and mudflats at high tide to quantify predation pressure outside the streams. A diagrammatic representation of our sampling scheme is shown in Figure 2.

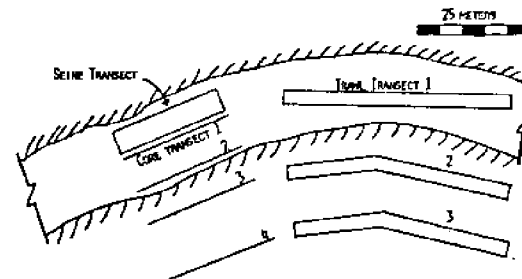


Figure 2. Typical Index Slough section showing seine, core sample, and trawl transects

Sampling will be conducted throughout the next year to monitor fish populations and to gather data on invertebrate populations before, during, and after the strong spring pulse in predator abundance. Eventually we hope to refine this approach to estimate the carrying capacity of the salt marsh for juvenile salmon.

Application of Information to Fisheries Management Problems

Most of the streams and rivers entering Puget Sound have--or once had--salt marshes of greater or lesser extent in the tidewater zone. All of these streams and rivers also support runs of one or more of the 5 species of Pacific salmon. Fishery biologists have sometimes noted large numbers of juvenile salmon in salt marsh streams (R. Orrell, 1976, personal communication) but evidence for utilization of marsh food resources by salmon has been lacking. Our initial sampling on the Skagit River delta (Spring, 1976) indicated that large numbers of chum and chinook fry were feeding in the marsh. We do not yet know how long the fish reside in the marsh, or what portion of total chum and chinook outmigration is involved. However, the high density of fry observed in tidal streams in late April (ranging from 200 to over 800 fry per 100 m² at some stations) and the higher percentage of fry with full stomachs suggest that the Skagit salt marsh may be an important foraging area for downstream migrants. More detailed information on the feeding of salmon fry in salt marshes will be valuable to agencies with responsibility for management of salmon resource, for several reasons.

First, if survival of outmigrants is enhanced by the presence of salt marsh habitat, this provides a strong argument for preservation of marshlands. In the absence of hard evidence weighing in favor of marsh preservation, a large portion of Puget Sound's marshlands have already been dredged, filled, or otherwise altered. Reclamation of the Skagit delta for farmland began in the 1800's; today less than twenty percent of the original marshes remain. The Green and Puyallup River marshes have been obliterated by industrial development, and much of the Snohomish River salt marsh has been altered by land fills and log raft storage. Because of continuing pressure for development of remaining delta areas, documentation of the ecological importance of salt marshes is essential.

The second major point is that understanding of interactions between juvenile salmon and their prey in the salt marsh, and beyond in the main estuary, would facilitate development of optimal rearing-and-release strategies for artificially propagated salmon. For example, the timing of releases of hatchery fish should be such that adequate natural food is available when they enter the estuary. At present we know very little about seasonal changes in the abundance of estuarine prey organisms. In contrast, Japanese chum salmon culturists are reported to carefully monitor the abundance of zooplankton in nearshore waters and to release fry only when conditions are judged favorable for their survival. It is not possible to specifically identify the benefits derived from this procedure, but certainly the Japanese chum salmon program has been an outstanding success, and high fry-to-adult survival rates have been achieved.

Development of optimal release strategies for hatchery fish will also require knowledge of the carrying capacity of salt marshes and of the littoral zone in the estuary, where Puget Sound chum and pink salmon fry concentrate their feeding activity (Feller and Kaczynski, 1975). Food availability in salt marshes and in the littoral zone may constrain the number of fry that should be released in any river system or part of the Sound. Although production of wild chum and pink salmon in the Puget Sound region is presently much below historical peak levels, artificial propagation of chum salmon may increase rapidly from the present level of about 20 million fry per year to over 500 million fry per year within the next decade. The Nisqually River system alone is believed to have enough available spring water to incubate 600 to 700 million chum eggs. More realistically, if the number of chum fry utilizing the Nisqually delta is increased by 150 to 200 million, how will populations of preferred prey organisms, such as *Corophium salmonis*, be affected? And if the growth and survival of fry is progressively reduced due to increased intraspecific competition for food, at what point will additional investment in hatchery facilities cease to be cost-effective? These are important questions, since a "crash" enhancement program could easily overshoot the optimal production level. The return of adults from a release of chum salmon fry is not known for 4 years, and even a strong downward trend in fry-to-adult survival would not be conclusive without 4 or 5 years of data. Hence, a rapid expansion of hatchery facilities could continue without contravention for 9 to 10 years after the optimal production level has been exceeded.

A tabulation of all the published literature would undoubtedly demonstrate that over 95% of the research completed on salmonid fishes has dealt with the freshwater phase of the life cycle. Yet, mortality rates during the estuarine or "early coastal" phase of the life cycle are believed to be extremely high and very variable from year to year (Parker, 1968; Royal, 1962). Despite the technical difficulties, much more effort must be put into identifying the factors that determine the estuarine survival of juvenile salmon.

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DISCUSSION: SESSION 1; PURPOSE AND SAMPLING DESIGN

A discussion ensued regarding the mouth size versus feeding habits of flatfish. The English sole and starry flounder were cited as examples of small-mouth fish, and sand sole and sanddabs as examples of large-mouth fish. One could reasonably expect the large-mouth fish to feed more intensively on fish than on crustaceans, which is the observed case. A trophic analyst ought to consider the functional morphology of the fish related to the food items it is capable of consuming.

Greg Cailliet mentioned that the fish residing in Elkhorn Slough are not adults, including English sole. The smaller fish live far up in Kirby Park, and as they get larger, they move offshore. By the time they reach a sub-adult size, they are on their way and become part of the fishery in and around the edge of the canyon. Starry flounders and perhaps a few of the sanddabs get older in the area, while the other species use it only in the juvenile stages of life.

Talvo Laevastu suggested that we ought to thoroughly examine the older European literature to see what other scientists have done--both to supplement our knowledge and to make certain that we are not wasting valuable research dollars by repeating some long-forgotten work. As an example he cited work done in the early 1900's by Petterson, published as Evaluation of the Sea I, II, and III. Steve Obrebski acknowledged the volumes, but said he had not found in them useful information regarding analysis of interacting communities.

Obrebski cited the work of Bob May (published in Nature and American Naturalist) regarding stability analysis. How valid are some of the current predicting devices of community structure when one is dealing with complex systems? Each complexity increases the difficulty of using models successfully. Dick Steiner agreed and further questioned the ultimate goal of science--is it to come from prediction or true understanding? The conclusion seemed to be that prediction itself ought to come from true understanding.

Joseph Durkin wondered what might be causing observed mortalities of

Juvenile salmon in estuaries. He cited the case of the Columbia River where freshwater predators end 20 miles upstream of the mouth and salt-water predators don't usually enter the estuary. If predators are the cause of the mortalities, might they be yearling fish feeding on the downstream migrants? Or perhaps might the mortalities be related to availability of food?

Durkin continued the discussion of availability of food as a limiting factor by suggesting that perhaps the young chinook and chum were over-utilizing what is available. He thought that perhaps the fish fed on *Corophium salmonis* (the documented preferred food item of young salmon on the West Coast as they feed in estuaries) when they come out of their tubes to molt. Jim Smith replied that the fish seem to go after the large males of *C. salmonis*, which are much more active on the surface and migrate around. The feeding fish seem to take full advantage of this behavior. Durkin wondered if there was any evidence of fish going in the mud after them. Smith answered that it was hard to say since the amphipods move around quite a bit and change their tubes often. Generally, it was felt that the young salmon feed on *C. salmonis* when they are out of their tubes on the surface for any reason.

Mike Healey of Nanaimo asked if anyone had ever actually observed coho feeding on pink and chum fry. Si Simenstad replied that he had never seen them in coho stomachs although he had observed them in the stomachs of *Leptoosteus*. He suggested that one ought to consider other predators in the system. Healey completed his question by stating that perhaps the general acceptance of coho preying on pink and chum fry is a motherhood myth in most cases.

Terrence Gjernes added that he had observed sockeye fry in coho stomachs in the Fraser River system.

Laevastu addressed the group and asked if anyone was simultaneously studying bird predation on salmon fry. Are there observations of salmon fry in bird stomachs? Jim Smith replied that this was probably true as well as predation on salmon fry by river otter. Few data are available, but he is interested in looking at that aspect of salmon predation more closely.

In reference to an earlier question, Jim Congleton stated that they didn't have as much data on biological interactions at high tide because of sampling problems. The group was in agreement that such samplers as beach seines and Eckman grabs do not work as well on a high tide. Cailliet mentioned the use of a pop-up net as described in Ecology. This required the setting up of permanent stations. Congleton said they were aware of this but had come across problems of fish not swimming over the net. The pop-up net is a design whereby the net remains collapsed until use. When the lines are pulled, the net "pops up" and purses the captured fish.

Bob Feller posed the idea that fish using the nearshore estuarine environ-

ment as feeding grounds might be the basis for preserving these areas. He wondered if any studies existed where such nearshore habitats did not exist but where pink and chum fry exist, feeding perhaps on zooplankton. He also wondered if feeding in a nearshore environment was actually part of their life histories or merely an adaptation to a particular environment. Congleton thought that fish were able to adapt to the resources within a particular ecosystem. Herbert Jaenicke asked how long chum fry will remain in these shallow, estuarine areas. He then cited the case in Bristol Bay where sockeye smolt move several hundred miles slowly in cold summers but faster in warm summers. This speed of migration seemed to have quite an effect on total marine mortality. How long did the young fish in Congleton's study remain in the Skagit area and what would be the effect of short-term starvation should food resources not exist? Congleton agreed that he also would like to know!

Howard Horton mentioned that a graduate student from Oregon State University--Range Byers--did a Master's project on the feeding habits of the great blue heron in the Yaquina Bay Estuary. He accomplished this by checking the food items that had been dropped from the heron nests. This was one method to estimate diet with non-destructive sampling. Bob Miller posed the question of how to determine the carrying capacity of a stream. Congleton stressed that the task would be tremendous but could be done. One way might be to estimate fish density, daily food ration, evacuation rates, and then compare to the production of invertebrates used as food in the area. Another might be to monitor the changes in prey abundance relative to changes in predator abundance.

Healey responded to an earlier question about residence time of young salmon in estuaries. In 1975 in the Nanaimo River Estuary chum fry (early run) stayed about 2 weeks, but most fish stayed less than a day. In 1976 the smaller early run stayed about a week on the mudflats and the later run fish stayed no time at all on the mudflats. Even those on the mudflats were moving progressively seaward. During this time, chum and chinook were putting on about 4-4 1/2 percent of body weight a day on the mudflats. Little difference in growth rate was observed between fish feeding on or off the mudflats. It was felt that most of the chum feed off the mudflat areas while the chinook fry do use the mudflat-marsh area. The chum seem to have a wider range of habitats. Healey felt that sloughs with water are the most attractive to young fish.

Gjernes presented an idea for sampling coho--the minnow trap with 1/4-inch mesh and salmon roe bait. This refreshed the memories of Horton and Jaenicke who recalled a study where the researcher used blended salmon roe as bait with some success. Bruce Hillaby commented that he had used minnow traps and found that they didn't work well for chum but worked very well for coho and chinook. His group even built a large minnow trap for an area where beach seining was impossible. One sampler they found to work very well for chum was a manual purse seine operated by three people. The seine was 50 feet long and 13 feet deep. He offered to send the dimensions to anyone who was interested.

Cailliet mentioned that he had used a similar net to study assemblages of fish associated with drift kelp in Monterey Bay, California. They encircled the drift kelp with a small Boston whaler and pursued the bottom up.

Simenstad returned to an earlier thought about food being a limiting factor in early life histories of fish. He emphasized that rates and rations have really not been studied at all. Some literature on rates and rations is available, but he didn't feel that it was worth much and in some cases was based on insufficient data. He had some ideas how to determine daily rations but presented the question to the group for suggestions. Gary Smith agreed that most food studies have, unfortunately, stopped short of consumption rate studies. Feller wondered how many published accounts of 24-hour diet studies were available.

Healey suggested that a fair amount of literature existed on diet and feeding, perhaps some of it European. He cited the chum workshop (held sometime prior to this workshop) as a good forum for information exchange. He had observed diet changes over a tidal cycle with chum feeding on large *Calanus plumochirus* in the early morning, then eating harpacticoid copepods midday and *C. plumochirus* again in the evening. He acknowledged that someone else might not get the same results. The observations could have been the result of the fish's or food's position during the tide, etc. Obrebski mentioned that someone from the Pacific Marine Station in Dillon Beach had studied food habits of fish in Tomales Bay. He had found that the oxygen levels in eelgrass beds dropped at night to 2 ppm and forced certain crustaceans out of the area. Caprellids, for example, swim away in droves. This could have quite an effect on where the fish feed.

Cailliet cited that more ration studies have been done in fresh water than in the marine environment. Al Ebeling, for example, has done some consumption studies. These are difficult to do because one might not catch the same fish over a 24-hour period. Not much is known about digestion rates, which for some species of predator and/or prey might exceed 24 hours. Bivalves were cited as a possible example. Laboratory studies can be performed, but one should remember that the fish might behave abnormally under artificial conditions. However, they are better than nothing. Laevastu stated that it is simple logic that quantitative estimates are not possible without good numbers. He continued along another line that if food is a limiting factor in the sea, then starvation plays a major role in health of fish stocks. Sex products may not develop at all with a starvation diet, or may be resorbed for added energy. We need much better numbers of feeding rates, food requirements, and behavior in absence of food.

Healey said that there is a wide literature on food rates and gastric clearance rates available. Perhaps the reason some researchers think it doesn't exist is because they have not checked carefully enough. Much of the literature is European, as mentioned before. For example, the Aberdeen Marine Station in Scotland has produced several papers on the feeding ecology of plaice.

SESSION 2

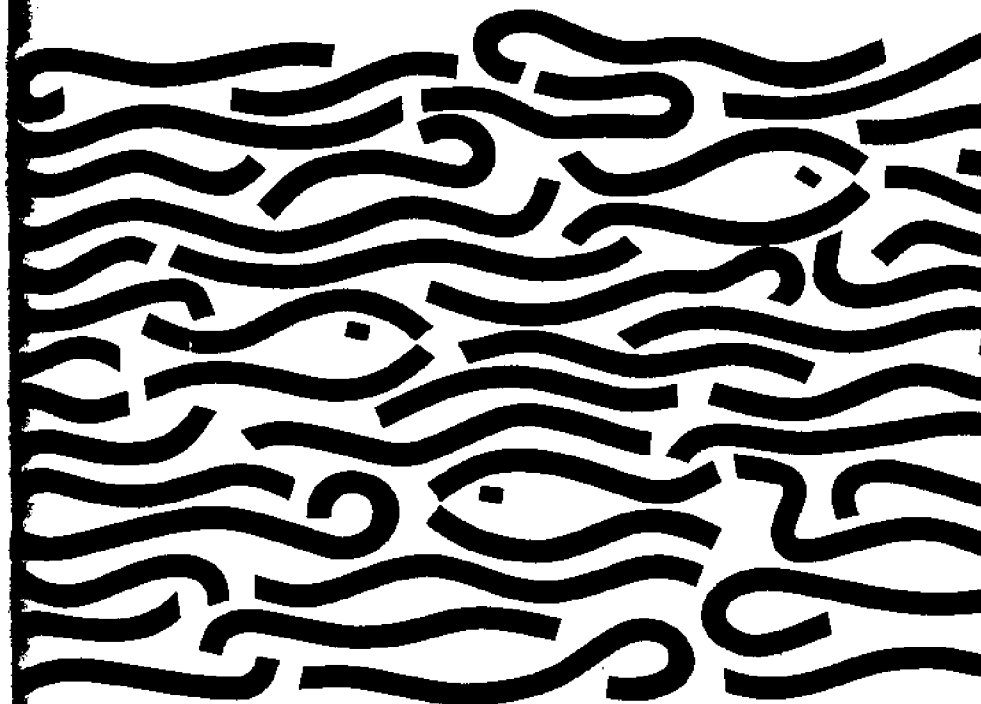
PREDATOR AND PREY COLLECTION

Cailliet supported this by saying that there is also a considerable group of literature coming from the fish larvae culture section at National Marine Fisheries Service in LaJolla, California (Reuben Lasker and John Hunter). He especially cited papers on *Engraulis mordax*. Most of the work is laboratory work.

Congleton mentioned that very few researchers have tried to combine field and laboratory studies. One might, for example, get estimates of evacuation rates in the laboratory and apply them to consumption rates derived from actual field observations. Simenstad agreed that simultaneous studies of a community should be initiated. Prey community composition is a very important thing to know.

Laevastu summarized by saying that study needs had been aired but we ought to order them by priority. He then suggested that might be one of the goals of the fish foods habits studies workshop.

One of the limiting factors of any study, of course, is funding. Researchers should carefully consider the benefit/cost ratios of any proposal and use research time and dollars wisely.



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AN EVALUATION OF BENTHIC INVERTEBRATE SAMPLING DEVICES FOR
INVESTIGATING FEEDING HABITS OF FISH

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Benthic invertebrate samplers and the information gained from their use can be extremely valuable to research conducted on feeding habits of fish. These samplers provide complete and undamaged specimens which can be accurately identified, and the data produced can be used to formulate detailed pictures of the community of organisms present in and on the surface of the sediment. This evidence of existing community structure coupled with inventories of the stomach contents of particular fish species can be used to determine selectivity in patterns of feeding for the fish species in question. However, many of the benthic samplers in use today do not function in the same manner, and as a result, unequally represent both the types of species and number of individuals captured. Therefore, data are somewhat biased by the type of sampling device employed and caution must be used in attempting direct comparisons between organisms found in the stomach contents of fish and those depicted by community members in benthic grab samples. The purpose of this paper is to review the results of a field comparison of benthic samplers and to discuss the inherent attributes and problems associated with several types of commonly used sampling devices as they relate to research on fish feeding habits.

Our study focused on three major types of benthic samplers: benthic grab samplers (eg. Van Veen, Smith-McIntyre, Ponar, Shipek, and Orange Peel), deeper penetrating sampling devices (eg. box core and anchor dredges), and shallow penetrating samplers (eg. epibenthic sleds and shell dredges, Fig. 1 a-g). These broad types of sampling devices function differently and emphasize different portions of the benthos. Therefore, some knowledge of both horizontal and vertical distribution patterns of organisms was required and was included in our field survey and discussion. Differences characterizing benthic grab devices are discussed next. Because these devices do not function in the same manner, we will briefly compare 6 frequently used benthic samplers based upon a set of criteria, and then designate which grab sampler we believe to be the most efficient and effective. Finally, a comparison of the broad categories of benthic samplers is presented, along with a rationale for choosing which benthic sampler should be used in the investigation of feeding habits of fish.

Types of samplers



Figure 1a. Orange Peel

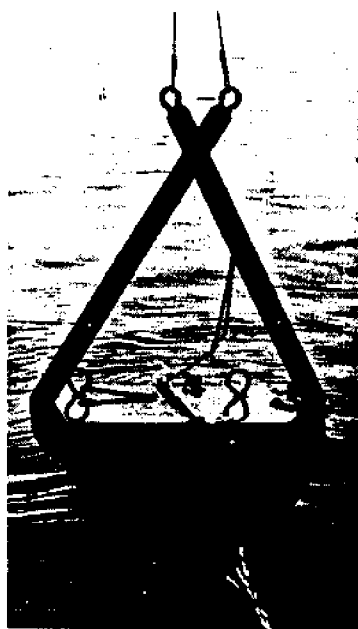


Figure 1b. Bar tripped Van Veen

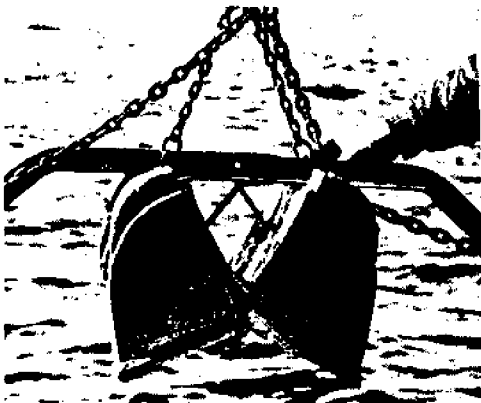


Figure 1c. Chain-rigged Van Veen

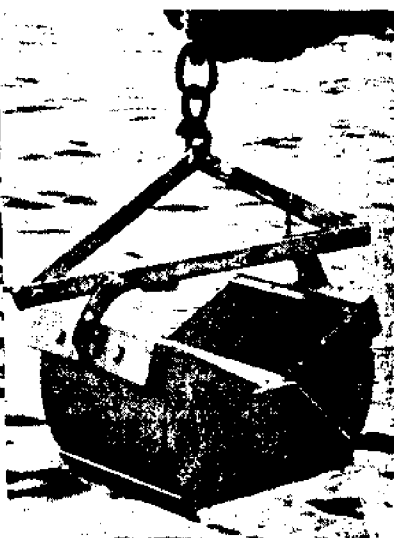


Figure 1d. Ponar

Types of samplers (cont.)

Figure 1e. Shipek

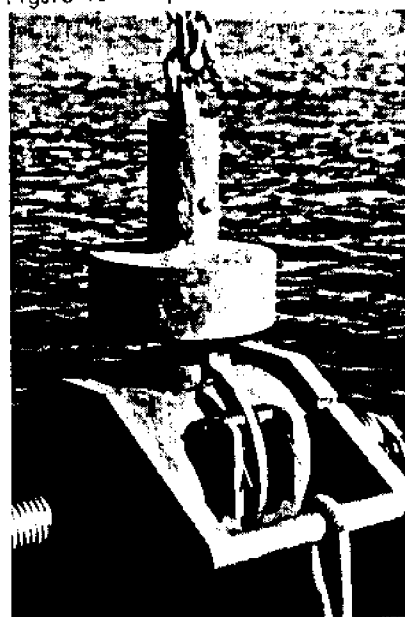


Figure 1f. Smith-McIntyre



Figure 1g. Box Corer

Methods

Our field study was conducted during 2 cruises in the winter of 1974 and 1975 (Word et al. 1976). Biological descriptions of an area of bottom are directly dependent upon the numbers and kinds of organisms present in benthic samples. Focused on: 1) Horizontal distribution patterns, investigated by taking 10 replicate 0.1 sq m samples at a shallow (12.0 m) sandy station in Santa Monica Bay, California; and 2) Vertical distribution patterns; determined through the analysis of benthic core samples (5.4 cm in diameter) taken at 3 stations, each representing a different sediment type (Figure 2 and Table 1). Six core samples from each station were sectioned at depth intervals of 2, 5, 10, 20, and 30 cm, and the organisms present in each of the sub-samples were identified and enumerated. The data on the number of species and individuals from each sample were combined to determine the numbers of replicate samples and the depth of penetration required to obtain species accounting for over 90 percent of the individuals at each station. Additional analyses were made to predict semi-quantitatively the combined effects of pressure waves, leakage, and surface disturbance on the organisms sampled (Word et al. 1976).

On the basis of these collections, certain criteria were formulated and used for selecting the most effective grab sampler. The more efficient devices are characterized by the following features:

1. Consistent sampling of the same surface area
2. Consistent sampling below the depth where the majority of species and specimens occur
3. Minimum surface disturbance caused by pressure waves
4. Minimum disturbance due to leakage

Horizontal Distribution Patterns

Horizontal distribution patterns of marine benthic invertebrates have been studied at many stations in a variety of manners (Greene, 1975; Smith and Greene, 1976; Boesch, 1973; Cassie and Michael, 1968; Fager, 1957). A common method of describing the biota at a benthic station is to collect replicate samples at a confined area until the asymptotic point of species acquisition has been reached. It has also been suggested that this point be used to indicate the number of replicates required to adequately describe a benthic station (Jones, 1961). However, the numbers of species present at a station is not the only important biological parameter. The species present at a station indicates that the two following conditions exist: 1) the species can tolerate the present environment, and 2) successful recruitment had occurred. This information does not indicate what organisms are most likely to be encountered in the area in large enough numbers or in sufficient quantities to be an available food source. Therefore, an additional important piece of information required is an estimate of the population size of the species present. Consequently we performed additional analyses on the relative population levels of the various species collected at 1 station, in addition to the analysis of the species acquisition curves.

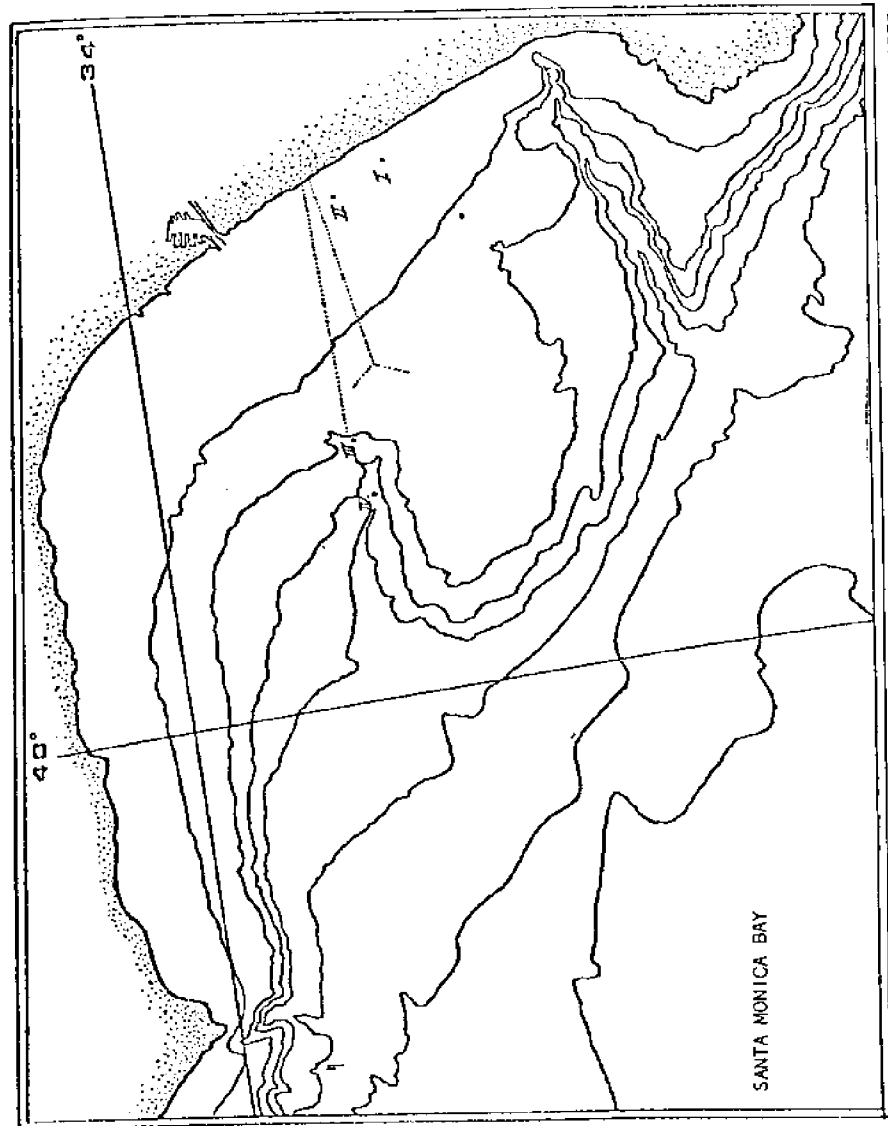


Table 1. STATION LIST: Comparison of grab sampling devices, Santa Monica Bay, December 1974 and March 1975

Station	Lat. N.	Long. W.	Description	Depth	Sediment Type
I	33°	118°	0.60 naut. mi., 048° T to end of El Segundo Pier. 1.75 km WSW, 0.75 km NNE from end of 1 mile sewer outfall (sampled in December and March)	12 Meters	Silty Sand
	54'	26'			
	15"	14"			
II	33°	118°	1.18 naut. mi., 135° T to end of El Segundo Pier	12.5 Meters	Outfall Sludge
	55'	26'			
	29"	42"			
III	33°	118°	5.25 naut. mi., 68.5° T to S. end of Marina del Rey break-water. Near end of 7-mile "sludge pipe" outfall	112 Meters	Outfall Sludge
	35'	30'			
	45"	25"			
IV	33°	118°	6.38 naut. mi., 0.70° T to S. end of Marina del Rey break-water. Edge of submarine canyon. (Sampled in December and March)	260 Meters	Silty Clay with Sludge
	55'	34'			
	30"	45"			

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We found that the asymptotic point of the species acquisition curve had been reached after 10 replicate samples had been taken at the shallow, sandy station. This indicated that 10 replicate samples were not adequate for capturing all those species that could occur at this station (Figure 3a). However, an additional analysis performed on these same samples showed that those new species added by each additional replicate did not account for a large proportion of the individuals. For example, the average of all second samples contained additional species accounting for only 10 percent of the individuals (Figure 3b).

Even sophisticated analytical techniques (eg. Smith and Greene, 1976), in which species or stations are clustered together based upon their relative similarities in distribution are most sensitive to those species that account for 90 to 95 percent of the total number of individuals sampled. Since the second sample yields species which account for 10 percent of the fauna, it would appear that for most purposes, a single sample or at most two will capture the majority of the fauna occurring at this type of station. It should be emphasized that different conclusions regarding the number of replicates needed can be derived from the type of analysis conducted, but it is our opinion that useful descriptive information is obtained with single 0.1 sq m benthic samples for at least some substrate types.

Vertical Distribution Patterns

The 3 stations sampled to study the vertical stratification of organisms depths within the sediment varied in sediment types and in sampling depths (from 12.0 to 260 m). In general, we found that although organisms burrowed

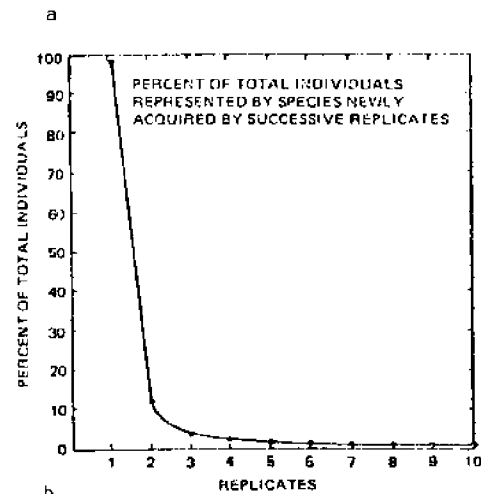
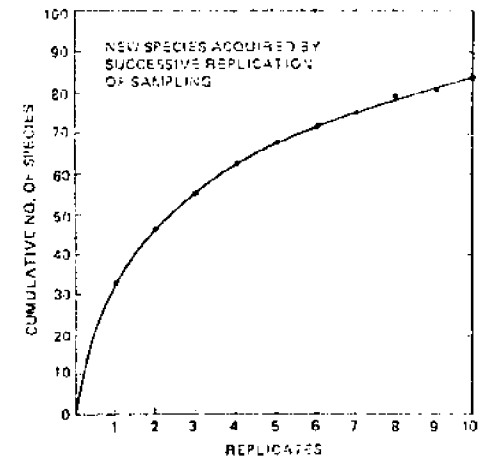


Figure 3. Species acquisition (a) and percent numerical acquisition (b) curves successive replication of sampling

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more deeply within the finer sediments, about 90 percent of the species and individuals were present in the upper 10 cm of sediment at all stations sampled (Figure 4).

Physical Functioning of Grab Samplers

Certain mechanical attributes of grab samplers affect their ability to capture organisms. Some of these are: pressure waves created by the sampler during its descent, leakage of sediment and animals from openings in the device, and disturbance of the sample once it is contained within the sampler (Holme, McIntyre, 1971).

Quantification of the effects of these mechanical variables is extremely difficult. We used information on the relative density or mass of organisms and their position vertically within the sediments to establish a useful index for measuring the relative effects of these mechanical sampling attributes on the organisms captured.

Two major groups of animals, microcrustacea and molluscs, are present in the upper 2 cm of sediment and are more susceptible to effects of mechanical variables than deeper burrowing animals (Word, 1976). The microcrustacea are less dense and as a group are more susceptible to losses resulting from pressure waves, leakage from the sampler, and disturbance of the sample than the heavier, more dense molluscs. As a result of these characteristics, a comparison of the abundances of these two groups of organisms will reflect the combined effects of the mechanical variables mentioned above.

Therefore, we determined the relative number of microcrustacea and molluscs collected by the different sampling devices at each station, and compared these results with our qualitative estimates of leakage, pressure wave effect, and sample disturbance based on direct field observations. Although a comparison of this type is unique and may be subject to various interpretations, the results did support the expected trends reflected in the qualitative physical sampling estimates (Table 2). This information showed that those samplers (Shipek, bar-tripped Van Veen, and Orange Peel) that we estimated to have the greatest combined amounts of surface disturbance, leakage, and pressure waves also yielded samples with the lowest microcrustacea-to-mollusc ratio. In contrast, samples taken with the Ponar, box corer, chain-rigged Van Veen, and Smith-McIntyre, had higher microcrustacea-to-mollusc ratios and little change as a result of the physical functioning of the sampler (Word, et al. 1976).

Selection of a Grab Sampler

Having considered the natural distribution of organisms in the sediment and the relative effects of certain mechanical parameters on organisms captured, we can select criteria for choosing the most effective sampler. The sampler should: (Table 3).

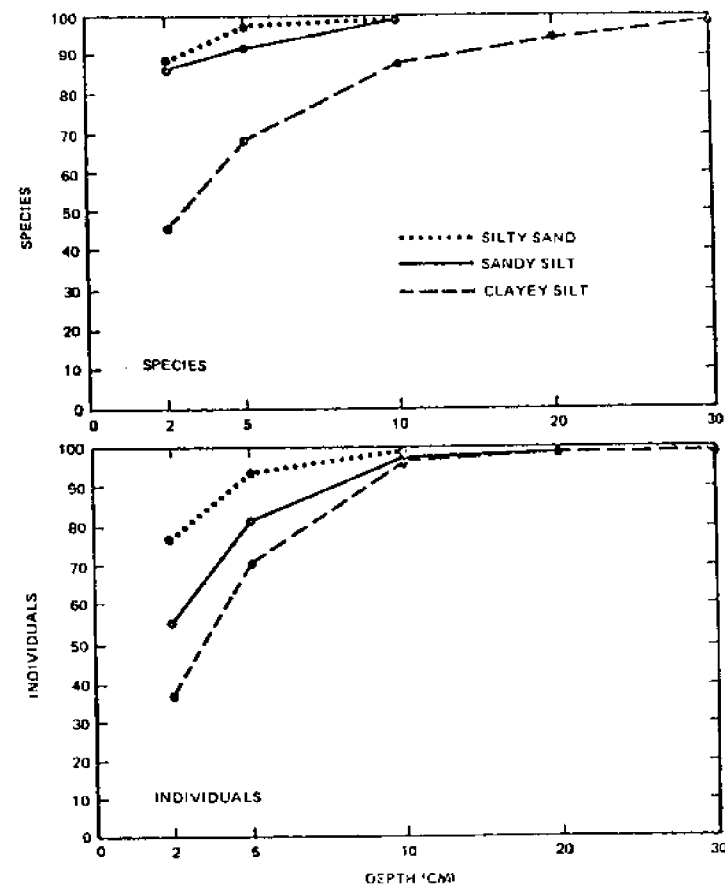


Figure 4. Percent of total benthic infauna species and individuals captured with increasing depth of penetration into sediments. Data from box corer samples.

Table 2. Comparison of grab samplers based on ratios of microcrustacea catch to mollusc catch and estimates of the amount of disturbance of the samples caused by the mechanical functioning of the device. The ratios have been ranked, with 1 representing the lowest and 5 the highest. The estimates have also been ranked, with 1 representing little or no effects from these factors. The number preceding the slash is the ratio rank, the number following the slash is the mechanical functioning rank.

Device	December 74			March 75	
	Silty Sand	Sandy Silt	Clayey Silt	Silty Sand	Clayey Silt
Ponar	5/4	5/4	5/5	NT*	NT
Box corer	4/5	4/5	4/4	NT	NT
Shipek	3/3	2/2	2/2	3/4	3/4
Van Veen 1	2/2	3/3	3/3	NT	NT
Orange peel	1/1	1/1	1/1	NT	NT
Smith-McIntyre	NT	NT	NT	4/5	4/5
Van Veen 2	NT	NT	NT	5/5	5/5

*NT = Not tested during this cruise.

Table 3. Criteria for a grab sampler and ratings of seven samplers commonly used off Southern California.

Criteria	Van Veen 2	Smith-McIntyre	Ponar	Van Veen 1	Shipek	Orange Peel	Box Corer
Little or no variation in amount of surface area sampled	Good	Good	Good	Good	Poor	Poor*	Good
Penetration to 10 cm	Good	Good	Poor	Good	Poor	Good	Good
Minimal amount of leakage	Good	Good	Good	Poor	Poor	Poor	Good
Little or no pressure wave created in descent	Good	Good	Good	Poor	Poor	?	Good
Low percentage of error resulting from variations in surface area covered or depth of penetration	Good, 25%	Good, 26%	Poor, 5-55%	Fair, 0-23%	Poor, 7-44%	Poor, 262%	Good, 0
Few operators required	Fair, 2	Fair, 2-3	Good, 1	Fair, 2	Good, 1	Good, 1	Poor, 3
High percentage of success in capturing samples	Good, 100%	Fair, 63-86%	Fair, 77-100%	Good, 100%	Poor, 20-100%	Poor, 48-100%	Good, 100%

*Barnard et al. (1959) states that area sampled with this device may vary as much as 50%.

1. Consistently sample the same surface area
2. Consistently sample deeply enough in the sediments to collect at least 90% of the organisms
3. Produce a negligible pressure wave
4. Have a minimum amount of leakage

We have found that 2 devices, the Shipek and the Orange Peel, samples a variable surface area. The area sampled by these 2 devices varied as much as 62% from that specified by their manufacturer (Table 3). Variations of this magnitude were considered unacceptable. In addition to the variation of the sampled surface area, the Shipek was not found to penetrate deeply enough in certain sediments. The Ponar did not vary significantly in area sampled, it did not however sample deeply enough within these sediments to capture the optimum number of species and individuals.

Two different types of Van Veen samplers were used during our tests: one was triggered by a chain-rigged mechanism; the second was triggered by a bar-tripped device. The chain-rigged Van Veen, in addition to having a different tripping mechanism, also had screens on the upper surface of the sampler. These screens served to decrease the pressure wave in front of the sampler during its descent. The bar-tripped Van Veen was found to have a large amount of leakage due to inadequate fitting of its parts; it had no screened upper surface so that its pressure wave was greater than that observed with the chain-rigged Van Veen. For these reasons, in addition to the fact that the bar-tripping mechanism is less safe to use, the bar-tripped Van Veen was considered unacceptable.

Eliminating these 4 devices (the Shipek, Orange Peel, Ponar, and bar-tripped Van Veen) leaves 2 samplers for consideration. The chain-rigged Van Veen and the Smith-McIntyre samplers were both found to give excellent penetration within the sediments, the surface area sampled did not vary, they had minimal leakage, and their upper surfaces were screened to decrease pressure waves during descent. In addition, there was also a high degree of success in taking samples with both devices. Comparison of the respective microcrustacea-to-mollusc ratios showed that the chain-rigged Van Veen was slightly more effective at capturing surface-dwelling microcrustacea than needed for Smith-McIntyre. In addition, the chain-rigged Van Veen was a simpler device to use, requiring 1 less operator than needed for the Smith-McIntyre, and also had a higher degree of success in taking samples at some of the deeper stations. Therefore, we selected the chain-rigged Van Veen as the most effective benthic grab sampler.

Comparison of Major Categories of Benthic Samplers

As described in previous sections, the different sampling devices obtained different relative abundances of organisms based upon their penetration within the sediment and also upon the surface area sampled.

Comparisons of the 3 major categories of benthic samplers (benthic grab devices, deeper penetrating burrowers or box coring devices, and the shallow penetrating epibenthic sleds) will be discussed in this section.

Benthic grab samplers, (eg. the chain-rigged Van Veen) efficiently sample the infaunal organisms to a depth of approximately 10 cm in most sediment types. These samplers are the generalist, that is they can capture the majority of different animals living on and in the sediments but they cannot be used to selectively sample the deeper dwelling organisms or those that live on the uppermost surface of the sediment.

To obtain information on organisms living deeper in the sediment a different type of sampling tool should be used such as the anchor dredge or the box corer. The box corer is driven deeply within the sediment as a result of its weight and momentum on being lowered to the bottom. These samplers are very effective at capturing organisms to depths of about 40 cm. The anchor dredge samplers are driven deeply within the sediment as a result of the force of the vessel pulling against a lever which forces the dredge into the bottom, also to depths of about 40 cm. However, both of these samplers are typically small in sampled surface area and as a result tend to miss some of the more mobile and sparsely distributed invertebrates.

The epibenthic sleds collect material from a minimal depth (about 1 cm) of penetration over a wide area of sampling, and therefore are integrative samplers. These devices will collect more surface dwelling animals and those mobile invertebrates such as the microcrustacea that are able to escape the more commonly used benthic samplers because they are towed over larger areas and are more likely to encounter and capture these animals.

In the final analysis, we have to consider what we want to learn from our sampling. After looking at the stomach contents of the fish species of interest, we can get an idea of the types of species, the size categories of the food, and whether it is stationary infauna, or a movable epifauna. If a comprehensive investigation of numerous fish is required, then a more generalized approach is necessary, and the use of a Van Veen sampler is advisable. If, on the other hand, the investigation centers around species of fish that feed primarily on epifauna or that feed on deep burrowing forms of invertebrates, then an epibenthic sled or deep-burrowing sampler might be preferable.

In this paper we have presented information on benthic sampling devices, the organisms they collect, and how these samplers can be used to assist investigations into the feeding habits of fish. It is hoped that further research and collaboration between fishery and invertebrate biologists will broaden our understanding of the use of these tools in investigating faunal relationships in the marine environment.

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FIELD METHODS FOR SAMPLING DEMERSAL FISH POPULATIONS AND OBSERVING THEIR BEHAVIOR

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While populations of shallow water organisms can be observed directly by divers using SCUBA equipment, deepwater demersal and benthic organisms must generally be sampled by remote methods. A number of sampling methods can be used to obtain information on the populations and behavior of demersal organisms. The objective of this paper is to describe the relative selectivity of these methods and to describe the types of methods that are appropriate for obtaining different types of population and behavioral information on these organisms.

Methods for sampling the larger organisms living near the bottom fall into two major categories--capture methods and observational methods. Capture methods result in the organism being brought to the surface, dead or alive, whereas observational methods allow the organism to remain alive and relatively undisturbed in its natural environment.

Capture methods used by the Coastal Water Research Project include small otter trawls and hook-and-line methods. The otter trawls used in our studies have a 7.6 m-(25 ft-) headrope and have a 1.25 cm-(0.5 in) cod-end liner; these trawls are generally towed at 4.6 km/hr (2.5 kn) along isobaths (SCCWRP 1973 a; Mearns et al. 1976). We have used 2 hook-and-line methods to sample demersal soft-bottom fishes (Allen et al. 1975); (1) We laid a 100-hook setline across the bottom to catch the species within the vertical range of the trawl that might avoid the net; and (2) we fished schools of fish located by sonar in the general vicinity of the trawl stations with rod and reel to collect species that either dwell in the water column above the vertical range of the trawl or are highly clumped and therefore might be frequently missed by the trawl.

We have also used a number of observational methods including direct observations by divers and remote observations from free-vehicle cine cameras and television cameras. Divers have photographed marine organisms around outfall pipes in Santa Monica Bay to 100 m using SCUBA equipment in shallow water and two-man submersibles in deep water (Allen et al. 1976). We have

used a baited free-vehicle automatic cine camera (Shutts 1973) to observe marine organisms attracted to bait at depths to 350 m on the Palos Verdes Shelf (SCCWRP 1973); this battery powered camera is left on the bottom for 24 hours where it photographs water around the bait for 15 seconds at intervals of 30 minutes or 1 hour. In addition we have used television to survey demersal organisms and to observe the behavior of these organisms with respect to the otter trawl (Allen 1975).

Relative Selectivity of Methods

We have conducted quantitative surveys of demersal organisms in Santa Monica Bay using 4 methods (otter trawl, rod-and-reel, set-line, and photographs taken by divers; Allen 1975). Thirty-one species of fishes were observed in photographs of the discharge pipes in Santa Monica Bay (Table 1). Rod-and-reel sampling on soft-bottoms yielded 15 species, and setline sampling yielded 11 species. A total of 23 species were taken by both hook-and-line methods, with only 4 species in common between the 2 methods: spiny dogfish (*Squalus acanthias*), sablefish (*Anoplopoma fimbria*), white croaker (*Gonyonemus lineatus*), and Pacific sanddab (*Citharichthys sordidus*). In contrast, 87 species have taken in Santa Monica Bay by otter trawl surveys conducted by the Coastal Water Project. Photographic and hook-and-line methods yielded only 2 species that were not taken by otter trawl in this area: Pacific hagfish (*Eptatretus stouti*), taken by setline, and an unidentified ronquill (*Rathbunella* sp.) observed in the photographs. Both species have been taken by otter trawl elsewhere. More species were taken per station by otter trawl (10.4 ± 0.4) than by rod and reel (3.6 ± 0.5) and setline (2.3 ± 0.7) methods, although time spent on the station varied considerably (otter trawl, 10 minutes; rod-and-reel, 4 hours; and setline, 1 hour).

Setlines were most effective at sampling wide-ranging species that forage on the bottom; the setline did not sample rockfish populations. Rod-and-reel fishing into schools located by sonar was effective at catching species such as rockfishes that range higher off the bottom and are generally clumped. Otter trawls were most effective at sampling small bottom fishes such as flatfish, sculpins, and small rockfishes.

Although we caught a proportionately greater number of large fishes with the hook-and-line methods than with the otter trawl, hook-and-line catches usually fell within the size ranges sampled by otter trawl. The hook-and-line catches showed that more large bottom-feeding fish (mostly spiny dogfish) occurred in shallow water than was indicated by otter trawling.

Photographic sampling was effective at showing the species (particularly invertebrates that cannot be taken by hook-and-line) found on hard substrate areas (such as outfall pipes) that cannot be trawled. This method was also very useful in showing where the organisms are living--information of this sort is almost always lost by capture sampling techniques. The disadvantages of photographic sampling include the difficulty in making accurate identifications of organisms observed and in getting size estimates on some species.

Table 1. Characteristics of fish surveys conducted in Santa Monica Bay, California, by the Coastal Water Research Project using different sampling methods, 1971-1975 (from Allen 1975)

Characteristic	Hook and Line			Submersible Photographs
	Otter Trawl	Rod and Reel	Set Line	
Total Samples	124	16	13	399
Depth Range (m)	20-190	20-190	20-190	10-100
Habitat	Soft	Soft	Soft	Pipe
Time Spent on Station	10 min.	4 hours	1 hour	-
Total Species	87	15	11	31
Species/Stations (Mean \pm Std. Error)	10.4 \pm 0.4	3.6 \pm 0.5	2.3 \pm 0.7	-

Video tapes of otter trawls in action suggested that many of the fishes and invertebrates encountered escape the nets. Larger fish species (such as the Pacific angel shark, *Squatina californica*) have been observed to swim into the net, become entangled and later swim out before the net is retrieved. Water column species often swim up and over the net. Smaller bottom species (such as speckled sanddabs, *Citharichthys stigmaeus*) swim slightly off the bottom in front of the net, trying to outswim it. Turbots (*Pleuronichthys* sp.), which are often buried, jump vertically from the bottom when the net approaches, only to fall within it. Sea pens and tube-dwelling polychaetes, which have a certain degree of attachment to the bottom, are not well sampled.

Sampling methods for different behavioral and ecological information

Different sampling methods yield different types of behavioral and ecological information including the presence of large predators in the area and the diel activity patterns, foraging behavior, and food preference of different species.

Large predators--large fishes that prey upon small species normally caught in small otter trawls are not frequently captured in these trawls. In part, this is due to their ability to outswim the net at the speeds towed, as mentioned above. In addition, however, this is also due to the low densities of their populations. Large bottom-foraging species generally require a larger foraging space (to obtain enough large food items) than do smaller species and thus occur in low densities. Information on the presence of these species in an area can be obtained by attracting them to a bait. The presence of large Pacific sleeper sharks (*Somniosus pacificus*) in deep water in southern California was not known until they were photographed by baited free-vehicle cameras (Isaacs and Schwarzlose 1975). We have found higher densities of spiny dogfish (*Squalus acanthias*), swell shark (*Cephaloscyllium ventriosum*), and sable fish (*Anoplopoma fimbria*) in frequently trawled areas than was indicated by the trawls. Set-lines also indicated higher densities of spiny dogfish on the shelf than was indicated by trawling.

Diel activity--differences in diel activity among fishes in the field have been observed by divers using SCUBA equipment in shallow water (Starck and Davis, 1966; Hobson, 1965, 1968, 1974), but diel activity differences among deep water species have been less frequently observed. Baited free-vehicle cameras left on the bottom for 24 hours (taking 15-second movies every half hour or hour) have shown diel differences in several species (SCCWPP 1973b, 1974). At a 23-m station senorita (*Oxyjulia californica*), blackeye goby (*Coryphopterus nicholsi*), and blue rockfish (*Sebastes mystinus*) were active only during the day while treefish (*Sebastes serriceps*), copper rockfish (*Sebastes caurinus*), and swell shark (*Cephaloscyllium ventriosum*) were active only at night. Television cameras dropped to the bottom at night have shown rattfish (*Hydrolagus collieri*) actively foraging and individual pink seaperch (*Zalambius rosaceus*) resting on the bottom. Trawls towed on the same stations during the day and at night have shown few major catch differences, presumably because the trawl does not discriminate between species that are active or inactive (generally seeking refuge on or slightly buried in the bottom). Major differences include increased abundances of spotted cusk-eel

(*Chilara taylori*), rattfish (*Hydroloagus collieri*), and northern lampfish (*Stenobrachius leucopsarus*) at night. Cusk-eels generally burrow into the sediment during the day and are thus unavailable to trawls, whereas the other species probably move into the trawl areas from deeper water at night.

Foraging behavior--observational and hook-and-line techniques have shown differences in foraging behavior among demersal fishes. Swell shark, spiny dogfish, sablefish, treefish, copper rockfish, and Pacific sleeper shark have been observed cruising above the bottom searching for food items on the bottom in baited camera films, while California scorpionfish (*Scorpaena guttata*) have been observed to ambush prey from the bottom and shortbelly rockfish (*Sebastes jordani*) to actively pursue small nektonic organisms in the water column. Large sablefish will bite into a large, dead bait fish, and spin their bodies until a chunk of flesh is torn off (Isaacs and Schwarzlose 1975) while Pacific hagfish (*Eptatretrus stouti*) will slide a knot down their bodies, forcing slime onto the bait and thus protecting the food item from competitors such as sablefish. Video tapes have shown spotted cusk-eels cruising slowly above the bottom, dragging their barbels along the bottom. The two hook-and-line methods demonstrated a difference in foraging behavior among the species taken; setline catches were dominated by wide-ranging bottom foragers while rod-and-reel catches were dominated by water-column foraging rockfishes such as bocaccio (*Sebastes paucispinis*) and vermillion rockfish (*Sebastes miniatus*).

Food preferences--by using different types of bait, some indication of food preferences can be determined. Whole Dover sole (*Microstomus pacificus*) used as bait in the baited camera study was consumed in one-fifth the time that stripe-tail rockfish (*Sebastes saxicola*) was consumed. Presumably the spines on the rockfish make the species less desirable to predators than Dover sole, which has no sharp spines. Spiny dogfish, sablefish, and Pacific hagfish were the only species observed eating the bait. Capture methods, of course, generally provide the best food habit information because the stomach contents of the fishes taken can be examined.

Conclusions

Of the 3 general methods (otter trawl, hook-and-line, and observational techniques), otter trawls are probably the best method of sampling small bottom fishes on soft-bottom areas--the trawls yield the greatest number of species and numbers of individuals from which additional measurements and analyses can be made. Small otter trawls probably do not efficiently sample large, fast-swimming species or species that burrow in the sediment. Large species found over soft-bottoms are often more effectively taken by hook-and-line techniques. Of these, setlines more effectively sample large, wide-ranging bottom feeders, which may escape the net; fishing by rod and reel in schools located by sonar is a more effective way to catch the highly clumped rockfishes that may be missed by chance in a trawl. Photographic and hook-and-line methods are both effective at sampling rocky bottom areas.

Sampling methods such as otter trawl or hook-and-line fishing allow accurate identification of specimens and measurement of size, examination for diseases, and analysis of stomach contents, although they give little information as to

the behavior of the organisms in their natural environment. Photographic sampling gives more information on the behavior of the species in their natural environment, but identifications can be less accurate, and fewer measurable data are gathered. A combination of sampling methods then would yield the most behavioral and ecological information on deepwater demersal fishes.

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SAMPLING INTERTIDAL SALT MARSH MACROBENTHOS

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My thesis work is the analysis of the community ecology of the benthic invertebrates of the salt marsh-mudflat system at the mouth of the Skagit River in Puget Sound, Washington. The river delta forms Skagit Bay, a 25-km² expanse of sand and mudflats ringed with salt marshes. Most of the perimeter of the bay is diked. Numerous small tidal streams cut deeply through the emergent marsh, spreading out and becoming shallow on the unvegetated flats. During the spring and summer, the tide streams contain large numbers of predatory fish, particularly starry flounders (*Platichthys stellatus*), staghorn sculpins (*Leptocottus armatus*), threespine sticklebacks (*Gasterosteus aculeatus*), and the juveniles of chum (*Oncorhynchus keta*), chinook (*O. tshawytscha*), and pink (*O. gorbuscha*) salmon. As part of my study, I am attempting to determine the impact of juvenile salmonid predation on the populations of the benthic intertidal invertebrates.

In planning the benthic sampling phase of my study, I had to consider six major problems common to any soft-bottom sampling program: (1) core depth, (2) screen size, (3) size of plot (or length of transect), (4) frequency of sampling, (5) core area, and (6) number of samples per plot or transect. I wanted to select a sampling procedure which would allow me to sample as many of the prey species as possible and to provide enough individuals per sample to make accurate population estimates and reasonably powerful statistical tests. I am reporting here the processes by which I chose my techniques for benthos sampling.

Core Depth

I took 10 cores, separating them into three depth intervals: 0-4 cm, 4-8 cm, and below 8 cm. The total depth of each core was 15 cm. The results are shown in Table 1.

Table 1. Vertical distribution of benthic Invertebrates. Data from 10 cores were pooled.

	0 - 4 cm	4 - 8 cm	Below 8 cm
Total number	966	41	26
Percent	93.5	4.0	2.5

Since over 97% of the animals occurred above 8 cm, I decided to sample only to that depth.

Screen Size

Screen size is a trade-off between efficient sampling and efficient laboratory treatment of the samples. I wanted to sample as many of the smaller species, including juveniles, as possible and yet pass enough sediment and detritus to expedite sorting. I tried several mesh sizes ranging from 4.0 mm to 0.149 mm and found that the smallest mesh sizes, though very efficient at retaining most juveniles, passed very little sediment. I decided to choose that mesh size which would sample a high proportion of the juveniles of two species of amphipods, *Anisogammarus confervicolus* and *Corophium salmonis*, which occurred frequently in stomach contents of juvenile salmonid fish from the lower Snohomish River. The results of successive screenings of four samples containing these amphipods through three mesh sizes are shown in Table 2.

Table 2. Efficiencies of three mesh sizes in retaining the amphipods *Corophium salmonis* and *Anisogammarus confervicolus*. Data from four cores were pooled. Both adults and juveniles were present.

Retained by 0.99 mm	<i>C. salmonis</i>		<i>A. confervicolus</i>			
	0.297 mm	0.175 mm	0.99 mm	0.297 mm	0.175 mm	
Total number	136	100	0	142	56	0
Percent	57.6	42.4	0.0	71.7	28.3	0.0

The 0.197 mm mesh retained 100% of the amphipods. Since it passed much of the substrate, I chose this sieve.

Size of Plot

In order to decide the scale over which samples are to be taken, some knowledge of the scale of patchiness is required. This is a complex question and

I had little time to consider it in depth. In the course of other preliminary work, I had taken several sets of samples over variously sized areas. Since samples taken over an area of 3 to 4 square meters had shown approximately the same species composition as samples taken over several hundred square meters, I assumed that the dominant patch size was probably less than several meters. I chose to locate samples along a 15-meter (50 feet) line, since this was a convenient length along which to sample. It was small enough to sample quickly, but large enough to prevent superimposing successive samples on previous sample locations.

Frequency of Sampling

To determine population parameters such as reproductive times, seasonal trends in abundance, and growth over time, sampling must be done at close intervals relative to the life span of the individual organisms. Since most of the invertebrates I am sampling are small and short-lived (on the order of a year), I decided to sample monthly.

Core Area

As a result of the extremely dense populations of macrofauna on the mudflats, I found that laboratory processing of standard 0.25-m² samples was too slow. I also tried plastic tubing which took cores of 38.5 cm², but with the screen size I wished to use (0.297 mm), this still sampled so many animals that it was impractical to take more than 2 cores per station. In general, unless accuracy and precision are sacrificed, it is better to decrease sample size and increase the number of samples. This provides a better idea of the variance of the population.

In order to justify my choice of a smaller corer (I wished to use 5.07-cm² plastic tubing), I took a series of 18 samples in which I nested small cores inside the large cores. Comparing the species list of the large cores with that of the small cores, I found that every species sampled by the large cores was also sampled by the small cores. Apparently no species was so rare that the small cores missed it. Also, no species was better able to escape from the small cores.

Edges of corers passing through substrate trigger avoidance responses in many animals, or destroy and push down animals that should have been included in the core. Since the ratio of circumference to area is larger for a small core than for a large one, this edge effect causes smaller cores to underestimate invertebrate abundances. I found that, for the 5 most abundant organisms sampled, the opposite was true; the large cores underestimated abundances. I believe that this was due to the greater difficulty in sorting the material from the large cores. Apparently any edge effect was small compared to this effect. Smaller samples often cause an increase in variance. However, I found that for the 5 most abundant species, the variances calculated from the small cores were never significantly greater than those calculated from the large cores (Moses Ranklike Test for Dispersion-Medians Unknown or Unequal; $\alpha = .05$).

Considering the above results, I decided the 5.07-cm² core was appropriate for my sampling program.

Number of Samples per Plot or Transect

To decide on the number of samples per plot, I took 2 sets of samples. First, I analyzed 20 cores and plotted the number of species sampled versus the number of cores in order to find the sample size at which the curve reaches an asymptote. Since the shape of the curve depends upon the sequence in which the cores are plotted, I randomly chose 3 sequences. The results are shown in Figure 1.

Since this habitat is characterized by a small number of very abundant species, the asymptote is shifted strongly toward the left. The first 2 or 3 cores sampled nearly two-thirds of all species. In all cases, the first core sampled the 5 most abundant species, which represent approximately 95% of all the individuals sampled.

I took a second set of samples to find the smallest sample size at which means and variances would stabilize. I collected a series of 18 cores from a single plot and calculated the means and variances for randomly chosen unequal sample sizes. Shown in Table 3 is a summary of results obtained when I compared a 5-core sample with a 13-core sample. For the 5 most abundant species, the medians were equal (Mann-Whitney U-test; $\alpha = .05$).

Table 3. Means and variances of the 5 most abundant species sampled in two unequal samples from the same plot.

SPECIES	MEANS		VARIANCES	
	Small sample (5 cores)	Large sample (13 cores)	Small sample (5 cores)	Large sample (13 cores)
<i>Corophium salmonis</i>	18.6	13.5	58.3	114.5
<i>Manayunkia aestuarina</i>	8.4	7.8	6.3	16.8
<i>Pseudoamphiteteis neglecta</i>	7.8	5.2	24.2	13.0
<i>Anisogammarus confervicolus</i>	27.6	24.2	29.3	180.5
<i>Macoma balthica</i>	2.4	1.8	5.3	1.4

For 2 of the 5 species, *Macoma balthica* and *Pseudoamphiteteis neglecta*, the variances calculated from the small sample were significantly larger than those of the large sample. I felt that since neither of these species had been found in juvenile salmon stomachs, 5 cores was an adequate sample size for the purpose of this study.

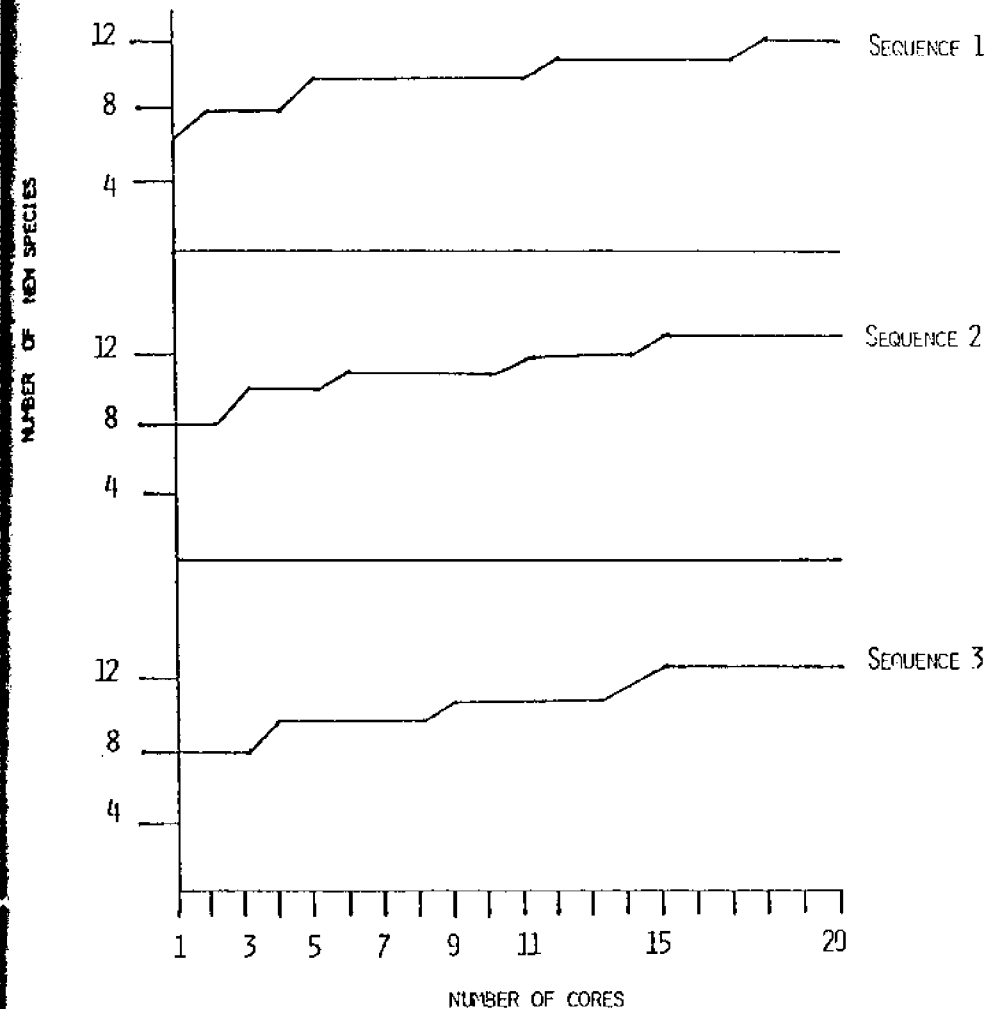


Figure 1. Number of species versus number of cores. The number of species (ordinate) is cumulative, but only increases as new species are encountered. The 3 plots represent 3 different randomly chosen sequences of the same 20 cores.

FEEDING HABITS AND SELECTIVITY OF PLEURONECTIDS ON THE OREGON SHELF:
A SUMMARY OF RESEARCH IN PROGRESS

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The purpose of this on-going study is to investigate feeding habits of fishes associated with either Dover or English sole. In particular, 3 aspects of feeding habits in each fish community are being considered: 1) vertical distribution of macroinfauna within the sediment (as sampled with a box corer), and these organisms' availability as fish food 2) diel periodicity of pleuronectid feeding, and 3) selectivity of food species and sizes by pleuronectids.

The sampling plan was designed to determine what potential food "choices" were available to demersal fish. What invertebrates does a fish actually "see" in its environment? To assess the benthic macrofauna, we used a 0.1-m² Bouma box corer and a 0.25-m² Hessler-Sandia box corer. To sample macroepifauna, we used an epibenthic sled. To collect fishes from the same area, we used a 3-m beam trawl.

Two stations were intensively sampled: SG-27 (44°26.0'N, 124°14.3'W, 62 m deep, sand bottom), an area of high catches of Pacific sanddab and English sole; and SG-29 (44°05.0'N, 124°35.0'W, 112 m deep, silty sand bottom), an area where Dover sole is abundant. Samples, taken day and night, included 18 beam trawls, 4 epibenthic sled hauls, and 20 0.1 m² box cores at each station.

For studies of vertical distribution of macroinfauna, cores were sectioned at 1-cm intervals for the first 10 cm, 2-cm intervals for the next 10 cm, and 4-cm intervals for the remainder of the core. Each section was then washed through a 1-mm sieve screen. If the number of sections were reduced, artifacts, contamination, and sample loss would probably decrease.

Usually, all fishes from a trawl were preserved. To insure rapid preservation of stomach contents, formaldehyde solution was injected into the body cavity with a size 16 hypodermic needle. Whole fish were then stored in formaldehyde solution.

Problems arise out of the scope of the sampling program. The area bounded by trawl tracks and box cores was small (6.5 km² for SG-27; 14.8 km² for SG-29), and each station was occupied only 30 hours. Patchiness effects may be present, since areas of box coring and beam trawling overlapped but did not coincide.

DISCUSSION: SESSION 2; SAMPLING OF BENTHIC PREDATORS AND PREY:
HOW DO DIFFERENT SAMPLERS AND SAMPLING TECHNIQUES
ALTER OUR IMPRESSIONS OF THE BENTHOS?

Steve Obrebski mentioned that while the benthic sampler used is important, the method by which the sample is processed is just as important. For example, sieving a fresh sample might allow the slimy, smaller organisms to slip through the mesh while preserved animals are stiffer and less likely to pass through. He further mentioned that a sieve size of 0.5 mm may not have a great efficiency for recovering numbers of organisms.

Jim Allen presented a brief overview of the Southern California Coastal Water Research Project (SCCWRP). The group was established to study the ecology of the Southern California Bight and the sources and effects of pollutants in the area. The funding comes by way of the southern California counties.

Regarding SCCWRP's use of the underwater towed camera system, Bob Feller asked if the group had ever reversed the direction of the cameras so that it recorded the fish's behavior when approached by the net. Allen said that instead of that they had attached it to the bridge to observe fish behavior. He agreed that some fish are able to escape the net.

Bruce Hillaby wondered if any of the attendees used the flotation method for initial sorting of benthic samples. Jim Smith replied that in his case the substrate was too full of organics so that by the time one had the proper concentration of sugar (or other materials) everything in the tray floated. Jack Word added that flotation or elutriation methods are unsuitable for molluscs. Hillaby then wondered if a combination of flotation and hand-picking might work. Word added that he isn't too crazy about flotation techniques. One technique that is coming into wider use is the elutriator or "bubbler." Air and water are jetted up a column containing the sample, forcing the lighter animals over the top of the column onto a collecting screen. While this method is adaptable to sand and gravel substrates, it does not work for vegetation. None of the attendees had any good system for sorting animals from vegetative material.

Taivo Laevastu suggested that benthic studies should be examined to see if

researchers could reduce the specificity of invertebrate identifications. He stated that working on benthic samples is very time-consuming and we should examine the goals of our projects to see if they can be achieved with less time spent. This time could then be devoted to other things. Jim Smith was asked how he avoided disturbing the area in which he takes core samples. He replied that he tries to prevent taking cores within 3 cm of a previous core. Disturbance of the sampling area is difficult to avoid since one is always kicking up sand and mud, which are then carried by currents to other parts of the sampling area.

Referring to an earlier suggestion of using exclusion cages, Obrebski asked if any of the benthic organisms were mobile. Smith replied that he believed some of the tube-dwelling amphipods and polychaetes moved around but he wasn't absolutely sure. Others in the room agreed that these animals do leave their burrows for varying periods of time. Obrebski then commented that exclusion cages might not be an effective tool. Smith replied that he was aware of the problems and hoped to come up with some correction factors.

Obrebski then mentioned that a student, Ralph Johnson, studied Tomales Bay and found that benthic communities are often associated with certain sediment types. Therefore, the species diversity of a particular benthic sample is dependent on the patchiness of the substrate. Some organisms are associated with several sediment types while others are more specifically associated with one or two. One might consider sampling the surrounding sediment along with the fish and benthic invertebrates.

Feller asked how Oregon State University's samples are preserved, to which Wendy Gabriel replied that they are washed through a 1-mm mesh screen, put in formalin, then changed to alcohol.

Word wondered about the value of geological analysis of sediment under the current technique of dropping the sediments in hydrogen peroxide and boiling out the organics. He claims that the invertebrates don't see that kind of substrate, they see the detritus, vegetation, etc. Currently, however, there is no better technique. It might be worthwhile for someone to work on a new technique for sediment analysis.

Gabriel commented that "...in some instances, if you can identify sediment from the geological point of view, that will give you some clues to the dynamics of the water mass movement in that area." For example, different grain sizes might be found behind banks, in areas of upwelling, associated with deep water currents, underwater transport systems, etc. These things may affect the short scale distribution of species.

Obrebski pointed out that Bob Whitlash of Woods Hole recently completed a thesis very pertinent to this question of distribution of infaunal organisms, mostly polychaetes, and their relationships to sediments. He took cores very carefully from intertidal areas, froze them, and very carefully sectioned them. Then he measured the three-dimensional positions of the organisms, sampled the sediment around them, and the sediment in

their guts. Finally, he measured the overlap in particle size distribution between species and at the same time determined, by nearest neighbors statistical technique, the differences in spatial configuration. The general result was that those species with the highest diet overlap are least likely to be nearest neighbors. For example, two spionid polychaetes, one large and one small, occur in similar areas. When they do occur near each other, the larger one whips with its palps and tears the palps from the smaller one. Small spionids, when close to large spionids, move away and therefore are not nearest neighbors.

Joseph Durkin mentioned that he had observed Pacific sanddabs feeding on fish in the area of the mouth of the Columbia River. Allen agreed that he had observed similar behavior in California but Gabriel had not looked at enough fish to say yet. Durkin also had noticed an inshore/offshore migration of some demersal fishes. For the moment, not much discussion was heard on this subject (it was brought up a little later).

Glen Van Blaricom brought up the subject of core samples once again and said that a fellow student at Scripps recommended laying them on their sides after collection to avoid traveling by the animals, thereby affecting their normal spatial distribution. If an animal responds to gravity, it can without changing its vertical position. Word said that they set the samples in dry ice and freeze them as fast as they can. Feller mentioned that freezing can "pop" some of the soft-bodied animals, which ruins them for later identifications. Word suggested capping the sample tightly but agreed that frozen samples are difficult to identify. Another problem arises with large or long animals. When the core is sectioned, these animals may appear in several of the subsections. How does one place the animal? This should be standardized although many people now use heads as indicators of total body placement.

Sandy Lipovsky mentioned a problem with polychaetes falling apart after being stored in the stomachs. The combination of digestive fluids and formalin is dynamite to soft-bodied animals. Word agreed but Gabriel uses a technique whereby the guts themselves are not injected but rather the stomach cavity, missing the gut. The entire fish is then stored in formalin in case a student later decides to do a morphometric study. They use a 10% formalin and seawater preservative. Upon hearing that, Word recommended that they lower the strength to 5%, then rinse the samples and convert to alcohol. Gabriel mentioned the volume of fish and lack of time for conversions to alcohol.

A discussion of buffers followed. Feller mentioned Hexamethaline tetramine which works fine but is expensive. Word expressed the views of many by saying that Borax works just fine and is cheap. There also is some natural buffering by seawater, which also reduces the osmotic change experienced with formalin-freshwater mixtures.

Laevastu discussed that in many ways epifauna may be more important as fish food than infauna. Little quantitative information is known about epifauna such as seasonal migrations and year-to-date changes in abundance.

Looking at seasonal migrations of some demersal fish, we assume that it is related to something physical as temperature, rains, storms, etc. Perhaps it is the epifauna that is sensitive to environmental signals and the demersal fish, in turn, follow the epifaunal food sources. Gabriel came back with another theory to explain some of the inshore/offshore migrations. Perhaps during storms, the fish move offshore, sacrificing their food rations for stability, especially if their habitat has been in relatively shallow water. In colder water, the metabolic requirements would be lower and the fish could afford to reduce the food ration. This may be more desirable to a fish than being covered up every few days by storm actions.

Simenstad returned to the problem of sampling epibenthos by explaining his problem of trying to sample in an area not suitable for an epibenthic sled. Some of the problems are shallow water, nursery areas, uneven bottoms, eelgrass, etc. His group is experimenting with an epibenthic pump which, when improved, may be a very useful sampler. It captures the juveniles of some invertebrates as well as the eggs of harpacticoids and gammarids. Obrebski wondered if pumping through a rotor might crush the organisms. The answer was yes but some pumps have collection chambers ahead of the rotor unit and some newer models are diver-held "vacuum"-style. The vacuum pumps are not too good in deep water, however.

Word introduced a new subject by stating that sometimes it is interesting to go beyond identifying animals by sorting them by sex composition. As an example of this, he stated that some male cumaceans and ostracods are pelagic dwellers while the females are benthic. If one examines a stomach full of males (cumaceans and ostracods), one can assume that the fish had fed up in the water column. If the stomach is full of females, that would indicate that the fish had been feeding along the bottom.

A short discussion of *Crangon* spp. ensued. Out of that came that the diet can be polychaetes, oligochaetes, nemertean, etc. These are all soft and can be ripped by the large *Crangon* spp. chelae. Another point was that juveniles and adults often occur in different depths of water.

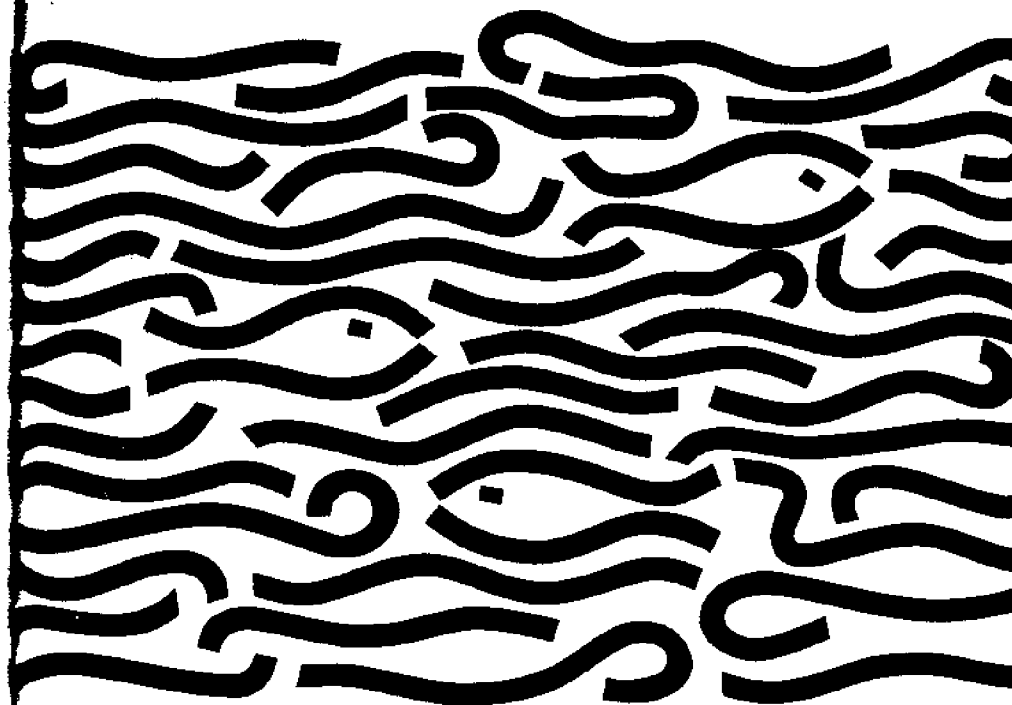
Laevastu wondered what causes separation of generations in terms of depth and area. Perhaps juvenile fish are found in shallower water to avoid cannibalism or perhaps it is a function of temperature. The warmer temperatures may optimize growth rates and conversion rates. Another idea was that perhaps the juveniles are more euryhaline than adults of the predator species and can therefore enter territory that the predators cannot. Obrebski cautioned that while we can show experimentally or otherwise that a fish is optimizing his existence, we shouldn't base that observation on a single factor. For example, photoperiod may be a better indicator of time of year than temperature. We also shouldn't worry if our theories will become out of date in future years. As long as our ideas are better than those that have existed to date, that is good and we ought to publish them.

The final discussion returned to epibenthic sleds and the problems involved

trying to quantify the data. It isn't possible since the area covered can't be measured and we don't even usually observe how the sled is traveling or if it has tipped on one runner, or if it is digging into the sand and sampling benthic invertebrates, etc.

SESSION 3

**LABORATORY
PROCEDURES AND
IDENTIFICATION**



SESSION LEADER:
Robin LeBrasseur

PARTICIPANTS:
Tony Phillips
Beverley Kask
John Johnson
Julie Ambler
Catherine Terry
John P. Ellison

A LABORATORY METHOD FOR THE ANALYSES OF FISH STOMACH CONTENTS

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During the 1969-1974, numerous studies were carried out on the estuaries and open waters of Georgia Strait and the west coast of Vancouver Island. These included the collection and analysis of the stomachs of juvenile salmonids, herring, stickleback, flatfish and many other species. Often these were caught in large numbers and it became necessary to develop a rapid method which would produce results comparable between areas and from year-to-year. In designing the laboratory techniques, we attempted to incorporate sufficient detailed analysis to allow a variety of treatments of the data, while maintaining sufficient speed and consistency. We endeavoured to keep subjective treatments to a minimum and establish a standardized approach that would reduce the variation between technicians. Concern as to the food sources of such commercial species as salmon resulted in the need to know not only the gross weight or numbers of diet items, but also to differentiate those found in the estuaries and nearshore areas from the pelagic sources. We therefore required information on the diets of individual fish, including the numbers, lengths and species of food organisms being eaten.

Materials and Methods

Laboratory technique--after the stomachs had been dissected from the fish, they were dried, using a damp towel, weighed on a Mettler P162 balance and put in Petri dishes. These were filled with water and placed on a mm grid under a dissecting microscope. Surgical scissors were used to open the stomach and a subjective estimate was made of the percent capacity utilized by the food bolus. The contents were then removed from the stomach using a probe. Gentle agitation usually separated the food items and spread them in the dish. Using the grid as a guide, the sample could then be moved back and forth under the microscope. Each field was examined and individual food items were identified and measured to the nearest millimetre. Manipulation of the food organisms was minimal and was usually necessary only when attempting to make identifications. The percent of the contents in an advanced

state of digestion was estimated subjectively. Where subsampling of the stomach contents was necessary, due to its volume, or large numbers of diet items, a Folsom plankton splitter was used. Subsampling was continued until 100 of the dominant food organisms could be counted, or until the volume reached a more manageable size. Alternately, in cases where there were large numbers of small food organisms e.g. tunicates, the subsampling was carried out by counting only a portion of the dish. In both methods, the total numbers of food items were calculated by multiplying by the appropriate splitting factor. The weight of the damp stomach shell was recorded, and this value, subtracted from the weight of the full stomach, gave the weight of the food bolus.

Recording and analysis of data--recording of data was originally on lab sheets on which the name of the food organism, the number and lengths were written. However, this proved to be too cumbersome when handling large numbers of stomachs. Hand tabulation and typing of tables for publication required many hours of preparation. Consequently it was necessary to design computed recording forms and devise a code to handle the analysis of large amounts of stomach analysis data.

On each coding sheet were recorded the sampling area, gear, station number, species of fish analyzed, length (mm) and weight (gm) of the fish, the number of the stomach, scale number, age, capacity of the stomach (%), the weight (mg) of the stomach, full and empty, the percentage of the contents that were digested, and the number of food categories. Each food category consisted of a category code, the size range (mm) and the number counted. Up to 23 categories could be listed from any one stomach analyzed.

The category code itself was designed to include fish, phytoplankton, zooplankton and benthos. Four separate sections of the code were set up, based on a three byte alphanumeric code. The first section, number-number-number, includes the fish of the marine waters of this coast, starting with 001 and ending with 999. The page numbers from Pacific Fishes of Canada by Hart (1973) were assigned to each species. Approximately 300 spaces have been reserved at the end of the code for freshwater species. 999 is given to "fish general". The second section is reserved for the benthos, and the codes are given as number-letter-number, encompassing 2,600 spaces from 0A0 to 9Z9. This section is not yet in use. The main body of the code, letter-letter-number is the section containing the phytoplankton, zooplankton, foraminiferans, radiolarians, ciliates, coelenterates, annelids and many others. There are 6,760 spaces in this section, and it expands into the next, letter-number-number, which contains another 2,600 spaces.

Spacing of assigned codes was arranged so as to allow for future expansion within each group, e.g. copepods. Identifications may thus be carried to group, species, or even life stage.

Discussion

While initially requiring the expenditure of considerable time at the microscope, this technique provides details which allow a selection of treatments

to be used in analyzing the results. These include calculation of the frequency of occurrence of each food organism by species, group, or size range and calculation of the biomass of each food item, per fish or in total. Information may be gained on energy requirements and food chain structures, both within the estuaries and in the open waters. By utilizing the same guidelines to measure the food organisms and those taken in the zooplankton tows, a comparison may be made between the food species available and those taken by the fish. Once familiarity is gained in using the keys to the various food groups, the time required for analysis is greatly reduced.

These methods have been a practical success and were used to describe the diets of fish from the Fraser (Environment Canada, 1975), Nanaimo (Environment Canada, 1974), Campbell (Goodman and Vroom, 1974), Squamish (Environment Canada, 1972), Somass (Kask and Parker, 1974), and Cowichan (in preparation) estuaries.

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METHODS USED IN STUDYING FOOD HABITS OF OREGON'S ESTUARINE FISHES

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My name is John Johnson and I am with the Oregon Department of Fish and Wildlife. I am involved with the Tillamook estuary study, which is a finfish and shellfish distribution and abundance study.

Along with our normal duties I started examining the stomach contents of various species of fish out of curiosity at first. I recorded my findings in vague terms like snails, shrimp, pill bugs, etc. Our first annual report was due and I wrote a short section about the food habits of fish in Tillamook Bay. Surprisingly many people thought this type of work enhanced our project in general and I was encouraged to continue the project in a more organized manner.

I was a wildlife major at Oregon State University and I did not have one course in invertebrates, so I knew I needed help from experts. I went to Joan Flynn, Oregon State University, and Sandy Lipovsky, National Marine Fisheries Service. They were both very patient and eventually they started me in the right direction.

I've been working with stomach analysis, on a part-time basis, for over a year now but still consider myself a beginner at best. I will explain the procedure I use for examining fish stomachs and give comments on gray areas I have questions about. I will give some suggestions that may help some of you that might be beginners as I am.

I am examining 5 species of fish: chinook salmon, starry flounder, English sole, surf smelt, and black rockfish; most of the fish examined are juveniles

We capture fish using gillnets, trawls, beach seines and SCUBA gear.

Juvenile starry flounder and English sole are preserved in a 10% formalin solution while chinook and rockfish are injected with pure formalin to stop the digestive process as soon as possible.

I examine the digestive tract of all fish from the top of the esophagus to the junction above the pyloric caeca. I put stomach contents into a watch glass and examine them with a binocular scope. I count and identify all organisms and record my findings.

I organize my data for a 1-year period of time (July 1975-July 1976) so that I know total number of food items for each species of fish and from that I can compute preferred food items for each species by percent. For example: I examined 71 starry flounder stomachs and found 851 food items. Preferred food items were as follows: corophid amphipods 53.6%, gammarid amphipods 13.6%, juvenile clams 11.5% and so on.

I had 3 basic sources of reference material. I used the third edition of Light's Manual which is an excellent source of information on invertebrates of the central California coast as well as the Oregon coast. Joan Flynn provided me with copies of detailed drawings of organisms she anticipated might be found in Tillamook Bay and I found these most useful. I often times referred to a reference collection of organisms found in Tillamook Bay which was composed by myself and Margaret Toner, OSU graduate student.

Here are some gray areas I have questions about. I would like to know how to stop the digestive process more rapidly than I do with present methods. I would like any suggestions you may have that would speed up the examination process. We spear black rockfish along jetties using SCUBA gear; however, I would be interested in finding other ways to capture rockfish in areas like this.

Here are some helpful hints for beginners starting work in stomach analysis. Go to experts and ask for pointers in all phases of the process. Find and use all keys you can get your hands on which pertain to the food organisms you happen to be working with. I have found my reference collection to be a real time saver in the keying process.

THE PREY OF DEEP-SEA MACROURID FISHES OFF OREGON

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This paper discusses the problems of identifying prey of deep-sea macrourid fishes. The results of this food habits study are published by W.G. Percy and J.W. Ambler in *Deep Sea Research* 21: 745-759, 1974. The prey of the deep-sea macrourids includes many taxa that inhabit the deep-sea floor and meso- and bathy-pelagic waters. Several major taxa were important prey: crustaceans, echinoderms, molluscs, polychaetes, and fishes. Taxa also observed included: foraminifera, nematodes, echinuloids, and plants. With such a wide variety of animals and the incompleteness of deep-sea taxonomy, several groups were given to specialists to identify. However, experience in sorting and identifying benthic invertebrates from beam trawls helped preliminary identifications. Recently published references will facilitate future taxonomic work for most of these animals.

Data Recorded for Each Fish Observed

For macrourids, an important fact is whether the stomach is everted, full, or empty. Since the swimbladder of a rattail expands when brought to the surface, the stomach is often everted. The percentage of everted stomachs varies with species of macrourid (Table 1, Percy and Ambler 1974). Data on fullness of the stomach in terms of 1/4, 1/2, 3/4, or full were subjective and not very useful. The size and species of macrourid observed were very important, because food habits changed with these factors (Table 4, Percy and Ambler 1974).

The most useful data for describing food habits were wet weight and frequency of occurrence of the prey taxa. Wet weights give relative importance of the major taxa which often include several species. Frequency of occurrence data can represent each species and type of prey. The wet weights did not correspond very well with frequency of occurrence (Table 3, Percy and Ambler 1974). The prey species of larger macrourids dominated by wet weight, when all size classes of a species are combined. The position of the prey in the stomach was also recorded to discover if

some animals always were in the anterior part of the stomach, which would imply feeding in the net. Copepods were suspected, but they were found from the anterior to the posterior part of the gut. The number of each prey taxa was recorded, but the variety of prey and presence or absence in the predator was more important (Table 2, Percy and Ambler 1974).

A higher percentage of unidentifiable gut contents occurred in smaller rattails than larger fish of the same species (Table 4, Percy and Ambler 1974). The unidentifiable material was called "grunge" and in some cases the origin identified: orange crustacean remains from pelagic crustaceans, fish or squid eyes, fish scales and vertebrae, and mud. A few commonly occurring items remained a mystery such as hooks and "copper wires".

Identification of Prey Species

For food habit studies of fishes, it is helpful to be familiar with the potential prey. For the macrourid fishes, benthic invertebrates caught in beam trawls and meso- and bathy-pelagic nekton caught in mid-water trawls were major prey items (see Table 2, Percy and Ambler 1974). Samples were also observed from a plankton net towed above the beam trawl. However, there was little correlation between copepod species in the fish stomachs and those in the plankton nets. *Gausssia princeps* caught in the plankton nets was never observed in the fish stomachs.

Identification of the prey to species may not always be necessary. From food habit studies, one wants to discover the major taxa of prey and its habitat. We wanted to know if the macrourids ate epibenthos, infauna, or nekton. It may be adequate to know that a particular species and size class of rattail eats deep-sea polychaetes and holothuroids rather than nekton. But, within a major taxa, some species may be more important food items than others. For example, the rattails only ate two of the holothuroid found in Cascadia Basin. Species identification of pelagic prey such as shrimps and cephalopods was correlated with the distribution of these animals in the water column. The occurrence of these mesopelagic animals in the guts of the rattails raised questions about their feeding behavior. Do rattails migrate to mesopelagic waters or do they eat the mesopelagic animals as carcasses?

The following is a list of taxonomic references which are general enough for the biologist who is a non-specialist. For deep-sea polychaetes, holothuroids, copepods, and amphipods, taxonomic specialists are essential. These references were recommended by people working with these taxa on projects at the School of Oceanography, Oregon State University, Corvallis.

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STOMACH ANALYSIS METHODOLOGY: STILL LOTS OF QUESTIONS

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There are two objectives in this presentation: One is to describe the methodology currently being used in our food web studies at the University of Washington's Fisheries Research Institute. The second is to bring up for discussion some of the questions and problems for which we haven't found adequate solutions.

Methodology

Preservation of specimens. Fish to be kept for stomach content analysis are placed in 10% buffered formalin in the field. With larger fish, formalin is injected into the abdominal cavity within 15 minutes of capture. The amount of formalin injected is recorded and its weight is subtracted from that of the fish when the fish is weighed. Fish are returned to the field lab where length, weight, and sex data are recorded. Small fish are tagged with a specimen number and a station location code. The tag is placed under the operculum and up through the mouth. Stomachs from larger fish are dissected from the abdominal cavity, cutting as close to the esophagus as possible and cutting just posterior to the pylorus. The esophageal end is tied by a string with a tag labelled as above.

Laboratory procedure. The stomach is removed from the fish and dried off. A damp weight is then taken to the nearest tenth of a gram. The entire stomach contents are removed and placed in a dish and the empty stomach is weighed. By subtraction this provides a total stomach contents weight including unidentifiable material and fluid. An evaluation of the stomach fullness is made and given a number scaled from 1 (empty to 7 (distended). The stomach contents are placed in a dish marked with a grid and sorted, separating all unidentifiable matrix from recognizable prey organisms. A subjective evaluation of the stage of digestion scaled from 1 (all unidentifiable) to 6 (no digestion) is made at this time.

Prey identification is made to the lowest taxonomic level possible given the digestive state and the ability of the sorter. For example, crab and shrimp are fairly easy to identify if they are intact, so these are taken to species if possible. Polychaetes are generally beyond recognition but we try to take these to family if we can. Amphipods are carried to suborder (gammarids, caprellids, and hyperiids) but no further. No attempt is made to identify other small crustaceans beyond the groupings of harpacticoid, calanoid, and cyclopoid copepods, mysids, cumaceans, tanaids, and euphausiids. Isopods are taken to suborder when possible. Molluscs are often relatively easy to identify and are taken to genus and species, though identification as a gastropod, pelecypod, or amphineuran is most common.

After prey have been sorted into groups and identified, they are counted. Counting can be a problem if the prey are pieces. In this case only a whole organism indicator--i.e., something the animal has one of--is counted. For example, heads for crustaceans, opercula or apical whorls for gastropods, hinge areas for pelecypods, central disks for ophiuroids, and Aristotle's lanterns for echinoids. When a prey was not eaten whole and only a part was ingested, the parts are counted and given special coding that indicates that it was only a part. This is especially useful for fish that prey on clam siphons and don't take the whole clam.

After the prey organisms have been sorted into groups and counted, the weight of each taxonomic unit is obtained to the nearest thousandth of a gram. The stomach contents are then placed in vials and kept for possible further identification of some of the difficult prey groups, such as gammarid amphipods, by experts in those taxonomic fields.

Stomach analysis data are recorded on computer-format forms with 10 digit numeric codes for both predators and prey (Figures 1a, 1b, 1c).

Time element for guts. Analyzing fish stomach contents using this method is slow work. We average 1 hr/stomach. This average is only this low when we include the time it takes to do an empty stomach, which is about 5 minutes. The minimum time we spend when a fish has food in its stomach is about 20 minutes. Juvenile flatfish and large rockfish eating large prey organisms usually fit into this time category. The maximum time we spend per full gut is 4-5 hours for large fish eating lots of small prey. This is common for adult embiotocids and processing time for these fish is very long. For example, one *Embiotoca lateralis* I did recently had 915 gammarid amphipods in its gut and took 5 to separate and count all the organisms.

Problem Areas

Identification. How far must you carry prey identification? Ideally, identification should be made to the species level except where damage by digestion has destroyed the specific characters. Practically, this is extremely difficult because of the taxonomic difficulty of many of the prey groups. The sorted prey would have to be given to experts in each taxonomic field, a single embiotocid may have 800-900 gammarid amphipod in its gut and it would likely take several months just to identify these organisms from one stomach. Yet if we're looking at interspecific competition for food, it

seems essential that we know exactly what species of gammarids are being preyed upon since there is such a great diversity of gammarids living in a wide variety of habitats. A possible alternative would be to identify the functional role (eg. pelagic, epibenthic, benthic) of a prey organism where morphological characters, are definitive. This, however, definitely complicates coding these organisms.

In addition to the taxonomic difficulty, there is the complicating factor of different levels of digestion. It is frequently impossible to identify a prey item beyond a broad category because of the advanced stage of digestion it is in. If in other stomachs we can identify organisms to species level how does one analyze the data? Do you throw out all specimens for which the prey are too well digested to be recognizable as individual species?

Organisms parts--how do you make counts of prey organisms which by their nature are not eaten whole such as pieces of algae, sponge, hydroids, bryozoans, holothuroid gills? We have been making very subjective estimates of what is "bite-sized" and then counting pieces this size. This is quite arbitrary and in some cases impossible to do. Recently, we had an *Enophrys bison* stomach which was full of sheets of *Ulva* and *Porphyra* and there was no way to estimate a number of bites of algae taken. In cases like this, our current method of trying to get both counts and weights breaks down.

Subsampling

Can you subsample when the stomach is packed with tiny prey? When stomach contents are removed from the stomach and placed in water, they do not spread out nice and evenly. Instead they tend to be very tightly clumped and one needs to carefully tease the organisms apart. It is the separation of the prey that takes the time with these guts. If we were to simply take half of the stomach contents and analyze them, we run a fairly high risk of error because the distribution of the prey organisms within the gut content often is not random. It is fairly common to see clumps or bands of certain prey types in the stomach contents. For example, with a plankton feeder, most of the stomach contents may be a mixture of copepods, *Oikopleura*, chaetognaths, and fish larvae and have a wide band of nothing but mysids placed somewhere in the stomach contents.

These are the questions that we still have about how it is best to do fish stomach content analysis and I hope that they will be part of the discussion that follows.

The use of discriminate analysis allows us more leeway than many other statistical tests, in that both enumerated and measured data may be utilized. For example, the diets of 2 or more fish may be compared using such data as reconstructed weight of the prey species, volumetric displacement, percent occurrence, percent volume of stomach, etc. as well as the numerical occurrence of the food items. Just as measured data provides a more valid interpretation of gut analysis so a statistic employing this type of data will result in a more useful test of difference or similarity.

In calculating our variable we multiply the number of each food item in the food groups by their estimated percent volume. Hopefully this will enable us to weigh the purely numerical data in order to get a more valid representation of the relative value of the various food groups.

Another advantage of discriminate analysis is that any one fish need not have every food group represented in its stomach. This allows the retention of minor food groups in the analysis rather than their combination into larger groups and the loss of information. It should be cautioned at this point that the proper food groups be chosen. For example, it may be valid in some instances to combine certain prey species into a common food group. In such cases the prey species should be looked at as an environmental rather than a taxonomic unit. On the other hand, it may also be possible that either sex or growth stage will separate a species into different behavioral and environmental units and necessitate its segregation into two or more food groups.

There are several considerations which should be kept in mind when using discriminate analysis. One is that the food groups chosen be distinct and with the least possible amount of overlap. This condition is sometimes difficult to meet in gut analysis as it is often necessary to combine badly mutilated and digested food items into higher taxonomic categories therefore creating possible overlap situations. Another aspect is that there should be as many cases as there are variables. So if you are comparing the diets of 2 species of fish and you find there are 20 food groups to deal with, then you should examine at least 20 full individuals of each species.

Our work to date at King Harbor has revealed 72 food groups in the collective diets of the 30 species of fish that we are concerned with. Our goal is to examine a minimum of 20 full individuals of each species. The resulting F values from the computer analysis of this data will enable us to determine which fish have different or similar diets.

DISCUSSION: SESSION 3; LABORATORY PROCEDURES AND IDENTIFICATION

The importance of a (prey) reference collection in facilitating the identification of food organisms from fish stomach contents was emphasized during the panel presentations.

Brock Bernstein, Jack Word and John Stephens pointed out the biases produced according to the time of predator collection, i.e., nocturnal feeders collected during the day, and the value of various indications evident in stomach examination such as state of digestion, position of prey in the gut or the intestine, etc. in elucidating the actual feeding chronology.

Several comments related to regurgitation, especially with collection of rockfish via spearing. Glenn Van Blaricom suggested using a hand net to contain fish and anything regurgitated; Greg Calliet and his associates were using quinaldine in squirt bottles to anesthetize fish underwater and then place them in bags, and Jim Congleton mentioned SCUBA divers using a baited line to lure fish into a net.

SI Stenstad and Catherine Terry suggested that low stomach fullness and a high incidence of empty stomachs in rockfish may be natural, considering their tendency to forage on large organisms.

Bob Feller asked if the Nanaimo group examined the hind guts of juvenile chum salmon (no) ...he suggested that there may be a sizable percentage of the total alimentary tract contents found in the hindgut.

A discussion among Feller and the Nanaimo group concerned the use of wet weights vs. dry weights and pointed out that while dry weights are less variable, fish are eating wet weights, not dry. So these should be related to the dry weights of the fish themselves. The alternative is a reconstruction of biomass by organism size. Mike Healey mentioned that for juvenile salmonids they were examining, stomach contents averaged 5% to 10% of the total fish biomass, whether measured by wet or dry weight.

Dave Levy mentioned the problem of dropping fish (especially cottids) directly into formalin for preservation as it will often induce regurgitation and an intermediate anesthetic is necessary.

Bruce Miller requested information of the Nanaimo group regarding prey coding errors. Beverly Kask verified that they ran cross references among their stomach examiners with no significant errors, though Healey noted that this is difficult because subsequent examiners ended up with fewer and fewer organisms to identify.

Back to a discussion of measuring weights, Jim Congleton asked if anyone had information showing a progressive decrease in dry weight with preservation in formalin. Cailliet mentioned that zoarcids shrank 10% and their food organisms 5% to 10% for a few days, but then decline quickly tapered off; he suggested using a volumetric instead of a gravimetric method, citing the drying of *Dikopleura* to essentially nothing. Johnson and Toner both suggested that the volumetric method was too time-consuming. Simenstad said that the volumetric method was also less precise than taking weights, and Terry thought you tended to contribute more water to the volume when you added an organism.

Considering stomach fullness, Cailliet mentioned that in studies of *Loligo* stomachs, use of fullness index from 0 to 4 provided generally the same conclusions as the percent total dry weight, with few discrepancies. Robin LeBrasseur said he had once tried measuring the maximum volume of salmon stomachs by pouring mercury in them, but that they always distended and subsequently exploded before they got full; their studies did show that the maximum stomach fullness of chum salmon in the wild was 6% to 7%, while experimental laboratory feeding situations went as high as 14% to 15% of body weight. Cailliet wondered about the use of subjective scales, especially the problems of "grey areas" with long scales. Terry explained that of their seven value fullness scales, only four were used very often and the others represented extreme cases not typically encountered.

Herbert Jaenicke said he had used the volumetric method of Yenchers and Herberts, measuring zooplankton dry weight over volume but that it was time-consuming and prone to error because of the need to pool samples. Sibert simply asked if anyone had done anything useful with the percent fullness index; i.e., why measure it? LeBrasseur suggested that it could be more useful to record fullness as a percentage of the fish's weight.

Steve Obrebski compared the subjective fullness index to that for percent cover used by terrestrial ecologists, saying that it had been shown that there were significant differences in the estimate, depending upon the observer, producing an element of error. He suggested that it would probably be wiser to go to some other method.

Laevastu reminded the group that the *Abderhalden* series in the German Handbook of Biological Methods, which was produced in Europe in the 1920's,

considered stomach analysis methods including many of the same problems being discussed. He continued that ICES and FAO have also reviewed these methods and that European literature should be checked, especially the documentation of food habits variability in space and time. He also noted that there is a crying need to summarize the existing data on fish food habits and orient current and future studies on more practical information, citing the lack of knowledge of North Pacific squid resources as either food organisms themselves or regarding their prey.

Sandy Lipovsky asked the Nanaimo group if they used a wet weight: dry weight conversion factor (no) and whether anyone had looked at annual or seasonal variations in such a relationship. No one knew of any data.

John Ellison mentioned that separation of the food bolus without breaking up the animals can be a problem and said that Reish's people used an extremely fine-meshed screen to wash it over, separating the food organisms without too much damage. He also said that he had never observed speared fish regurgitating and that allowing them to "suffocate" appeared to be preferable to direct preservation in formalin as far as reducing the chance of regurgitation. Stephens concurred.

Word asked if anyone had ever seriously looked into net contamination of fish stomach contents, by consumption of either net-caught items or other fishes' (regurgitated) food items. Laevastu reported the incidence of large and small pollock being caught in trawls and the problem of interpreting the evident cannibalism.

Word also mentioned the superiority of Keen and Coan's "key to the genera" for identifying small pelectpods.

Primed by a coffee break, the participants entered into a lively discussion concerning the optimum level of taxonomic identification of prey organisms. Word presented the view from the taxonomist's angle, that prey should be identified to species, in fact all the way to sex if the stage of digestion permits. His argument was that there are often distinct life history or ecological differences in congeners or between the ♀ and ♂ of the same species (specifically citing amphipods and cumaceans), which would imply differential exposure to predation. He maintained that the prey should be taken to that level and lumped back up according to life history information, and that one shouldn't "stop somewhere along the route and say, okay, this is the most time-applicable approach to looking at stomachs."

Others questioned the feasibility of this time-consuming and expensive approach as most of us are involved in ecological rather than taxonomic studies. Several suggested compromises in these analyses. Simenstad recommended a two-tiered system where subsamples of representative prey were retained after a detailed sorting (counts and weights) procedure, to be identified further by a specialist. Unfortunately, as several pointed out, quite often the specialist never gets them. Stephens suggested going to species when possible according to the stage of digestion, as often as possible. This would then require using the data in several ways, eliminating data from certain kinds of analysis, especially since the precision of the data "simply depends on (the) purpose of the analysis anyway."

LeBrasseur wondered about the cost of such precision, estimating that, given a \$25/hr specialist taking 40 hr per sample, a 20 fish sample would bring the cost of \$20,000 per sample! Word replied that the specialists don't see everything, that a several staged sorting process guarantees that the experts should only see 5-10% of the sample. Word further noted that people seldom go back to the sample after the processing and use what is on the data sheet and that is the most important part of a study on stomach contents. Ellison also reminded Word that, as a benthic ecologist, he is interested in everything that is there while in our analysis of fish stomachs the emphasis involves the major organisms of "interest" to the predator.

Getting down to the meat of the discussion, Obrebski pointed out that the objectives of a food habit study determine the way the data are analyzed and, thus, should dictate the sampling design (e.g. sample sizes, precision of taxonomy, etc.); "I think one of the general problems in agonizing about this is that people do not generally have a sufficiently distinct idea about what it is that they are going to use the data for; they are not sufficiently familiar with methods for analyzing the data and, hence, they are overly concerned with generalizable problems of precision, which add a great deal to the labor involved and are counterproductive for the reasons we are discussing, mainly, trying to optimize getting some kind of information within some fixed limits of cost and other aspects of logistics." Rather than accumulating a lot of data before looking for the appropriate statistics, he felt sampling and other techniques should be designed to make maximum use of whatever the appropriate statistics are, around an a priori idea of what the objective is. Callilet suggested that although it is necessary to say, with some reasonable probability, that the interpretations and conclusions are right, people shouldn't get so wrapped up in statistics that that is all they are doing; the two extremes should merge.

Stephens cautioned that researchers shouldn't neglect collecting certain bits of (easily obtained) information that may not seem useable at the time, but may prove valuable later. Obrebski said that a good statistician might find ways of designing sampling less around hard-to-get data and more to make maximum use of a limited amount of information. Sibert and Healey argued that there is a certain amount of data being gathered on fish diets just for the sake of doing it, most of it worse than useless and counterproductive, when, in fact, "the kinds of methods they use and the sorts of information they collect should be directly relevant to whatever problem or hypothesis they are attempting to tackle" e.g. a specific hypothesis to test about the intersection of the biology of a predator and its prey. Healey also criticized the use of words such as *selectivity*, *competition*, *selectivity*, *diet*, *overlap*, *preferred food*, etc. when this information can't be from the stomachs, especially considering the biases of sampling gear and the true abundance, relative proportion, and availability of organisms in their communities. Obrebski supported this, citing a California agency's mandatory requirement for cluster analysis of benthic community data a technique which he considered useless out of context; whereas, an intelligent ecologist's approach would

be to use cluster analysis to focus efforts on major organisms in the community.

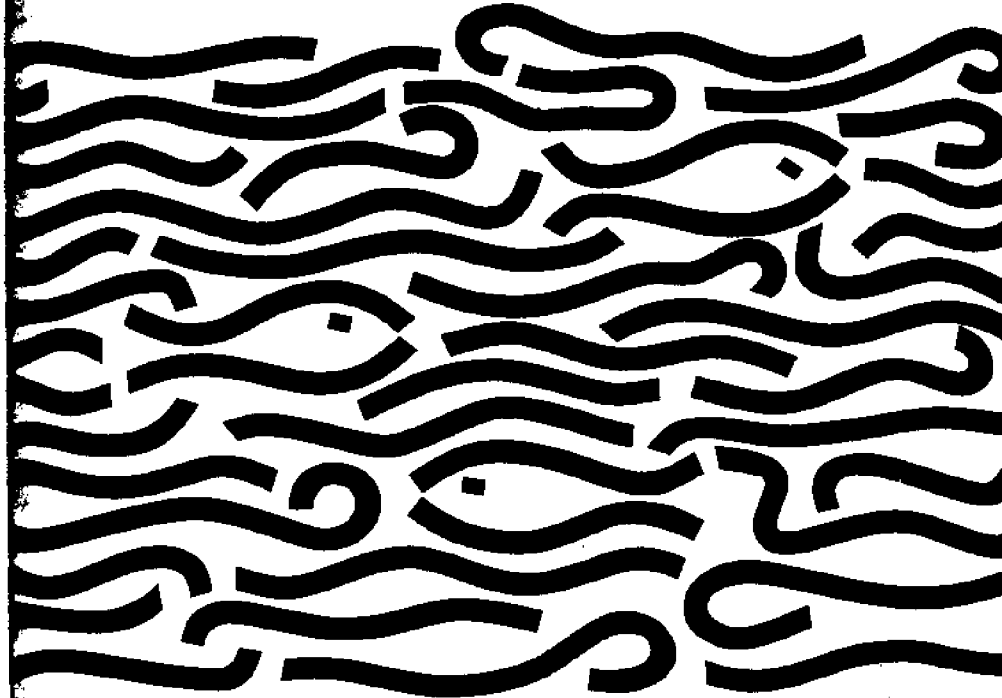
While Allen indicated that species which coexist in the softbottom demersal communities tend to have different foraging behavior, Stephens argued that there apparently are different problems in rocky shore sublittoral communities where they've observed many fishes (seemingly) foraging in the same place at the same time.

Noting the apparent switching behavior in feeding by hexagrammus, as evidenced in the arrangement of prey in the stomach, Simenstad asked if we couldn't be getting more information out of our analyses. Obrebski cited Murdoch and others' investigations on optimization of foraging behavior and said that many of these developments in other areas of ecology are not part of our consciousness. Laevastu argued that if we accept concepts such as selectivity, food preference, and food as a limiting resource, when the modeler comes to programming and constructing a complete ecosystem model, it is necessary to account for all organism groups. Thus, any information, quantitative or qualitative, should not be thrown away but recorded in order to provide some feedback to their feelings about the model.

Healey closed out the discussion session by disagreeing with the generality that fish populations are food-limited and asked for evidence to that effect.

SESSION 4

**DATA MANIPULATION
AND PRESENTATION**



SESSION LEADER:
M. James Allen

PARTICIPANTS:
Jack Q. Word
John Sibert
Taivu Laevastu
Charles A. Simenstad

A PROGRAM FOR STANDARDIZING THE IDENTIFICATION OF MARINE INVERTEBRATES

Jack Q. Word
Southern California Coastal Water Research Project
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Around wastewater discharge sites the types of organisms, their population sizes and their distributional patterns are being used to determine the extent of change in the environment (Smith and Green, 1976). In 1973, the Coastal Water Project examined the ecology of the Southern California Bight, particularly emphasizing alterations in the kinds of animals living around these discharge sites. It was thought that comparative analysis of these data would provide valuable information. It was later determined, however, that not all of the changes observed in species composition were actually due to environmental changes; instead, some reflected inconsistent or inaccurate identifications of some of the over 4,000 species of invertebrates in southern California. (Word and Charvat, 1974; Word, 1975; Word, et al., 1976).

In order to correct this problem and increase the value of these data, we started the Taxonomic Standardization Program to facilitate the exchange of taxonomic information and promote uniform identification among 150 practicing southern California taxonomists.

This program standardizes the level of identification and the names used for each particular species through a series of publications and workshops with various taxonomic experts. Workshops are typically scheduled every 2 months at which presentations are made and keys are distributed among 30-40 participants. After the formal presentations the group of organisms under discussion are looked at in the laboratory and the keys critically examined. Information presented during the workshops, including the keys, any modifications to them, and new taxonomic information are then published in the bi-monthly Proceedings of the Taxonomic Standardization Program which is mailed to over 200 participants in the program. The proceedings are meant to be stimulants for interest in a particular group of animals and hopefully the interest created will result in comments about particularly difficult couplets in the keys or specimens which do not fit the keys. They are additionally intended to provide up-to-date, accurate taxonomic information.

Contribution Number 78, Southern California Coastal Water
Research Project

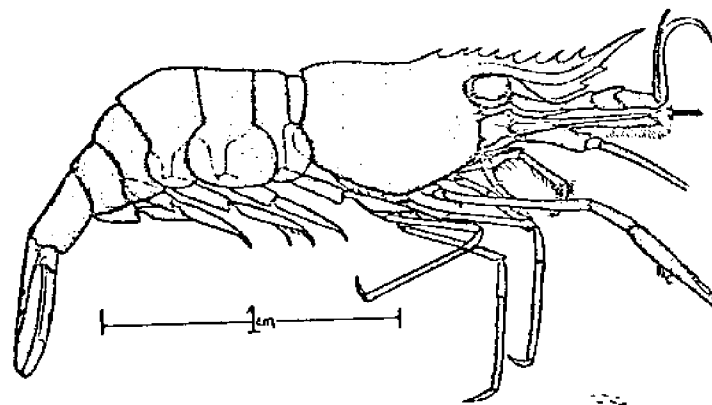
An outgrowth of the Proceedings is our final document on identification of species groups, The Invertebrates of Southern California Coastal Waters (Word and Charwat, 1975, 1976). These volumes include all the necessary information (eg. figures, keys, glossaries, etc.) required by the non-expert taxonomist to quickly and accurately identify specimens of the species contained in each book. All information on each species has been confined to a single page, contained in a looseleaf binder (Figure 1a and 1b). This will allow us to revise, add, or delete species from the volumes without requiring a complete revision of the publication.

We believe that the main reason for the success of this program has been our direct interaction with the scientists doing the identifications. By using the knowledge accumulated by these scientists and through its sharing at the workshops all of the active participants in the program have improved their identification abilities and increased their efficiency. Many of the systematic problems recognized in past years have been corrected and the analysis and comparison of data collected by the many different organizations in southern California is becoming feasible.

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Palaemon ritteri Holmes, 1895
Common Name - No common name in use.



Additional Diagnostic Characters:

Color: Translucent white; eggs when present are pinkish in color

Size Range: up to 4 cm in total length

Habitat: A common rocky intertidal and brackish water inhabitant of both coasts of Baja California. It has been found in southern California at San Diego Bay.

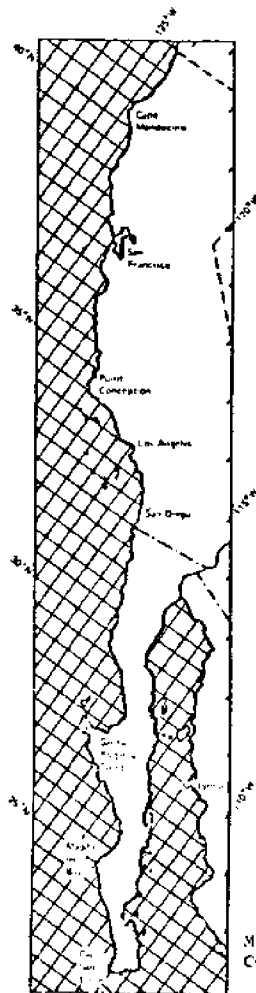
Remarks: very similar in appearance to many shrimp species of the family Hippolytidae. Members of the family Hippolytidae have multisegmented carpi on the 2nd walking leg.

Miscellaneous: Bopyrid isopod parasites are commonly found under the carapace near the branchial chamber.



Figure 1a. Sample species sheet from keys to invertebrates of Southern California coastal waters

Palasmon ritteri Holmes 1895



SYNONYMS

Leander ritteri Nobili 1901. Non Palasmon ritteri? Rathbun 1910; of Schmitt 1939.

DISTRIBUTION

RANGE: From San Diego, Calif. to Magdalena Bay, and in the Gulf of Calif. to Guaymas. From intertidal to 30 m. From Holmes 1895: San Diego, California.

From Rathbun 1904: San Bartolome Bay and Magdalena Bay, Baja California, and La Paz Harbor, Gulf of California.

From authors' data: Algodones Bay, Guaymas, Sonora, Mexico (intertidal zone).

Sexual or juvenile dimorphism:

Museum specimen number 1353 (SCCWRP)
Computer code number 18010301004001 (EPA-OHIO)

Figure 1b.

FREQUENCY DISTRIBUTIONS OF FOOD ITEM COUNTS IN INDIVIDUAL FISH STOMACHS

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Stomach contents analyses are conducted for many reasons. The results of such studies are usually statements about the suite of food items consumed by fish and statements about the amount of a particular food item consumed by a particular species of fish in relation to another species of fish or in relation to the same species, taken in a different sample. The statements about range of food items preferred are rarely, if ever, presented in a simple, clear, quantitative fashion. Similarly the statements concerning the amount of a particular food item are rarely accompanied by the additional information required to evaluate the significance of any observed differences. These observations are not necessarily intended as criticisms but rather should be taken as comments and reflections on the complexity of the problem.

In this paper, we report some preliminary results of work in progress on the variation of stomach item counts between individual stomachs. The purpose is threefold: 1) to "get a feel" for the range of variation in a rather large body of data; 2) to search for a method of representing the central tendency and dispersion for stomach contents data; 3) to explore the statistical properties of the data prior to the application of multivariate pattern-recognition techniques. We do not propose any definitive solutions to the problem, but we may indicate some promising avenues for further inquiry.

Methods

The data consist of the results of the dissection and analysis of approximately 17,000 fish stomachs collected from 7 estuarine areas on the Strait of Georgia. The fish species involved are principally juvenile salmonids, herring, stickleback, perch and sculpins. These data were collected and

used for the preparation of environmental impact statements in relation to proposed developments in the Fraser, Nanaimo, Campbell and Cowichan River estuaries (Goodman and Vroom, 1974; Environment Canada, 1974, 1975). This study begins a second more leisurely, and perhaps more rigorous, examination of the data.

A subset of 14 stations in the Nanaimo estuary on eastern Vancouver Island was selected from the data base (Fig. 1). Four stations (4, 13, 14, 15) were in deeper water seaward of the delta face and were sampled by purse seine at both high and low tides. The remainder of the stations were intertidal and were sampled by beach seine and pole net at low tide. All samples were obtained from March through July of 1973.

The laboratory procedures for analysing these samples are discussed by Kask in these proceedings. The data subset discussed in this paper is basically the same as that presented by Obrebski and Sibert also in these proceedings.

Before beginning the analysis of the individual frequency distributions, the data set had to be condensed further. The fish species list was shortened from 71 to 8 (Table 1). The potential food category list containing 157 entries was reduced to 20 by a process of ranking. Ranks were obtained for the total count, biomass and incidence for each of the original 157 categories. The ranks were then summed and the 20 items having the lowest sum of ranks were selected (Table 2).

Results

The final data subset consists of 1,712 fish stomachs. The contents of these stomachs are summarized in Table 3. There are evident similarities and differences, but the significance of some of the differences is impossible to evaluate from the data presented, except on the basis of intuition.

The characteristics of the data are perhaps better illustrated by frequency histograms; 4 of such histograms are presented in Figure 2. There are two aspects of these distributions which are immediately apparent. First is the high proportion of zero counts. Second is the long tail containing a relatively large number of extremely high counts.

The high proportion of zero counts may be misleading since it is calculated by difference from the total numbers of stomachs and the sum of all non-zero observations. It indicates, however, that the fish are probably full of something else, since for most species, the proportion of totally empty stomachs was always rather low (Table 3).

The long tail is suggestive of a contagious distribution. There are many contagious distributions available in the statistics literature and one could contrive mechanisms of predator-prey interaction which would produce a particular distribution of food items in a fish stomach. That is an interesting, but often misleading, exercise; and it is equally desirable to fit some frequency distribution merely to achieve a parsimonious condensation of the data. One of the best-known contagious distributions is the negative binomial (NBD).

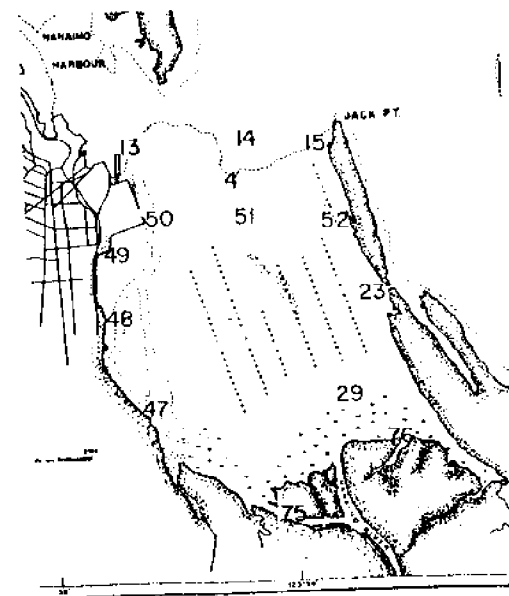


Figure 1. Map of the Nanaimo River estuary showing sampling stations

Table 1. List of fish species included in the data set

Herring
 Chum salmon
 Chinook salmon
 Coho salmon
 Threespine stickleback
 Shiner perch
 Prickly sculpin
 Pacific staghorn sculpin

Table 2. Ranking of food item by count, biomass and incidence

Category	RANK		
	Count	Biomass	Incidence
1. Harpacticoid copepods	2	6	1
2. Tunicate (<i>Dikopyleura</i>)	3	5	5
3. Unidentified egg	1	1	14
4. <i>Anisogammarus</i> spp.	8	8	2
5. <i>Calanus glacialis</i>	5	5	10
6. <i>Corophium</i> spp.	10	10	3
7. <i>Euphasia pacifica</i>	5	9	19
8. Shrimp larvae	6	15	9
9. Chironomid larvae	14	7	11
10. Zoëa	11	19	7
11. Herring larvae	29	2	8
12. Unidentified fish larvae	26	3	12
13. Diptera	18	20	4
14. <i>Eurytemora</i> sp.	7	15	20
15. Cypris	13	26	6
16. <i>Exosphaeroma</i> sp.	7	15	20
17. <i>Pseudocalanus minutus</i>	9	18	23
18. Fish egg	27	14	16
19. <i>Centropages abdominalis</i>	12	21	29
20. <i>Parathemisto pacifica</i>	23	22	14

FOOD	FISH							
	Herr.	Chum	Stickl.	Chin.	Shiner	Coho	Prickly sculp.	Stag. sculp.
HARPACTICOID COPEPOD	2.8	13.9	58.9	28.4	60.3	3.8	0.3	3.6
TUNICATA	2.9	30.4	9.6	0.0	0.0	46.7	0.6	0.0
UNIDENTIFIED EGG	68.9	40.2	9.6	0.2	0.0	0.0	0.0	0.0
ANISOGAMMARUS SP.	10.0	0.7	2.7	15.4	2.2	7.4	40.4	49.0
CALANUS GLACIALIS	10.0	3.1	0.5	7.1	0.0	12.1	0.0	0.0
COROPHIUM SP.	0.0	0.0	2.8	7.8	11.4	0.4	36.8	28.3
EUPHASTIA PACIFICA	0.5	7.5	0.5	0.1	0.0	0.1	0.0	0.0
LARVAL SHRIMP	5.9	0.3	1.9	0.8	8.7	0.0	0.0	6.0
CHIRONOMID LARVAE	0.0	0.0	1.6	9.6	1.0	1.0	10.7	9.6
CHAB ZOEL	3.7	0.0	0.2	5.1	4.1	9.5	1.4	0.0
HERRING	0.0	0.0	0.0	4.1	0.0	11.8	0.0	0.0
UNIDENTIFIED FISH LARVA	0.1	0.1	0.4	1.3	0.2	1.5	0.2	0.0
DIPTERA	0.0	0.3	3.7	19.8	0.0	0.3	0.0	0.0
EURYTEMORA SP.	1.8	1.3	1.1	0.3	2.2	0.3	0.0	0.0
BARNACLE CYPRIS	0.0	0.0	0.0	0.2	10.0	0.4	7.7	3.6
EXOSPHAEROMA OREGONENSIS	0.5	0.0	5.2	0.0	0.0	0.0	0.0	0.0
PSEUDOCALANUS MINUTUS	2.0	0.8	0.4	0.0	0.0	0.0	0.0	0.0
CENTROPAGES ABDOMINALIS	45.0	14.0	11.0	5.0	100.0	15.0	3.0	3.0
Empty stomachs	267.0	402.0	302.0	184.0	285.0	106.0	116.0	50.0
Total stomachs	51250.0	105272.0	58660.0	1997.0	8900.0	2654.0	1587.0	251.0
Total food								

Table 3. Percentage composition of stomach contents sample

	Herr.	Chum	Stickl.	Chin.	Shiner	Coho	Prickly sculp.	Stag. sculp.
Harpac.	.076*	.138	.139	.021*	.062*	.011		.103
Tunicate	.022*	.065*	.034*					
7 egg	.016*	.014*	.017					
Anisogam.	.114	.096	.096	.080	.100	.069	.860	.552*
C. glac.	.023	.044	.023			.027		
Coroph.		.067	.095	.067	.099*	.024	1.004	.533
E. pac.	.032	.031	.025*			.026		
Shrimp l.	.061	.045	.030*	.027				
Chir. l.		.028	.059	.013	.021	.012	.079	.099
Zoea	.085	.061*	.085	.023		.016	.018	
Herr. l.	.012	.017		.060		.131		
U.F.L.		.044		.023		.073		
Diptera		.177	.066	.083		.029		
Euryt.	.011	.017	.025					
Cypris.	.106	.084	.120	.054	.011	.059		
Exosph.				.015	.024*	.033	.323	.214
P. minutus	.015	.010*	.027					
Fish egg	.088	.071	.068					
Cent.		.011	.010					
Parath.	.082	.088	.035*					
No. of stomachs	267	402	302	184	285	106	116	50

Table 4. Values of the parameter of the negative binomial distribution. Asterisks indicate cases where departure from expected is significant at the $P < .05$ level by a Chi-squared test for goodness of fit. Blanks occur where there were insufficient data

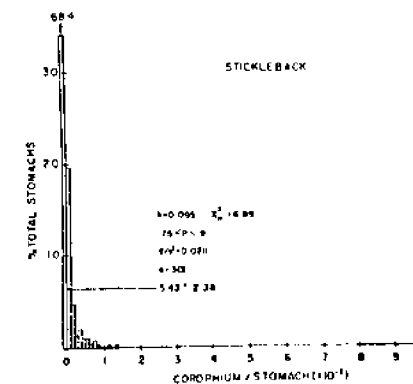
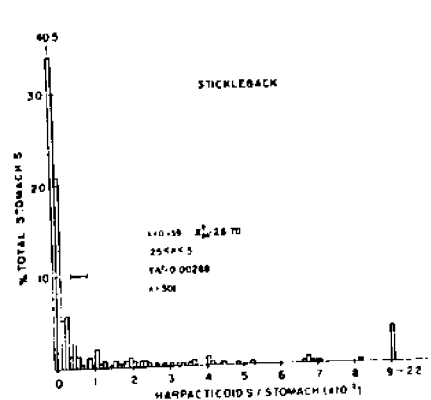
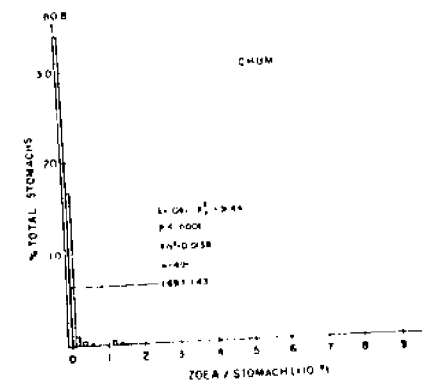
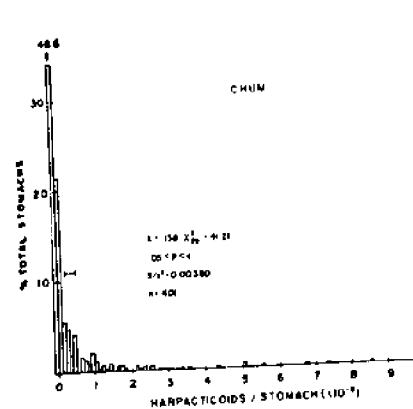


Figure 2. Histograms of the frequency of counts in individual fish stomachs

The Chi-squared statistics on the histograms (Fig. 2) indicate the goodness of fit of the data to the NBD. Table 4 contains maximum likelihood estimates (Bliss and Fisher, 1953), of the parameter k of the NBD. The agreement of the data with the NBD seems generally good, although not as good as one would like for certain key combinations of fish and food species (eg. harpacticoids in shiner perch and chinook salmon).

One of the desirable properties of the NBD is that two other well-known frequency distributions can be derived as limiting cases of the NBD (Fisher et al. 1943). In particular, if the parameter k is zero, the limiting case is Fisher's logarithmic series distribution (LSD). It can be seen from Table 4 that most values of k are rather low, suggesting that the LSD would more accurately represent the data. This distribution has been widely used to describe the distribution of individuals in species and its parameters have been shown to behave in such a way as to suggest reasonable biological interpretations, (Williams, 1964). Hopefully we can have the same success in this application.

Conclusions

The usual method of summarizing a set of data is to calculate the mean (i.e. arithmetic average) and the variance (i.e. mean squared deviation) and these two statistics can be shown to contain as much information as the original data provided certain assumptions about the data are satisfied. In this case, these two statistics are woefully inadequate. The bars on the histograms indicate the mean and 99% confidence limits. If the sample size were smaller, one could accept a hypothesis of zero mean, which is clearly a misrepresentation of the data. Clearly, a better way to summarize this kind of data must be found. These data are not normally distributed and no reasonable transformation can make them so. The solution will probably lie in the properties of some other distribution function.

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EVALUATION OF STANDING STOCKS OF MARINE RESOURCES IN THE EASTERN BERING SEA: USING A STATIC-TROPHIC NUMERICAL BULK BIOMASS MODEL (BBM)

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ABSTRACT*

Standing stock size of any marine ecological group is dependent, besides recruitment, on ecosystem internal consumption and growth, and on mortality rates. Growth-rate data are generally available, as are fishing and natural mortality rate estimates. The ecosystem internal consumption can be determined by food requirements (for growth and for maintenance) and composition of food of all components of the marine ecosystem. A static-trophic numerical Bulk Biomass Model that computes the ecosystem internal consumption is programmed and uses an iterative technique to derive plausible standing stocks of various ecological groups, using growth and mortality data (Fig. 1). Model computations indicate that the availability of food is the main factor limiting the size of standing stocks of most ecological groups above herbivores; the need for further research on food coefficients, composition of food, and feeding habits is emphasized.

Model results indicate that: 1) only a small fraction of the annual phytoplankton production is used directly by herbivorous zooplankton and pelagic fish (<10%), and the bulk of this production must go to a regeneration cycle or sink to the bottom where it is consumed as detritus by benthos (Table 1); 2) the estimated consumption of zooplankton is considerably higher than the standing stock and production (as ascertained from available data) would permit, indicating that the present quantitative zooplankton data are deficient and/or starvation is rather common in the sea; and 3) there must be considerable standing stocks of squids and small pelagic fish (Pacific herring, *Clupea harengus pallasii*; capelin, *Mallotus villosus*; smelt, family

* The complete paper by Laevastu and Favorite is too long for reproduction in the proceedings. Therefore only the abstract with 1 figure and table are presented here. The complete paper has been reproduced as a Northwest and Alaska Fisheries Center Processed Report and is available by writing to the authors.

Osmeridae; etc.) in the Bering Sea ($>3.5 \text{ ton/km}^2$ and ca 8 ton/km^2 , respectively) to satisfy the food requirements for other ecological groups grazing upon them.

Plausible standing stocks of various ecological groups in the eastern Bering Sea are presented. In general, it can be postulated that the food coefficients of the fish (both for growth and maintenance) are lower (i.e., fish is more efficient in food utilization) than assumed heretofore and that a considerable part of the biomass of fish is in recruitment juveniles, which have high growth coefficients.

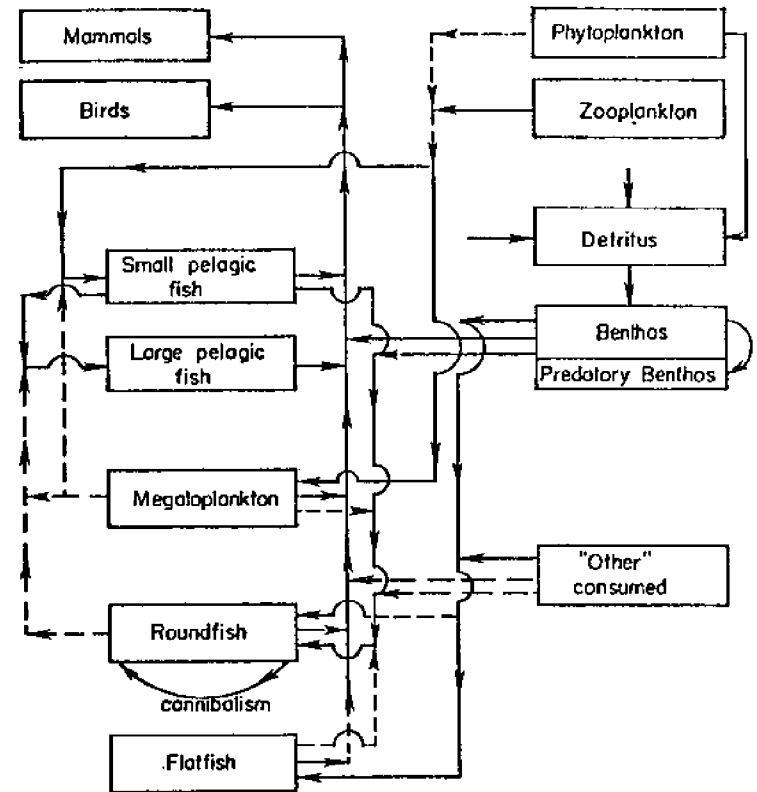


Figure 1. Schematic food flow diagram for BBM model
 major contribution ----- minor contribution

Table 1. Annual mean consumptions, standing stocks, and mean annual turnover rates (kg/km²) in Eastern Bering Sea (as computed with BBM model)

Ecological group	Monthly mean standing stock	Annual consumption ^{1/}	Mean natural annual turnover rate ^{2/}
Phytoplankton	(2,000) ^{3/} 100,000	36,850	(0.4)
Zooplankton (copepods, euphausiids)	(400) ^{3/} 20,000	85,630	4.3
Megaloplankton (squids, etc.)	3,800	4,800	1.3
Small pelagic fish (herring, etc.)	8,200	12,960	1.6
Large pelagic fish (salmon, etc.)	760	155	(0.2)
Benthos	200,000	25,980	—
(predatory benthos)	(50,000) ^{4/}	(148,570) ^{5/}	(0.8)
Roundfish	9,800	5,290	0.5
Flatfish	4,700	(1,200) ^{6/}	(0.3)
Others	?	14,300	?

^{1/} All exclude fishery

^{2/} Standing crop/consumption (excluding fishery)

^{3/} mg/m³

^{4/} Predatory benthos

^{5/} Total consumption, including consumption by predatory benthos

^{6/} Cannibalism and consumption by roundfish, mammals ("incidental")

A STORAGE/RETRIEVAL/PROCESSING SYSTEM FOR STOMACH ANALYSIS AND OTHER FISH DATA

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Elaborate, ecosystem-wide environmental surveys generate a profusion of biological data which can be handled only by computers. Such large data bases are particularly complex when they deal with the in-depth examination of the interactions between components of various trophic levels and their relationship to the driving variables and nutrient inputs responsible for their maintenance. This is certainly the case with food habits studies where the diet of an individual predator can be related to 1) physical and chemical parameters in the environment, 2) temporal and spatial aspects of predation, 3) the composition of the guild or community of which the predator is a part, 4) the composition and abundance of the available prey community, and 5) the prey spectra of conspecifics and cohorts. In these circumstances the ability to interpret a species' observed diet depends upon the efficient retrieval of data subsets from a large, diverse data base and subsequent input into a processing system.

I would like to describe briefly a data manipulation system presently being developed at Fisheries Research Institute at the University of Washington, which is designed to handle data from an extensive survey of nearshore marine fish communities in northern Puget Sound, including multispecies food habits information.

Objectives of the System

The data manipulation and processing system, called SSRP, is designed to facilitate:

1. Screening of the data for unacceptable variable values
2. Sorting of fish data (including stomach contents) according to temporal, physical, or chemical variables associated with their collection
3. Retrieval of data subsets associated with a particular species, life history stage, or other fish characteristic (i.e. sex, age, length, weight, etc.)

4. Interfacing of these data subsets with processing programs providing statistical summarization
5. Input of the summary values into programmed plotting routines.

The SSRP system components are respectively named UPDATE, USCREEN, RIRS, DATAPROC, and SIMPLOT. The complete technical descriptions of the SSRP system and its components will be available soon from FRI's Data Processing Center. They will, however, be described briefly here.

UPDATE (Control Data Corporation, 1975) is a system which is used to create and maintain libraries of programs or data. UPDATE permits one to modify a single card image in a data base without manipulating the whole body of information. Erroneous records detected by program USCREEN can be "withdrawn" from the data base, corrected, and "re-inserted" with minimal effort. This facility is invaluable in dealing with a 40,000- or 60,000- record data base-- the alternative being to search by hand through 20 to 30 boxes of data cards to find errors!

USCREEN is a series of FORTRAN programs designed to test whether data of a certain record type meet the range and value criteria specified for each variable. The testing for anomalous data is of course directly related to the precision of the screening criteria, i.e., the broader and more diverse the expected values, the more difficult it is to detect aberrant data. There is a separate USCREEN program for each record type in our data base.

RIRS (Gales, 1975) is an information retrieval system especially well suited to retrieving small data sets from very large data bases. It is organized around a series of data blocks which are linked by a common set of variables called sort key variables. RIRS employs three types of retrieval functions-- serial, random, and indirect.

Serial retrieval functions scan in turn each record in a data set in order to extract the desired subset. Typically, serial functions can operate on any variable in a record, but are prohibitively expensive for data sets with more than, say, 10,000 records. Random retrieval functions operate on a data base organized into separate data blocks and stored on a random access device-- for example, a magnetic disk. Associated with each data block is a pointer, which in turn is determined by the values of the sort key variables. Random functions scan through the list of pointers only rather than all the records in each data block; as a result these functions can only operate on sort keys, but they are extremely fast and are suitable for data bases in excess of several hundred thousand records.

Indirect retrieval functions are a composite of random and serial functions and operate as follows. First, a random function is used to extract a small data block, called a directory, from the data base. The directory contains non-sort key variables specifying collection and environmental information, in addition to the sort keys. Then a serial function which may operate on any variable is applied to the directory to obtain a subset of the directory, called the sub-directory. The subset of sort key values which occur in the sub-directory then guides a random retrieval function which extracts all data blocks from the data base whose sort keys match a portion of this subset.

Thus, the sort keys in the directory serve as pointers to other data blocks in the data base. By combining fast random retrievals and slow serial retrievals, one can economically extract almost any small data subset from the data base.

DATAPROC This is a package of data processing programs which summarize the various record types forming our data set. DATAPROC and USCREEN are the only parts of SSRP which are tightly tied to the types and form of data we are accumulating in our Puget Sound fish investigations, although similar data could be easily adapted for DATAPROC by changing its input format. At present, DATAPROC consists of three processing programs which describe and summarize 1) physical and environmental conditions of the collection (information contained in the RIRS directory deck); 2) catch composition and the statistics of the species' total abundance and biomass; and 3) statistical summary, by prey organism and overall, of the composition, abundance, and biomass of fish stomach contents. Appendix I provides example output for each of these processing programs.

SIMPLOT (University of Washington, 1973) is a general purpose plotting program which produces computer plots from sets of input plot directives and x and y coordinates. In our case, SIMPLOT is directed to displaying a variety of catch statistics and diversity indices computed by DATAPROC, as a function of time. These statistics and indices include the mean, standard deviation, and coefficient of variation of catch abundance, weight, and number of species, and the Simpson, Shannon-Welnea, Hills, and Heaps diversity indices for abundance and weight.

The overall structure and operation of the system are shown in figure 1. The dotted arrow represents information which aids the user in correcting data errors; the dashed arrow represents information used by the computer to aid in retrieving data; and the solid arrows represent flows of data and computed information.

Conclusion

The SSRP system is an economical and flexible system for storing, retrieving, computing, and displaying information from a large biological data base. Some of the system components (UPDATE, RIRS, SIMPLOT) are very general systems which can be readily adapted for different data formats and variables, and which can easily be interfaced with a wide variety of special purpose error screening and processing programs.

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SSRP SYSTEM STRUCTURE

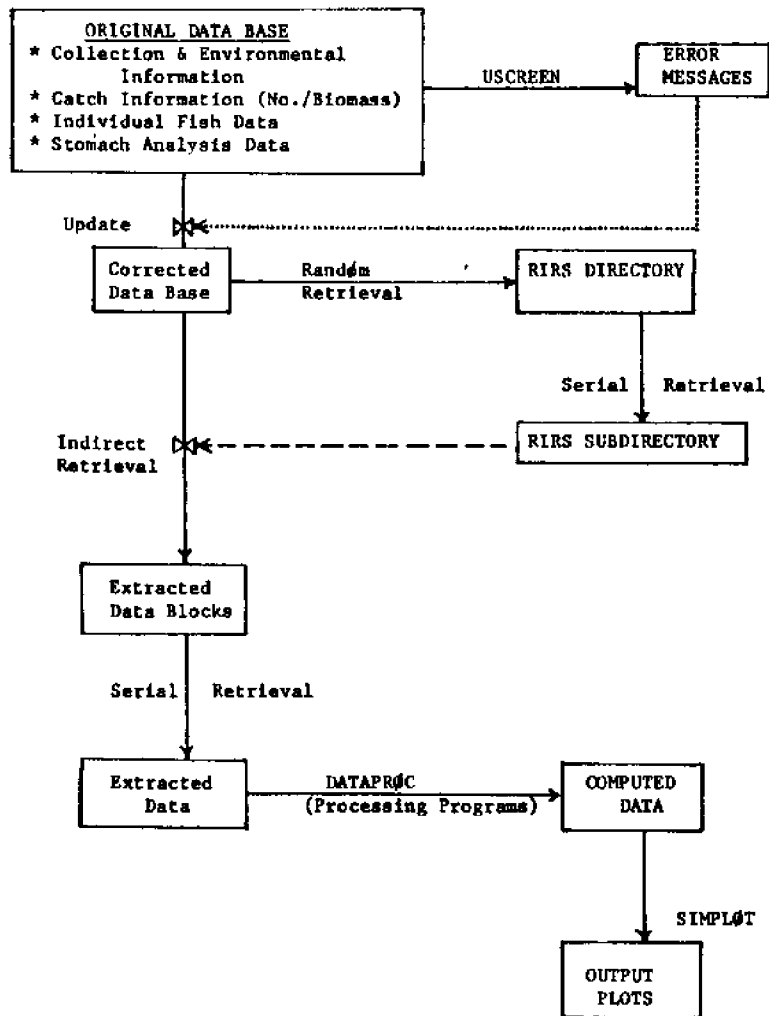


Figure 1. Overall structure and operation of the system

Appendix 1. Sample output for SSRP processing program package, DATAPROC

COLLECTION INFORMATION				LOCATION		BOTTOM TYPE	
NUMBER	HAUL NUMBER	DATE DAY MONTH YEAR	SUBAREA	SITE	HARTLEY		
75799	1	73 9 75		96-PT. GEORGE	SAN JUAN	1-ROCKY/KELP RED. EXP.	1-ROCKY
75799	2	73 9 75		96-PT. GEORGE	SAN JUAN	1-ROCKY/KELP RED. EXP.	1-ROCKY
75800	1	73 9 75		38-WFSTICOTT BAY	SAN JUAN	2-MUD/FEELGRASS, PROT.	2-LOOSE MUD
75800	2	73 9 75		38-WFSTICOTT BAY	SAN JUAN	2-MUD/FEELGRASS, PROT.	2-LOOSE MUD
75801	1	74 9 75		70-DEADMAN RAY	SAN JUAN	3-GRABVEL/MON. EXPANSED	3-MUD/CLAY
75801	2	74 9 75		70-DEADMAN RAY	SAN JUAN	3-GRABVEL/MON. EXPANSED	3-MUD/CLAY
75802	1	74 9 75		65-FAGLE COVE	SAN JUAN	2-SAND/FEELGRASS, PROT.	2-SAND
75802	2	74 9 75		65-FAGLE COVE	SAN JUAN	2-SAND/FEELGRASS, PROT.	2-SAND
75803	1	74 9 75		64-AMERICAN CAMP	SAN JUAN	2-CORALLE. EXPANSED	2-GRABVEL
75803	2	74 9 75		64-AMERICAN CAMP	SAN JUAN	2-CORALLE. EXPANSED	2-GRABVEL
75804	1	74 9 75		92-BURROUS I. NS FISH	BELLINGHAM	1-ROCKY/KELP RED. EXP.	1-ROCKY
75804	2	74 9 75		92-BURROUS I. NS FISH	BELLINGHAM	1-ROCKY/KELP RED. EXP.	1-ROCKY
75805	1	74 9 75		9-AIRCH RAY	GEORGIA ST.	2-SAND/FEELGRASS, PROT.	2-GRABVEL
75805	2	74 9 75		9-AIRCH RAY	GEORGIA ST.	2-SAND/FEELGRASS, PROT.	2-GRABVEL
75806	1	74 9 75		12-CHEERY PT.	GEORGIA ST.	2-CORALLE. EXPANSED	2-GRABVEL
75806	2	74 9 75		12-CHEERY PT.	GEORGIA ST.	2-CORALLE. EXPANSED	2-GRABVEL
75807	1	74 9 75		2-LUMMI RAY	BELLINGHAM	3-MUD/FEELGRASS, PROT.	3-LOOSE MUD
75807	2	74 9 75		2-LUMMI RAY	BELLINGHAM	3-MUD/FEELGRASS, PROT.	3-LOOSE MUD
75808	1	74 9 75		16-PT. MUGLEY	GEORGIA ST.	1-ROCKY/KELP RED. EXP.	1-ROCKY
75808	2	74 9 75		16-PT. MUGLEY	GEORGIA ST.	1-ROCKY/KELP RED. EXP.	1-ROCKY
75809	1	75 0 75		17-VILLAGE PT.	GEORGIA ST.	3-GRABVEL/MON. EXPANSED	3-MUD/CLAY
75809	2	75 0 75		17-VILLAGE PT.	GEORGIA ST.	3-GRABVEL/MON. EXPANSED	3-MUD/CLAY
75810	1	75 0 75		92-BURROUS I. NS FISH	BELLINGHAM	2-SAND/FEELGRASS, PROT.	2-SAND
75810	2	75 0 75		92-BURROUS I. NS FISH	BELLINGHAM	2-SAND/FEELGRASS, PROT.	2-SAND

COLLECTION CHARACTERISTICS

Sample DATAPROC output.

PAGE 1

COLLECTION NUMBER	HAUL NUMBER	BOTTOM DEPTH (M)	COLLECTION DEPTH (M)	GEAR TYPE	DISTANCE FISHED (M)	START DURATION (HRS)	FISHING DURATION (MIN)	ADFA FISHED (50 M)	VOLUME SPAINED (CUBIC M)	HANDLING OF CATCH
75700	1	20	3	5-TOW NET (3-1X6-1M)	-000	2030	10	-000	11499	-0
75700	2	12	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75800	1	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75800	2	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75801	1	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75801	2	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75802	1	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75802	2	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75803	1	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75803	2	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75804	1	12	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75804	2	12	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75805	1	2	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75805	2	2	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75806	1	8	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75806	2	8	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75807	1	6	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75807	2	6	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75808	1	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75808	2	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75809	1	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75809	2	20	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75810	1	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0
75810	2	4	3	5-TOW NET (3-1X6-1M)	-000	2040	10	-000	11499	-0

MEAN 10.0 3.0
STANDARD DEVIATION 7.1 3.0
RANGE 2-20 3-30

-999 INDICATES MISSING DATA

ENVIRONMENTAL INFORMATION

Sample DATAPROC output.

PAGE 1

COLLECTION NUMBER	HAUL NUMBER	SURFACE TEMPERATURE (C)	TIDE STAGE	TIDE (M)	VISIBILITY (M)	TEMPERATURE (C)	SALINITY (PERCENT)	OXYGEN (PERCENT SATURATION)
75700	1	10.6	1-ERR	1.3	-000.0	10.4	21.9	66
75700	2	10.6	1-ERR	1.3	-000.0	10.4	21.9	66
75800	1	13.2	1-ERR	.5	-000.0	11.2	20.3	114
75800	2	13.2	1-ERR	.5	-000.0	11.2	20.3	114
75801	1	10.7	2-ERR SLACK	.2	-000.0	10.7	21.6	172
75801	2	10.7	2-ERR SLACK	.2	-000.0	10.7	21.6	172
75802	1	10.3	3-FLOOD	.4	-000.0	10.3	22.9	47
75802	2	10.3	3-FLOOD	.4	-000.0	10.3	22.9	47
75803	1	10.3	3-FLOOD	.8	-000.0	10.3	23.2	73
75803	2	10.3	3-FLOOD	.8	-000.0	10.3	23.2	73
75804	1	10.1	3-FLOOD	1.4	-000.0	10.1	22.8	72
75804	2	10.1	3-FLOOD	1.4	-000.0	10.1	22.8	72
75805	1	13.2	1-ERR	1.8	-000.0	11.2	20.5	121
75805	2	13.2	1-ERR	1.8	-000.0	11.2	20.5	121
75806	1	12.3	1-ERR	1.4	-000.0	12.3	20.8	109
75806	2	12.3	1-ERR	1.4	-000.0	12.3	20.8	109
75807	1	12.1	1-ERR	1.5	-000.0	12.1	21.9	81
75807	2	12.1	1-ERR	1.5	-000.0	12.1	21.9	81
75808	1	11.3	1-ERR	.6	-000.0	11.3	21.5	54
75808	2	11.3	1-ERR	.6	-000.0	11.3	21.5	54
75809	1	11.1	1-ERR	.4	-000.0	11.1	20.3	75
75809	2	11.1	1-ERR	.4	-000.0	11.1	20.3	75
75810	1	11.7	2-ERR SLACK	.2	-000.0	11.7	20.7	89
75810	2	11.7	2-ERR SLACK	.2	-000.0	11.7	20.7	89

MEAN 11.4 21.4
STANDARD DEVIATION 10.3-13.2 20.3-22.9
RANGE 2-1.8 0-1.0 10.1-17.7 20.3-22.9 54-172

-999 INDICATES MISSING DATA

COLLECTION NUMBER 75806 DAY/MONTH/YEAR 7/ 9/75
 HAUL NUMBER 1
 CODE-SPECIES
 39-SOTINCHUS TMLICHTHYS LONGFIN SMELT 2-JUVENILE 1 1.50
 158-LEPTOCOTTUS ARMATUS PACIFIC STAGHORN SCULPIN 3-ADULT 1 45.00
 TOTAL 2 46.50

HAUL NUMBER 2
 CODE-SPECIES
 159-LEPTOCOTTUS ARMATUS PACIFIC STAGHORN SCULPIN 3-ADULT 1 175.00
 26-CLUPEA HADENGUS BALTICUS PACIFIC HERRING 2-JUVENILE 1 31.00
 39-SOTINCHUS TMLICHTHYS LONGFIN SMELT 2-JUVENILE 2 3.00
 73-TRICHODON TRICHODON PACIFIC SANDFISH 3-ADULT 1 25.00
 28-ONCORHYNCHUS KEPA CHIN SALMON 2-JUVENILE 1 40.00
 TOTAL 11 274.00

AVERAGE HAUL OF 2 HAULS Sample DATAPROC output.

SP-STAGE	HAULS	MEAN	S.D.	NUMBERS	RANGE	COEFF. VAR	MEAN	S.D.	RANGE	WEIGHTS	COEFF. VAR
24-2	1	3.0	4.2	6	1-6	1.4	10.50	14.85	21.00-21.00	21.00	1.41
26-2	1	1.5	.7	1	1-2	1.6	20.00	28.24	44.00-40.00	40.00	1.41
39-2	2	1.5	.7	1	1-2	1.6	2.25	1.06	1.50-1.50	3.00	.47
73-2	1	1.5	.7	1	1-2	1.6	12.50	17.64	24.00-25.00	25.00	1.41
158-2	2	2.0	1.6	1	1-2	1.7	90.00	63.64	45.00-135.00	135.00	.71

STAT AVERAGE
 OVER HAULS IN THIS COLLECTION
 MEAN 135.25 S.D. 7.28
 ABUNDANCE 135.25 COEFF. VAR 1.04
 WEIGHT 125.51
 N OF SPEC. 3.50 2.12

DIVERSITY INDICES COMPUTED CONSIDERING LIFE HISTORY STAGES
 SIMPSON INDEX 17200
 SHANNON-WIENER INDEX 2.0224
 PILLIS BATIO 2.1162
 WEIBS EVENNESS INDEX 1.0930

SPECIES: 24-CLUPEA HARENGUS PALLASI PACIFIC HERRING
 FROM COLLECTIONS: NUMBER HAUL DAY MONTH YEAR NO. SPECIMENS

NUMBER	HAUL	DAY	MONTH	YEAR	NO. SPECIMENS
75799	2	23	9	75	1
75805	1	24	9	75	1
75806	2	24	9	75	4
75808	1	24	9	75	1
75809	1	25	9	75	2
75810	2	25	9	75	0

LIFE HISTORY STAGE: 0 UNSTAGED
 0 LARVAL
 18 JUVENILE
 6 ADULTS

TOTAL SAMPLE SIZE: 24

MEAN RANGE S.D.
 2.0 1-5 1.2

CONDITION FACTOR (1-7, EMPTY-DISTENDED) 2.0 1-5 1.3

DIGESTION FACTOR (1-5, COMPLETE-NONE) 2.0 1-5 1.3

TOTAL CONTENTS WEIGHT (GRAMS) .03 .00-.08

TOTAL CONTENTS ARUNDANCE 2095.4 75.0-.11

(NUMBERS) 2906.0 1077.3

NUMBER OF EMPTY STOMACHS: 9
 PERCENTAGE OF EMPTY STOMACHS: 37
 ADJUSTED SAMPLE SIZE (STOMACHS CONTAINING PREY): 15

STOMACH ANALYSIS

PREY ORGANISM	LIFE HISTORY STAGE	TOTAL OCCUR	MEAN	RANGE	S.D.	TOTAL MEAN	RANGE	S.D.	AVE. BIOMASS MEAN	S.D.	PERCENTAGES OCCUR COMPO- RENCE SITION COOP
CRUSTACEA	3-70EA	.07	5	1-5	1.3	.00	.00	.00	.00	.00	.17
			2026	175.1	14	.11	.01	.00	.02	.00	59.72
COPEPODA	0-ADULT	.40	5	1-5	1.0	.00	.00	.00	.00	.00	.17
			999	300.2	99	.07	.00	.00	.00	.00	29
HYPERIDEA	0-ADULT	.13	25	1-7	3.0	.00	.00	.00	.00	.00	.86
			12	1-5	1.5	.00	.00	.00	.00	.00	.14
PLATYHELMINTHES	0-ADULT	.20	2	1-2	1.0	.00	.00	.00	.00	.00	.07
			700	46.7	700	.03	.00	.00	.01	.00	24.04
CUMACEA	0-ADULT	.07	15	1-15	3.0	.00	.00	.00	.00	.00	.52
			100	6.7	100	.00	.00	.00	.00	.00	3.44
COPEPODA	1-EGG	.07	20	1-20	2.8	.00	.00	.00	.00	.00	.96
			20	1-9	2.0	.00	.00	.00	.00	.00	.14
PERICARIDA	0-ADULT	.07	20	1-20	2.8	.00	.00	.00	.00	.00	.14
			20	1-9	2.0	.00	.00	.00	.00	.00	.96
OSTRACODA	0-ADULT	.07	20	1-20	2.8	.00	.00	.00	.00	.00	.14
			20	1-9	2.0	.00	.00	.00	.00	.00	.96
MANDIBULATA	0-ADULT	.07	20	1-20	2.8	.00	.00	.00	.00	.00	.14
			20	1-9	2.0	.00	.00	.00	.00	.00	.96

SPECIES: 24-CLUPEA HARENGUS PALLASI PACIFIC HERRING

UNIDENTIFIED MATERIAL

TOTAL NUMBER OF PREY CATEGORIES: 9
 SHANNON-WEINER DIVERSITY INDEX (NORMALIZED): 1.23

NUMBERS: 1.23
 BIOMASS: 1.79

DISCUSSION: SESSION 4; DATA MANIPULATION
AND PRESENTATION

Responding to questions about the new Southern California Coastal Water Research Project (SCCWRP) taxonomic keys, Jack Word explained that although the keys emphasize the southern California groups, the SCCWRP staff is adding northern California groups and is including only reliable literature references. He said that the extent of the subtidal coverage depends upon the group, e.g., Volume 2 (Shrimp) includes intertidal to 600 feet in depth, including midwater shrimp. Three of the 25 project people are involved in taxonomic studies--not a high percentage. As to subsequent volumes, Word says he has:

an ophiuroid key (76 species) completed,

a microcrustacea (cumaceans, ostracods, and pagurids)
key partially completed and,

plans for a key to the major groups of invertebrate
organisms.

Until recently, there has been little interest in funding publication of these keys; however, since the first two keys have been circulated, interest in publishing is increasing and appears feasible at this time.

During a discussion of the implications of a lot of zeros in data, Greg Cailliet asked of John Sibert whether, even though the mean of a group of numbers is a measure of central tendency, isn't it still a fact that, if in a skewed array of data, the mean is a lot less because of all the zeros? Cailliet further asked if it didn't still reflect that in a lot of guts studied there were not very many animals? Sibert replied that the median is simply half the distance in a total range and doesn't have any meaning. Steve Obrebski suggested normalizing transformations on data of that nature but indicated that skewed distribution and large numbers of zeros still create problems.

Bob Feller asked Sibert, "Are distributions of a large number of fish over a short period of time any different than from 4-to 5-month pooled data?"

Sibert replied, "Distributions are similar except that the effects of lumping data give more zeros and high numbers. If you reduce sample size, it still retains the general shape. If you looked at a thousand fish, all collected on the same day at the same location at the same time, you would still find a positively skewed distribution."

Obrebski reminded the group that most distributions of benthic organisms look skewed and that is one reason a negative binomial is a widely used distribution. The usual procedure is to normalize the data with the log transformation and use the log-transformed data, keeping in mind that the log of zero doesn't exist and it is necessary to add 1 to each number before transforming it. Sibert reinforced his earlier thoughts by stating, "You'd be better off to use statistics appropriate to that particular distribution or use a non-parametric method."

John Stephens asked, "For example, could one use the slope of the curve of the frequency distribution?" Sibert suggested that some two-parameter formulae could be used to describe such a curve. Stephens then asked, "Why would a benthic population necessarily approximate that particular frequency distribution?" Obrebski replied "Because the organisms are patchily distributed and, when you sample for patchy distributions, some samples have very few organisms and other samples have a large number of organisms. The variance of the distribution is the sum of the deviations from the mean. When you have high patchiness, then that variance is high and you have a situation where the variance is very high in proportion to the mean." Although this is from the point of view of community sampling, "usually the sampling distribution reflects the actual distribution of organisms in space." If the organisms are distributed at random, some other distribution, such as the Poisson distribution (in which the variance to mean ratio is equal) is the parent distribution. It should be pointed out that all these distributions are limiting forms of each other, so that the value of k , as it goes to larger numbers, soon begins to reflect data which fit a Poisson distribution. The parameter k has been used, for instance, by Lloyd in an article on something called "mean crowding"--which was in the Journal of Animal Ecology in 1967--to deal with the problem of describing the patchiness of organisms in space. Obrebski pointed out that the underlying distribution in this patchiness situation was the negative binomial. Overall, the patchy character of most sampling situations is something that people should be aware of because it detracts from the procedure of estimation which they're using.

Greg Cailliet suggested that individual stomach contents are not adequate samplers of prey items. Perhaps one way to overcome this would be to pool guts, say in 5-gut intervals, so that the chance of having one frequency class dominate the data would be less. Si Simenstad observed that it would be intriguing to measure overall prey distributions on the basis of an entire fish school, i.e., *Cymatogaster* sp. or juvenile chum salmon, compared to individuals passing through the same prey community. Cailliet agreed and also suggested that if one did that, it might be possible to use parametric statistics and measure central

tendency to see if rankings were similar.

Gary Smith noted that the problem of comparing significant differences in proportions is much more easily handled; i.e., the occurrences or nonoccurrences of food items in the stomachs ought to follow a binomial probability distribution. Then one can look up the confidence intervals graphically. Graphic determinations can also be used to determine the sample size required to meet proportion limits when one has predetermined precision objectives.

Jack Word asked John Ellison whether he showed that the two fish described in his study were feeding differently. Ellison replied that, although he showed that their numbers were significantly different, he still isn't sure about the existence of competition. "You say these things (wanting to test if there is any competition) in the beginning and then, when you finally go through there, and you look at the data, and you look at the statistics, and you read up on competition and everything, you're afraid to make any definite statement, 'Yes, there was competition.' I did show that the two diets were significantly different; I found certain food groups which were essential in the analysis in that they helped discriminate between the two diets."

Brock Bernstein asked Ellison if he had any indication of the mechanisms of partitioning, such as feeding in different parts of the habitat. Ellison described the different feeding morphologies and behaviors of the whitefish and brook trout, including the differences in mouth structure (subterminal vs. terminal) and size of mouth and the fishes' position in the stream (on bottom in deep pools vs. in riffles). He said that he also looked at differences in prey size frequencies, but that the variance within the stomach of any one fish was so great that, if partitioning was based on size of prey item, it certainly didn't show up in his data. He pointed out that the commonly eaten items were not necessarily of the same habitat, i.e., those of terrestrial origin (Hymenoptera for the brook trout) versus benthic (insect larvae) for the white fish. This assumes, of course, that of the variables you've plugged into the analysis, you've included the most important, principal food items.

Obrebski asked Ellison about evidence of temporal changes in the items that allowed Ellison to discriminate between the two fishes' diets. Ellison replied that he intended to look at the feeding periodicity of the two fish to see if it corresponded with the results of Banker's work in Convict Creek, which suggested that fish feed all the time but possibly stop feeding just before dawn. Ellison said that his sampling over 24 hours, however, provided no obvious trends; feeding in both fish was apparently at random, with both fish feeding most of the time.

Asked whether he could detect temporal changes in the rank order discriminator with change in time, diet items disappearing, etc., Ellison commented that the drift fauna and benthic fauna--the food groups that constitute the principal discriminators--change rapidly in a short period

of time but the overall diet compositions remain basically the same. He did examine summer-winter differences in whitefish diets and found, not surprisingly, significant differences there.

Obrebski noted that several papers by Roger Green in Ecology documented the use of the discriminate function in ecological applications, i.e., effect of temporal changes in environmental variables that affect the structure of biological communities.

Ellison said that he is now involved in a project gathering data from King Harbor (California) where they are accumulating both frequencies for prey organisms in each food group and an estimated percentage of stomach volume; the investigators are interested in combining both kinds of data with a view toward getting a more valid indicator than can be obtained by using enumerated or volumetric data alone. Along this line, Obrebski brought up the work of Schoener and others on optimal foraging strategies because Obrebski felt that the issue under discussion directly related to what fish theoretically optimize during feeding activities. Under this approach, the ultimate thing is net caloric gain relative to caloric output in obtaining food; that ratio should be optimized and thus the optimum measure would be a conversion of biomass to caloric equivalent.

Concerning Taivo Laevastu's discussion of a bulk biomass model, Gary Smith questioned the sensitivity of the standing stock estimates to small differences in food abundance and growth coefficients. Laevastu replied that the standing stock is very sensitive to the growth coefficient so that, in order to iterate to a steady state (within annual fluctuation), you have to take the growth coefficient to the second decimal point. Obrebski suggested that such a compartment model is typically very sensitive to the respiration rate and since it is very difficult to measure this in the marine environment, the use of that technique usually greatly underestimates the actual rate. And, as a result, Obrebski doubted whether we had any data on energetics of communities of any sort that can do anything other than create a model of that sort as an academic inquiry into factors that might affect stability in ecosystems. In defense of this "exercise," Laevastu noted that when it comes to management decisions, we hadn't time to wait for determination of a critical coefficient to the sixth decimal place and that this model was a step toward providing some of these answers now. He also said that the use of respiration rates from the current literature was solely to set limits on the system.

Laevastu asked Simenstad if the nearshore fish data base currently being compiled by the University of Washington's Fisheries Research Institute (FRI) might be compatible with the Northwest Fisheries Center (NMFS) data base. Simenstad replied that both the data format and the processing software are quite flexible and shouldn't pose any constraints on combining or comparing the two.

In a general discussion about the kinds of data that should be collected,

all agreed that the measures of diet composition to a large extent depend upon the question being asked. If one is inquiring about the selectiveness of the predator, it is necessary to know the size and number of items; if it's the "importance" of a prey item, you need a combination of numbers, volume and frequency of occurrence; and if it's regarding the nutritional or trophic role of a prey item, biomass and/or caloric values are required. Cailliet pointed out that many of these parameters are all combined in the Index of Relative Importance (I.R.I.).

Returning to the question of the applicability of the trophic model described by Laevastu, Steiner mentioned that there are fundamental problems associated with these types of models, that they are dynamic only as a thermostat on the wall is dynamic. A thermostat has a fixed rate and the energy going through is modulated around that, whereas, biomass estimates are variant temporally and spatially such that, as Steiner noted, "Even if your biomass estimates are right on the nose, then you're still not dealing with dynamic terms because your 'system' is being driven by static inputs, e.g., biomass values, growth coefficients, etc." Laevastu described details of how he thinks the model compensates for temporal changes although there are some options that would be difficult and expensive to handle, like considering year classes of dominant species. As it is now, it has taken 30 hours on the CDC 6500 to run just one cycle!

Jim Allen questioned the validity of always lumping prey items according to taxonomic characters, which he saw as leading to many errors. Instead, he proposed a system of grouping predators according to morphological characters indicative of the predators' food habits. Thus, once you had the predator and the food items identified to species, you could sort out the prey organisms with appendages which indicate active swimmers, burrowers, crawlers, etc.. Allen went on to suggest that if you were to take this approach you might not need to identify a prey organism to its taxonomic limit; you would look at the prey organism's morphology as an indication of its activity in the environment. Cailliet cited another example, Brooks and Dodson's classification of copepods into size classes and comparison of predator mouth size and size of copepods eaten. Obrebski recounted his experience with the Brooks and Dodson data. He calculated the diversity (Indices) of "alewifed" and "alewifeless" lakes to test the hypothesis that selective predation would affect the plankton community by increasing diversity. At that time no one had developed equations for calculating expectations and variance for the Shannon-Wiener function so they couldn't detect significant differences. Obrebski found that if you corrected for lake size and depth (which affect diversity), lakes with alewives did have higher diversities. Colin Levings told how he used mean weights of prey found in flounder stomachs to generate frequency histograms of numbers of organisms in specific weight categories. He compared histogram curves for what was in the guts versus what was in the environment (grab samples) and found that it coincided during several months. Taking it further, Levings discovered that cutting off the upper and

lower limits indicated that the whole community changes when fish moved in and grazed down the common items (of 77 total species, the polychaete species were preferred).

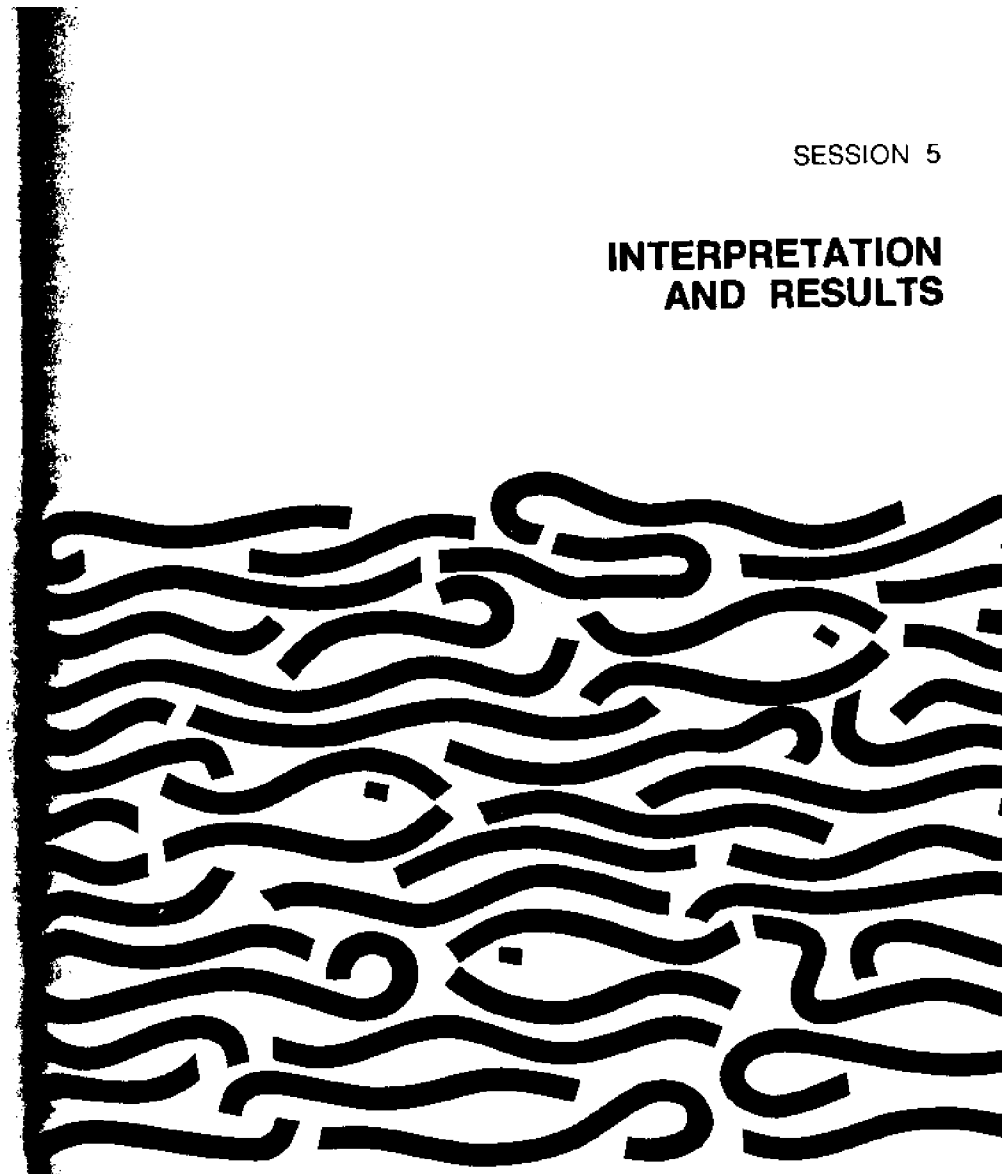
Allen suggested that a fish stomach could be treated like any selective sampler--trawl, grab, etc.--such that a lot of the same community analyses could be applied to these data. Cailliet pointed out that this was exactly what Hurtubia did in the Ecology (1974) paper discussion of lizard food habits. He assumed that each individual stomach was not a random sample but a very select sample; an individual stomach would not have all the prey items, but when stomachs were pooled, there was a point at which the pooled stomachs would represent the total assemblage of prey that were found in the population as a whole and at that time you could compare two species, two locations, etc.. Cailliet suggested that this points out several ways of comparing prey assemblages, from presence/absence data, which is what a lot of the similarity indices use, to the use of proportions. As we've seen, however, Sibert's talk illustrated that maybe the ranks by proportions aren't so realistic. Cailliet went on to point out that if we can get around the specific problem brought out by Sibert and generate some ranks, then we'll be able to compare ranks by similarity indices that deal with relative proportions, and thus extend our use of rank correlation techniques.

The group then outlined the various statistical techniques applicable to food habits analysis. Cailliet questioned the possibilities of using a Chi-square analysis to compare frequencies in different species categories between different predators, setting up one predator as the expected. Sibert suggested making it an N x N contingency. Robin LaBrasseur mentioned that they were using Chi-square to test replicate pump samples, to see if the first was the same as the last; as it turns out, each pump sample was an independent one. Cailliet said that a lot of similarity indices have been used in taxonomic studies to compare an array of meristic characters in one species to another; perhaps you could think of these in terms of being prey categories. Cailliet also noted that there was a paper in Ecology by Sale (1975), who included the use of Euclidian distance (which is the sum of the proportion of a prey item in one predator minus the sum of the proportional of that item in another predator) and derived significance levels to compare prey species composition in reef fishes. Wendy Gabriel mentioned that Overton (Forest Ecology, OSU) has developed a program treating proportions as vectors, where the cosine of the angle between the two vectors is a correlation coefficient; Obrebski brought up the use of Morisita's c as a covariance statistic in a matrix format. Bob Feller suggested using some of the ordination classification techniques, Q-mode and R-mode, outlined in the basic statistical ecology texts such as Poole (1974). Obrebski noted the use of the scaled Kolmogorov statistic, which can be used to test size frequency distributions but, given a large enough sample size, will almost always show different significant figures. Cailliet asked about the use of rank correlation techniques, i.e. Spearman and

Kendall; Simenstad recommended that a combination of rank correlation and overlap indices (using Shannon-Wiener), both of which have established tests of significance, may be necessary to detect shifts in prey organism rank and diversity of the prey spectra.

SESSION 5

INTERPRETATION AND RESULTS



SESSION LEADER:
Mike Healey

PARTICIPANTS:
Steven Obrebski
Colin Levings
Glenn R. Van Blaricom
M. James Allen
Charles A. Simenstad

DIET OVERLAPS IN COMPETING FISH POPULATIONS IN THE
NANAIMO RIVER ESTUARY

Steven Obrebski, University of the Pacific, Pacific Marine Station
Dillon Beach, CA

John Sibert, Department of the Environment, Fisheries and Marine Service
Pacific Biological Station, Nanaimo, B.C.

An expanding ecological theory concerning factors affecting the composition and stability of natural communities exists (see May, 1974; Cody and Diamond, 1975; Goodman, 1975 for recent reviews) and a major goal of ecology is to test its validity. For example, when sufficient information on resource utilization by competing species and resource production is available, the use of competition theory to predict species abundance is feasible (Pulliam, 1975). It is of related practical interest to know the degree to which marine fish compete for food resources. For instance, the stickleback is known to be an important competitor for food of the sockeye salmon (Foerster, 1968). Fish food habit studies might not only provide information for testing ecological theory but also for optimizing fisheries management procedures if methods for minimizing competitive food utilization by other fish and enhancing growth of exploited fish populations could be developed. Could selective removal of adult stickleback improve growth rates of young fingerling sockeye salmon in lakes or juvenile salmon in estuaries? With such ideal long range research goals in mind our purpose in this paper is to outline some of the problems of measuring food resource overlap in co-occurring populations of various fish species in the Nanaimo River Estuary on Vancouver Island, B.C., in Canada.

Samples of 9 species of fish were collected in the Nanaimo River Estuary in 1972-1974. Generally beach seines were used in shallow intertidal areas and purse seines in subtidal areas. Data on diets of fish collected every 2 weeks between March and July, 1973 are available. This information forms the basis of the present analysis. Details of sampling procedures and identification are available in Anonymous (1974). The data include 79 samples of individual fish species with counts and biomass measurements of gut contents for over 100 diet species. The fish sampled were herring, 3-spine stickleback, shiner perch, Pacific sand lance, prickly sculpin, Pacific staghorn sculpin and juvenile chum, chinook and coho salmon.

The sampling stations are shown in Sibert and Obrebski (these proceedings). Four stations (4, 13, 14, and 15) were in deeper water and were sampled with

a purse seine. The remainder were Intertidal and were sampled by beach seine and pole net at low tide.

We were interested in measuring the amount of competition for food resources between the juvenile salmon and the other fish species sampled. To estimate diet overlap we used an index of association due to Morisita (1959). The index, C_λ is

$$C_\lambda = \frac{2 \sum x_i y_i}{\sum x_i^2 + \sum y_i^2}$$

where x_i and y_i are measures

of the proportions of the i^{th} food category or item in species x and y , respectively. The data used was the percent biomass of diet items for all items represented by 0.1% or more of total biomass in a particular fish species. The index C varies from 0 when there are no food items in common to 1 when all food items are common to both species and occur in the same proportions.

A serious problem in any comparison of diet overlap between any two species results from the sensitivity of item abundance to the number of specimens from which the diet list is obtained. In Figure 1 we plotted the number of diet items in samples of fish species against the number of fish upon which the diet list was based. The results suggest either an exponential or power curve relationship between number of items observed and fish sample size.

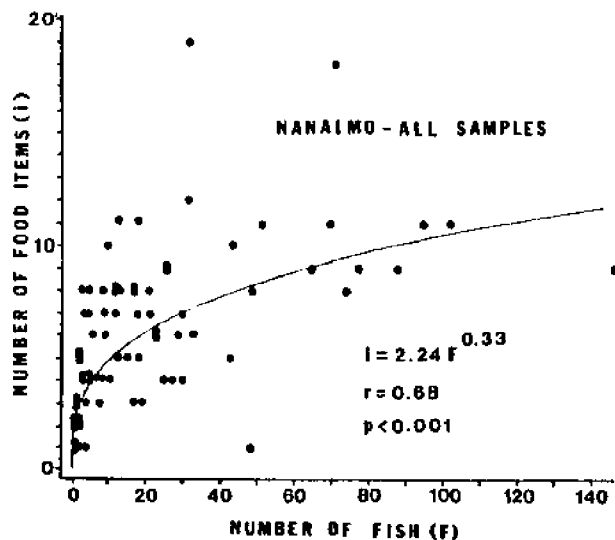


Figure 1. Relationship between the number of items observed in the diet of a sample of fish and the number of fish upon which the estimate of diet item number is based

Least squares fits to the data graphed yielded correlation coefficients of 0.49 for an exponential regression and 0.68 for a power curve, both coefficients being highly significant ($p < 0.001$). We chose the power curve to represent the relationship because of the higher correlation. The great amount of scatter around the regression should also be noted. On the basis of this analysis we eliminated samples involving fewer than 10 fish in comparisons of diet overlap to reduce the effects of small sample size in underrepresenting the number of diet items. Since the index used is based on the number of items in common we wanted to decrease potential variation in overlap due to variation in sample size.

Calculations of C_λ for fish collected in the Nanaimo River Estuary are summarized in Table 1 from which a few single species pair results are omitted. Inspection of the table shows that C_λ varied from 0 to 0.99. Of particular

interest is the recurrence of very high indexes of overlap between chum salmon and 3-spined stickleback indicating that at times these 2 species share many of their food items and take them in similar proportions as measured by food biomass. We chose to focus on feeding relationships between these 2 fish. Calculations of C_λ for all dates and localities for chum salmon and stickleback were made irrespective of sample size. The results are summarized in Table 2. To test the potential effect of small sample size in reducing C_λ we calculated correlation coefficients between sample size

and C_λ in two ways. First, correlations between the sum of numbers of both species of fish and C_λ were computed. Then, correlations between the number of rarer species and C_λ were made. The correlation coefficients were not significant in both cases, suggesting that sample size is not a serious problem in this case although it should be kept in mind that a correlation coefficient would have to exceed 0.5 to be significant if based on 14 pairs of comparisons. Inspection of Table 2 indicates that one half of the estimates of overlap are 0.80 or higher. While diet overlap between the 2 species is often very high, temporal variations are often considerable also. Variations in C_λ within species sampled in different localities are also evident. Chum

salmon and stickleback in subtidal and intertidal stations are compared for the 1-15 June 1973 sample in Table 3. While chum and stickleback in subtidal localities have an index of overlap of 0.99, within species overlaps for the 2 species from the different stations were 0.13 and 0.23, respectively! These considerable excursions in diet overlap and variations within species from different localities suggest that rapid and extensive changes in feeding behavior may be taking place over short periods of time. The foregoing analyses emphasize the need for standardization of sample size before extensive surveys of feeding competition between natural fish populations are made. Recurrent high values of C_λ strongly suggest that the

stickleback is an important competitor for food of the chum salmon, but how reliable is this measure as an indicator of competition? It might be conjectured that if food resources are not limited, and if feeding efficiency is in part density dependent, mixed species groups might increase feeding efficiency of both species. For instance, mixed populations of chum and stickleback, feeding on benthic faunas, might increase food availability for both species by increasing disturbance of the substrate surface. Both

TABLE 1

DIET OVERLAP BETWEEN FISH SPECIES IN HANAIMO RIVER ESTUARY, B.C. IN
MAY TO JULY, 1973

Legend: 3SST- 3-Spined Stickleback; CHIN - Chinook ; SHPE- Shiner Perch; PAST- Pacific Staghorn Sculpin; PRSC- Prickly Sculpin; HERRI- Herring; Morisita's measure $C\lambda$ is used throughout. No comparisons are made where one of a pair of fish is represented by less than 10 specimens; (*) - $0.01 > C\lambda > 0.001$; (**) - $C\lambda < 0.001$; N- No. specimens.

16-31 May 1973 Intertidal Stations

Species	N	3SST	SHPE	COHO	PAST
CHUM	18	0.81	0.81	0.02	0.12
3SST	44	----	0.97	0.03	0.12
SHPE	26	----	----	0.04	0.13
COHO	23	----	----	----	0.13
PAST	26	----	----	----	----

1-15 June 1973 Intertidal Stations

		3SST	CHIN
CHUM	32	0.21	0.05
3SST	71	----	0.25
CHIN	32	----	----

16-30 June 1973 Intertidal Stations

		CHIN	SHPE	PRSC	PAST
3SST	17	0.33	0.35	0.36	0.07
CHIN	13	----	0.53	0.62	0.69
SHPE	13	----	----	0.31	0.39
PRSC	78	----	----	----	0.72
PAST	11	----	----	----	----

1-15 July 1973 Intertidal Stations

		3SST	SHPE	PRSC
HERRI	23	0.08	0.39	*
3SST	17	----	0.17	0.14
SHPE	144	----	----	0.60
PRSC	30	----	----	----

TABLE 1 (CONTINUED)

1-15 June 1973 Subtidal Stations

		CHUM	3SST	CHIN	COHO
HERRI	43	0.99	0.24	**	*
CHUM	74	----	0.99	*	*
3SST	33	----	----	**	0.00
CHIN	12	----	----	----	0.26
COHO	15	----	----	----	----

16-30 June 1973 Subtidal Stations

		CHUM	3SST	CHIN
HERRI	100	0.07	0.12	0.18
CHUM	52	----	0.80	*
3SST	70	----	----	*
CHIN	88	----	----	----

TABLE 2

DIET OVERLAP BETWEEN CHUM SALMON AND 3-SPINED STICKLEBACK

Date	Intertidal Localities			Subtidal Localities		
	Number CHUM	3SST	$C\lambda$	Number CHUM	3SST	$C\lambda$
1-15 March 73	18	18	0.95			
16-31 March 73	26	3	0.97			
1-15 April 73	17	?	0.08			
16-30 April 73	21	5	0.23	3	2	0.04
1-15 May 73	49	12	0.96	29	2	0.10
16-31 May 73	18	44	0.81			
1-15 June 73	32	71	0.21	74	33	0.99
16-30 June 73	2	17	0.00	52	70	0.80
1-15 July 73	1	17	0.03			
16-31 May 74	10	1	0.82			

TABLE 3

WITHIN SPECIES BETWEEN STATIONS OVERLAP

1-15 June 1973, $C\lambda$ for Intertidal (I) and Subtidal (S) Localities	
CHUM(I) vs. CHUM(S) - 0.13	CHUM(I) vs. 3SST(I) - 0.21
3SST(I) vs. 3SST(S) - 0.23	CHUM(S) vs. 3SST(S) - 0.99

species would then have high diet overlaps but partition resources in some other way. In Figure 2 we present another method for comparing the feeding of these 2 species. Food items for the times listed in Table 2 were arranged for each species according to the order of decreasing importance as indicated by their contribution to the percent of total biomass in the diet. Successive biomass percentages for these serially arranged items were summed until the sums accumulated to 90% or more of total biomass. The successive sums were plotted against the serially arranged items in Figure 2. The results show that in 10 of the 14 cases the chum salmon required fewer items to accumulate 90% or more of its biomass. This suggests that in comparison to

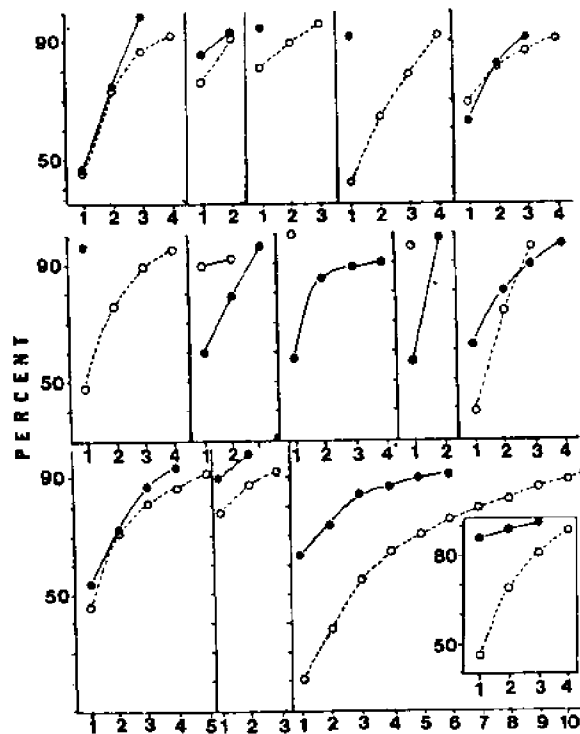


Figure 2. Feeding selectivity and specialization in chum salmon (○) and 3-spined stickleback (◻). Cumulative percent biomass of food items is plotted against food items arranged serially in descending order of contribution to total food biomass. Note that it generally takes fewer food items to accumulate 90% or more of total food biomass in the chum salmon than in the stickleback.

the stickleback, chum are specialists, concentrating on fewer food items to get most of their food. Thus, while the measure of overlap fluctuated considerably, being high only half the time, chum specialized more than stickleback in 70% of the cases examined. We have no information about the actual locations of these potentially competing populations while they are feeding. When diet overlap is high, it would be of interest to know if the species feed in different places or at different times.

The foregoing analyses indicate that rapid changes in diets of fish species can occur in short periods of time. While chum salmon and stickleback had high overlaps ($C_{\lambda} \geq 0.80$) in half the samples analysed (Table 3), the rest of the time overlaps were skewed towards rather low values ($C_{\lambda} \leq 0.23$). Diet overlaps shift radically and frequently and are skewed towards either high or low values. When feeding specialization is compared switching in the degree of specialization also occurred although the chum appeared generally to be more specialized than the stickleback.

There is evidence for the existence of short-term functional responses to changes in prey density involving switching of attacks by predators to concentrate disproportionately on the more abundant prey (Murdock, Avery, and Smyth, 1975). Werner and Hall (1974) showed that size selection of prey in the bluegill sunfish is related to optimal allocation of time spent on searching and handling prey. At low prey abundances different sizes were eaten as encountered but at high densities larger prey were selected. Ivlev (1961) summarizes data showing that at low densities fish electivity for food items decreases to zero. Beukema (1968) found that an important characteristic of stickleback prey searching behavior was its non-random movement. The fish avoided re-visiting areas recently foraged, most fish restricting their activities to areas where prey were abundant. Keenleyside (1955) found that sticklebacks guided each other to areas of high prey density! These studies indicate that complex behavioral factors have to be considered in interpreting fish diet data. We speculate that groups of fish species feeding in areas like Nanaimo River Estuary might not only partition resources in various ways (Schoener, 1974, review) but could change their feeding habits radically and rapidly over short periods of time or over short distances associated with rapid changes in food density and composition. In mixed groups of fish diets may not only change as a result of competitive interactions between species and changes in food availability. It is possible that mixed species groups might facilitate their joint feeding efficiency. For instance dense mixed groups of fish could make more benthic prey available by sufficient disturbance of the bottom than would ordinarily be available at lower densities of only one feeding species. Such possibilities could be evaluated from experimental and field observations of feeding of mixed groups of species.

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A "BUG'S-EYE" VIEW OF FISH PREDATION

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Understanding the dynamics of marine food webs involves an elucidation of the fates of biomass produced by invertebrates. Thorson (1966) concluded that fish predation had a minor influence on the population dynamics of marine invertebrates, but data gathering in many local studies emphasizes this particular route (especially via juvenile salmonids) for biomass loss. Changes (decreases) of prey populations frequently coincide with the arrival of migratory fish (e.g. Muus, 1967), providing an inference that fish are "controlling" prey communities.

An examination and review of the life history and ecological features of two species of gammarid amphipods demonstrates that an understanding of secondary production requires data on a variety of processes in addition to salmonid predation. Especially in estuarine habitats, suggestions that biological interactions are a primary factor in modifying benthic communities are in conflict with theory stating that these assemblages are physically "controlled" (Sanders, 1968). Recent research on certain of these topics at the Squamish River estuary in British Columbia shows that tidal creeks are useful experimental tanks for *in situ* studies.

At the Squamish estuary, the amphipod *Anisogammarus confervicolus* has ecological features that enable the species to minimize predation by fish, especially juvenile salmonids. The biomass distribution of the amphipod is related to river flows, since portions of this species population are "exported" and retained according to prevailing currents and habitats (Levings, 1976). The amphipod's distribution is also closely related to vegetation patterns (especially sedge, *Carex lyngbyei*), providing refuges for the species at both high and low tide. Clumping of prey (e.g. in refuges) can reduce predation (Taylor, 1976). In addition, structurally complex environments might decrease the foraging efficiency of salmonid predators; Ware (1972) demonstrated that trout forage less efficiently in more complex habitats. Tide pools are relatively uncommon in the estuary, so the amphipod is almost totally unavailable to fish when the tide is out.

These features seem to "buffer" the amphipod population from the effects of salmonid predation. Life history observations on *A. confervicolus* show that biomass increase (Fig. 1a) can occur at seasons when juvenile salmonids (especially chum *Oncorhynchus keta*) are most abundant in the estuary (April-May; Goodman and Vroom, 1972). Juvenile amphipods (Fig. 1b) are the main prey for the young chum salmon. Cottids (mainly *Leptocottus armatus*) are the other major fish predators in the estuary (Lavy, in progress). Predatory invertebrates are rare in the estuary.

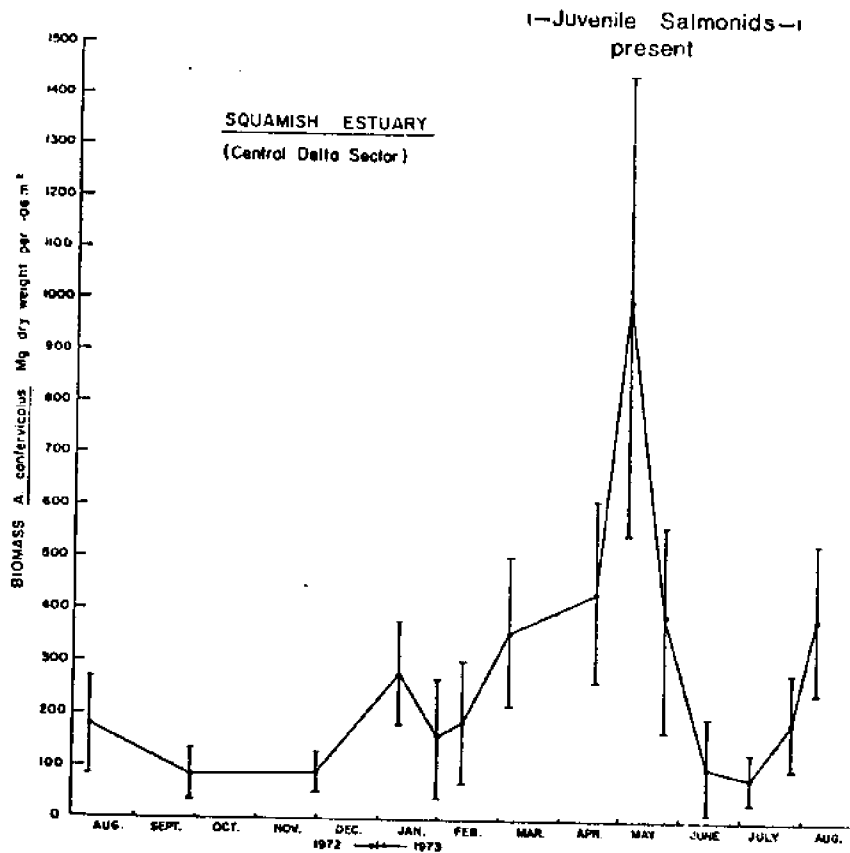


Figure 1a. Temporal change in biomass (mg dry wt/0.06 m²) of *Anisogammarus confervicolus* at the Squamish estuary (central sector). Samples were obtained with quadrats at low tide in sedge rhizome mats (Levings, 1973). Mean values (n=10) and 95% confidence limits for each sample are shown.

In contrast, the population dynamics of an Atlantic amphipod (*Photis reinhardi*) living in marine, subtidal habitats, reflects the effects of seasonal fish predation by winter flounder (*Pseudopleuronectes americanus*) (Levings, 1974). The flounders, which were the most abundant fish predator in the study area, immigrated to the habitat when the amphipod population was dominated by ovigerous females. The predators removed these large individuals, thus contributing to a decline in biomass (Fig. 2a, b). *P. reinhardi* has few refuges in its habitat. The amphipod builds diminutive burrows, but its level-bottom muddy habitat is relatively unstructured, so that the species is more accessible to predation. The habitat is subtidal, so fish predators can operate more consistently. Several predatory species of invertebrates (e.g. nereid polychaetes and nemertean) are present.

Data on mortality rates are required to calculate secondary production, and it is of interest to compare the significance of the various factors for the two

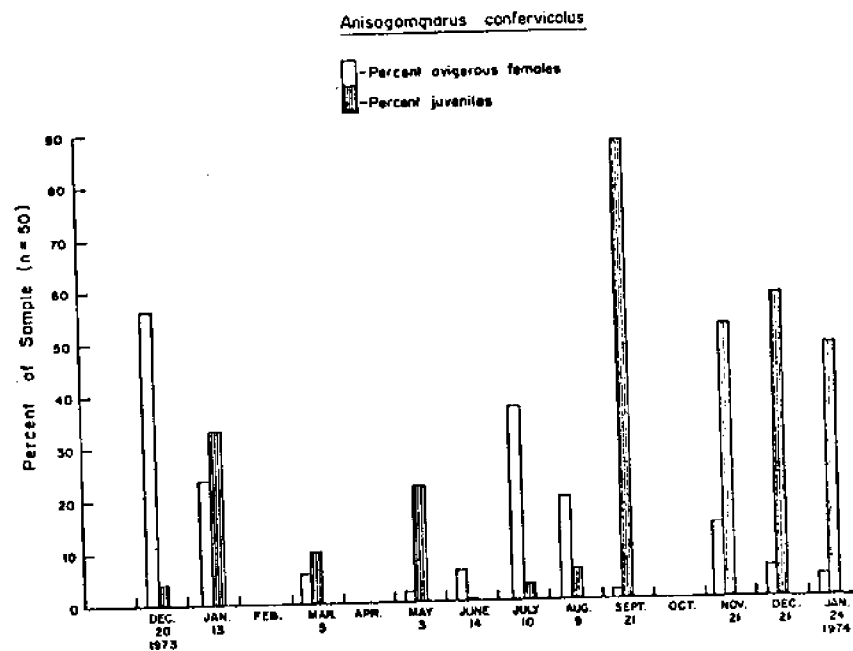


Figure 1b. Temporal changes in frequency of juveniles and ovigerous females for *A. confervicolus* at the Squamish estuary (central sector). Juveniles defined as organisms passing through a 1.7 mm mesh screen.

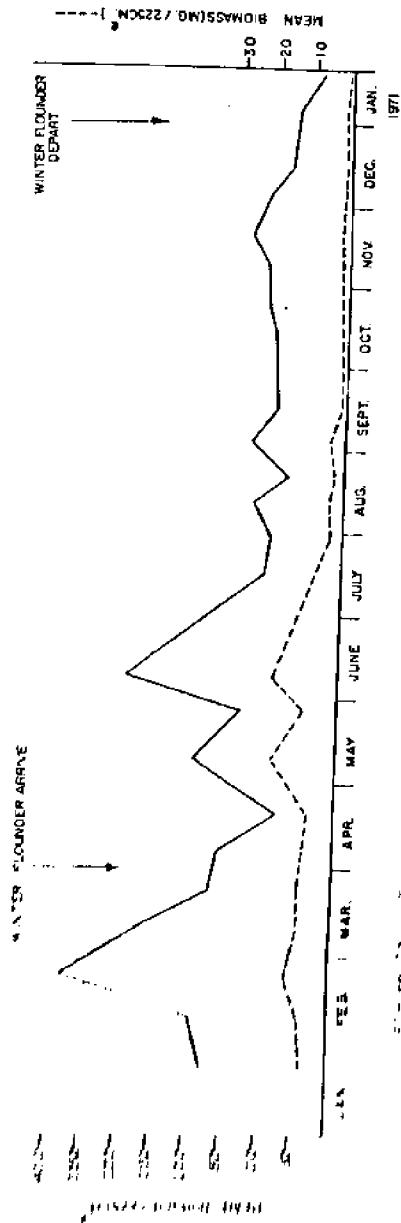


Figure 2a. Temporal changes in abundance (number, biomass) of *Photis reinhardi* at St. Margaret's Bay, Nova Scotia. Winter flounder immigrated to the study area in November, and were absent in winter months. Samples were obtained with an Ekman dredge, and mean values per 225 cm³ (n = 5) are shown.

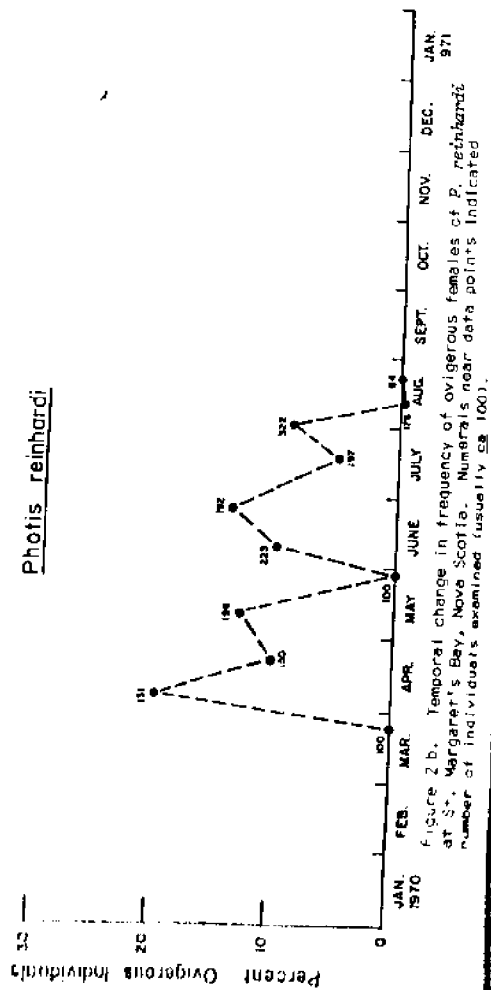


Figure 2b. Temporal change in frequency of ovigerous females of *P. reinhardi* at St. Margaret's Bay, Nova Scotia. Numerals near data points indicated number of individuals examined (usually ≤ 100).

amphipods. For a given time interval, instantaneous mortality rate (m) can be dissected as follows:

Anticammarus confervicolus: $m = Sp + Cp + Ap + L + N$, where
 Sp = salmon predation, Cp = cottid predation, Ap = avian (bird) predation,
 L = loss term due to tidal "export" from the estuary, and N = "natural"
mortality (disease, senescence).

Photis reinhardi: $m = Fp + Ip + N$, where
 F = flounder predation, I = invertebrate predation, and N is as above.

Measurement of the loss term for the estuarine amphipod is a major difficulty, given the vagaries of estuarine circulation.

Tidal creeks penetrate the marsh habitats at the Squamish estuary, and those features have been used as experimental tanks in fish feeding experiments. A beach seine was used to block the seaward end of the creek. At high tide, juvenile chum salmon conditioned in the laboratory to a variety of prey were introduced behind the net. Through careful selection of times and tides, experiments lasted up to 14 hours, spanning light and dark conditions. Fish collected at low tide when the creek drained, and about 20% of experimental fish were recovered. More fish could be recovered if concrete or wooden rims were constructed. Preliminary results show that juvenile chums fed mostly on the organisms they were conditioned to. The technique could be used to determine rates of a number of feeding processes e.g. consumption.

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PRELIMINARY OBSERVATIONS ON INTERACTIONS
BETWEEN TWO BOTTOM-FEEDING RAYS AND A
COMMUNITY OF POTENTIAL PREY IN A
SUBLITTORAL SAND HABITAT IN SOUTHERN CALIFORNIA

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The development of standard techniques for fish diet evaluation is a vital step toward the understanding of a larger issue, the nature of interactions between fishes and the communities they exploit for food. The preferential removal of certain kinds of prey from a broad spectrum of potential prey can have a key role in determining demographic and distributional patterns in prey communities (for example, Brooks and Dodson, 1965). Direct observation of prey consumption by fishes is difficult to accomplish on a regular, quantitative basis. As a result, stomach content study is a primary tool for describing fish diets. However, an investigator relying exclusively on stomach content data assumes that the impact of fish predation on a potential prey assemblage can be fully characterized in terms of prey eaten by the fish. This assumption may be inappropriate for certain systems involving demersal predatory fishes.

During some three hundred SCUBA dives on the subtidal sand plain near LaJolla, California, USA, I have observed the round stingray *Urolophus halleri* (Cooper) and the bat ray *Myliobatis californica*, (Gill) making extensive bottom excavations, apparently to expose and capture prey items. Walford (1935) describes this behavior in *Myliobatis* and relates it to feeding. The digging behavior involves rhythmic flapping of the rostrum and pectoral fins and is similar in both species. The underlying sand is swirled to the front and sides of the digging ray, uncovering deeply buried infauna and leaving a pit of characteristic shape which is visually distinct from other sedimentary structures in the area. In response to these observations, I set up preliminary sampling schemes and experiments to test the assertion that the foraging behavior of the two rays constitutes a disturbance of significance to abundance patterns of benthic species rarely or never ingested by the rays.

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Methods

All benthic sampling and behavioral observations were done at the primary study site directly offshore from the Scripps Institution of Oceanography in LaJolla. The study site is sixteen meters deep with a bottom of well-sorted fine sand of low organic carbon content (< 0.25%), and is roughly midway between the Scripps and LaJolla submarine canyons.

Rays used for stomach content evaluation were collected at or near the main study site by spearing or with bottom-anchored set lines checked at 2-3 hour intervals. Stomachs were removed immediately after collection and fixed in 10% formaldehyde solution for 1-2 days, then dissected and analyzed. For each prey species, numbers of individuals and percent of total stomach content volume were determined. Prey species importance was indexed by multiplying prey frequency (percent of all non-empty stomachs which contained the species) by mean percent volume of stomach contents for the given species.

Benthic animal densities were determined by collecting replicate sets (n=2 or 3) of hand-operated cores. The cylindrical cores were of two sizes (large: 0.018 m² surface area; small: 0.008 m² area, both penetrate 10-12 cm into sediment). Cored sediments were screened (mesh openings 0.5 mm), fixed in 10% formaldehyde solution for 1-2 days, then stored in 70% isopropanol prior to sorting and counting. Coring techniques were used to assess recovery of benthic populations in both natural and simulated (holes formed by hand-fanning bottom sands until the dimensions of natural holes were obtained) ray disturbance sites. Small corer arrays were used to determine the spatial extent of faunal disturbance associated with ray feeding holes for both Myliobatis (corer array shown in Figure 1) and Urolophus.

Rates of ray disturbance were determined in two permanent contiguous 1 X 25 meter belt transects at the main study area. Extant ray pits were marked with small stakes such that on a subsequent resurvey (usually 2-5 days later) new pits could be counted and measured, allowing computation of a disturbance rate, expressed as percent of total transect area disturbed per day.

Results

The ten prey categories most important in the diets of a modest sampling of Urolophus (n=11) and Myliobatis (n=26) are shown in Tables 1 and 2. Table 3 lists the ten most numerous benthic species in large cores collected in June-August 1976 from the main study area. Data in Table 3 are for cores taken in "baseline" locations, i.e., in areas which have not received recent disturbance from feeding rays. None of the important

Table 1. Principal Prey Items Found in Stomachs of Urolophus halleri¹

Importance Rank	Prey Category	Frequency of Occurrence (%)	Mean # per Stomach	Mean % Volume per Stomach
1	<u>Nototropis</u> sp. ²	20	206.0	92.5
2	<u>Blepharipoda occidentalis</u> Randall ⁵	30	8.67	43.3
3	<u>Harenactis attenuata</u> Torrey ⁴	10	1.0	100.0
4	<u>Dispio uncinata</u> (Hartman) ⁵	10	25.0	90.0
5	<u>Pectinaria californiensis</u> Hartman ⁵	20	2.5	40.0
6	<u>Leptosynapta</u> sp. ⁶	30	2.0	23.3
7 (tie)	<u>Megaluropus</u> sp. ²	20	17.0	25.0
	<u>Plinixa</u> sp. ³	10	5.0	50.0
9	Unidentifiable polychaete parts	40	-	10.0
10 (tie)	<u>Anchicolurus occidentalis</u> Calman ⁷	20	6.0	10.0
	<u>Cancer</u> sp. ³ (juveniles)	20	4.5	10.0
	<u>Monoculodes</u> sp. ²	10	18.0	20.0
	Decapod megalops larvae	10	2.0	20.0
	<u>Alpheus clamator</u> Lockington ⁸	10	5.0	20.0

(1) Empty stomachs (n=1) excluded from data, (2) Gammarid Amphipod, (3) Decapod crab, (4) Coelenterate, (5) Polychaete annelid, (6) Holothurian echinoderm, (7) Cumacean crustacean, (8) Decapod shrimp

Table 2. Principal Prey Items Found In Stomachs of *Myliobatis californica*¹

Importance Rank	Prey Category	Frequency of Occurrence %	Mean # per Stomach	Mean % Volume per Stomach
1	<u>Leptosynapta</u> sp.	64	5.3	59.3
2	<u>Lolligo opalescens</u> Berry ²	27	4.5	83.0
3	Ophiuroidea	27	2.2	31.0
4	Large unidentifiable bivalves	18	1.3	46.3
5	Unidentifiable polychaete parts	36	-	13.9
6	<u>Listriolobus pelodes</u> Fisher ³	14	3.3	35.0
7	<u>Isocholes pilosus</u> (Holmes) ⁴	4.5	1.0	40.0
8	<u>Crangon nigromaculata</u> Lockington ⁵	4.5	1.0	20.0
9	Unidentifiable fish parts	4.5	1.0	10.0
10	<u>Phyllospadix torreyi</u> Watson ⁶	23.0	-	1.4

(1) Empty stomachs (n=4) excluded from data, (2) Cephalopod mollusc, (3) Echiurid, (4) Pagurid decapod crab, (5) Decapod shrimp, (6) Marine angiosperm plant

Table 3. Abundant Benthic Animals from Core Sampling of Primary Study Area¹

Mean Abundance Rank	Species	Mean # per Core	Range	Frequency %
1	<u>Paraphoxus abronius</u> Barnard ²	79.6	21-133	100
2	<u>Tellina carpenteri</u> Dall ³	19.8	10-28	100
3	<u>Acuminodeutopus heteruopus</u> Barnard ²	16.1	5-27	100
4	<u>Rutiderma rostrata</u> Juday ⁴	7.8	5-17	100
5	<u>Ampelisca compressa</u> Holmes ²	5.8	1-22	100
6	<u>Mysella tumida</u> (Carpenter) ⁵	5.5	2-10	100
7	<u>Synchelidium</u> sp. ²	4.5	1-11	100
8	<u>Mediomastus acutus</u> Hartman ⁵	4.5	0-8	83
9	<u>Nebalia pugettensis</u> (Clark) ⁶	4.1	1-12	100
10	<u>Edwardsiella</u> sp. ⁷	4.0	0-9	83

(1) Based on 12 large (surface area 0.018 m²) core samples for crustacea, 6 large cores for other species., (2) Gammarid amphipod, (3) Bivalve mollusc, (4) Ostracod crustacean, (5) Polychaete annelid, (6) Leptostracan crustacean, (7) Coelenterate

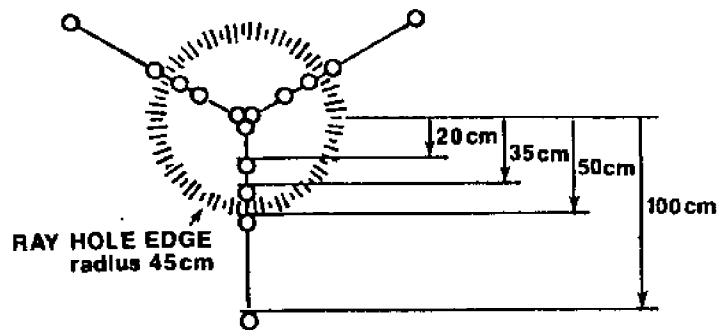


Figure 1. Sampling layout of *Myliobatis californica* disturbance site. Small circles represent positions of cores relative to the ray hole. Distances shown were measured between the ray hole center and the inner edge of each core.

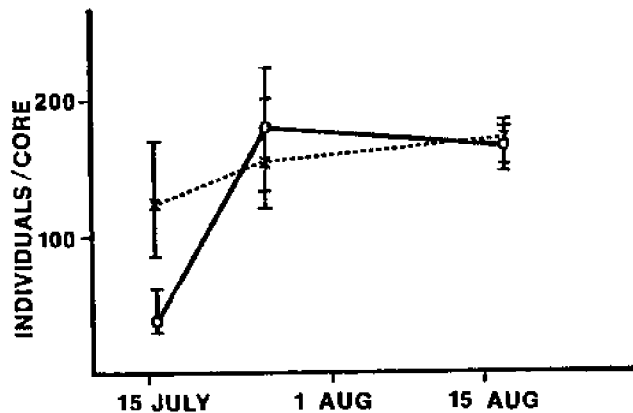


Figure 2. Recovery of benthic crustaceans (sum of all species) in natural ray disturbance sites. Sample means from disturbance sites are represented by open circles and solid lines, those from adjacent undisturbed areas by crosses and broken lines. Vertical bars show ranges for each triplicate sample set.

food species for either ray appears in the list of abundant benthic fauna. With the exceptions of *Monoculodes* sp. ($f = 67\%$), decapod megalops larvae ($f = 25\%$), and *Leptosynapta* sp. ($f = 16\%$), none of the prey species listed had a frequency greater than 10% in the summer 1976 "baseline" core samples, and most had frequencies of zero. Data from core samples taken in a number of locations on the subtidal sand habitat near LaJolla suggest that the preferred prey are uniformly rare rather than occurring in isolated high-density patches (such patchiness might explain the importance of the prey species if rays were able to locate areas of locally high abundance). Data from vertically partitioned cores indicate that virtually all infauna (including most species found in Tables 1 & 2) live within 5 cm of the sediment surface. Thus it is doubtful that the rareness of the exploited species is an artifact of inadequate corer penetration into the sediments.

Most of the preferred prey species for both rays have body sizes many times larger than any of the species listed in Table 3. Thus the most common benthic species may escape consumption by foraging rays as a consequence of their small size. However, data from core samples from natural and simulated ray holes of varying ages suggest, when compared with "baseline" samples, that ray disturbance has important and complex effects on populations of the abundant species.

Figure 2 shows summed abundances of benthic crustaceans in triplicate sets of large core samples taken from natural ray holes and "baseline" areas during summer 1976. All ray holes sampled were newly formed in the permanent belt transects between 14 and 16 July 1976. No ray hole was sampled more than once. Data show an initial depression of crustacean numbers in ray holes relative to undisturbed sediments. Ten days later, the summed densities had recovered, but individual species abundances in the ten-day ray hole samples differed considerably from "baseline" cores, with numbers of the gammarid amphipods *Synchelidium* sp., *Monoculodes* sp., *Uristes entalladurus* Barnard and *Acuminodeutopus heteruropus* Barnard exceeding normal levels and accounting for most of the recovery. In the 31-day samples the crustacean fauna of the ray disturbance sites closely resembled "baseline" abundances, both in summed density and in numbers and ranks of component species.

A similar pattern appeared in a ray disturbance simulation experiment run during winter 1976. On five dates replicate pairs of cores were taken from simulated ray feeding pits (dug on 29 Jan.) and adjacent undisturbed sands. Figure 3 shows that the initial depletion of summed crustacean numbers was followed by a recovery phase in which abundances exceeded baseline levels. Three of the four species which were early colonists of natural ray holes (*U. entalladurus* was the exception) plus two others (the amphipod *Megaluropus* sp. and the cumacean *Diastylopsis tenuis* Zimmer) were responsible for the over-compensation in the simulated disturbance pits. The excess summed crustacean levels and the high densities of early colonizing species persisted through a second sampling date, 22 days after the disturbances were made. The 33-day samples showed no important differences in the crustacean fauna of disturbed and

undisturbed sediments.

The response of combined polychaete densities to simulated ray disturbance, shown in Figure 4 was somewhat different than that of crustaceans. Numbers were initially depressed by the disturbance event and recovered slowly, converging with undisturbed densities in the 22-day samples. Abundances of component polychaete species in disturbed and undisturbed sands were similar at the time the summed densities converged.

Small core sample arrays collected from feeding holes formed by Urolophus (pit radius 20 cm) and Myliobatis (radius 45 cm) provided evidence that the areal extent of disturbances approximately corresponds to the visually perceived dimensions. These patterns were consistent for all crustacean, bivalve and polychaete species which were sampled in numbers sufficient to determine spatial patterns.

Nine pairs of transect surveys were made to determine rates of ray disturbance to the sediments by foraging rays. The mean rate was 0.55% of bottom area disturbed per day (range: 0-1.69%), with highest rates occurring during the warm water months of August and September in both 1975 and 1976. The size frequency distribution of ray holes is bimodal, with peaks at radii of 15 cm (probably due to Urolophus feeding) and 30 cm (probably caused by the much larger Myliobatis). Most of the ray holes (89%, N=150) were included in the small radius mode, suggesting that Urolophus is more important than Myliobatis as a source of benthic community disturbance.

Discussion

A system described by Orth (1975) is similar in many ways to the situation I have discussed for southern California. Orth has described the foraging activities of groups of cownose rays (Rhinoptera bonasus) which frequent the shallow sediments of Chesapeake Bay during summer months and employ foraging techniques (described by Bigelow and Schroeder, 1953) which apparently resemble those I have observed in Urolophus halleri and Myliobatis californica. During the summer of 1973 large groups of R. bonasus damaged or eliminated large stands of eelgrass (Zostera marina), to the considerable detriment of associated epifaunal and infaunal assemblages, while digging for their preferred bivalve prey. Stomach content study showed that most species reduced in abundance were unimportant as prey for R. bonasus.

Data from my preliminary work in southern California lend support to the notion that feeding activities by two rays in a sublittoral sand bottom community provide predictable physical disturbances to the rays. As a result, rigorous experimental testing of this hypothesis is now underway. Techniques include the controlled use of large cages which protect areas of the bottom in the main study area from the disruptive effects of foraging rays. Replicate sets of experimental and control cages are now in place and will be sampled in early November, 1976. These

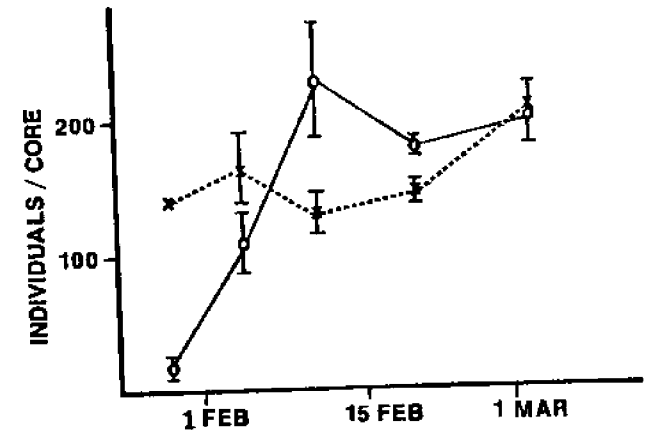


Figure 3. Recovery of benthic crustaceans (sum of all species) in simulated ray disturbance sites. Sample means from disturbance sites are represented by open circles and solid lines, those from adjacent undisturbed areas by crosses and broken lines. Vertical bars show ranges for each sample pair.

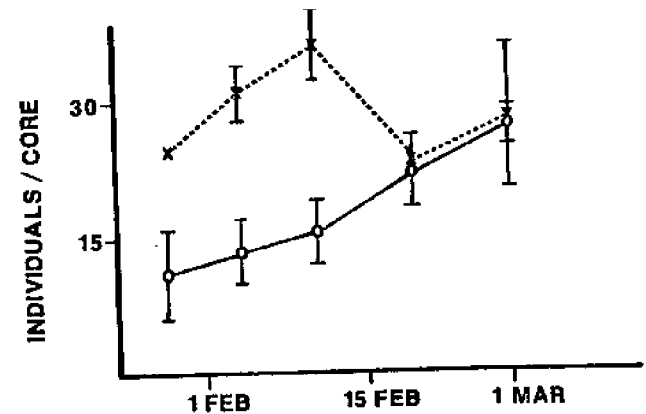


Figure 4. Recovery of benthic polychaetes (sum of all species) in simulated ray disturbance sites. Symbols are the same as those in Figure 3.

studies are being supported by expanded collections of rays for more satisfactory dietary characterization, and by extensive core sampling of benthic fauna.

It is apparent that the effects of predatory fishes on the structures of communities of potential prey populations cannot, in some cases, be adequately described by analysis of stomach contents. A full understanding of a fish's function in a prey community requires knowledge of the impact of foraging activity on populations which are not preferred as food. Thus, the improvement of fish diet analytical techniques must be accompanied by expanded studies on the nature and consequences of fish feeding behavior.

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PREY ORGANISMS AND PREY COMMUNITY COMPOSITION OF JUVENILE SALMONIDS IN HOOD CANAL, WASHINGTON

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For the past 2 years, investigators at Fisheries Research Institute have conducted intensive sampling of migrating juvenile salmonids, principally chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*), during their early marine life in northern Hood Canal, Washington. These studies have been funded from the OICC Trident Environmental Monitoring Program. The objectives of these studies are to monitor the movement of juvenile salmonids along the stretch of Hood Canal which is the site of the U.S. Navy Trident submarine base; and to evaluate the potential impairment to this migration caused by activities associated with the construction of piers, wharves, and docks along the base's Hood Canal shoreline, including the effects of dredging, of the impact of the installations themselves, and of the proposed 24-hour lighting of the shoreline environs at these facilities.

In conjunction with this sampling program, representative specimens of juvenile salmonids were retained for quantitative stomach analyses in order to document the importance of nearshore shallow sublittoral and neritic prey organisms in the critical early marine life of these fish.

In addition to the view of the juvenile salmonids' early marine habits from the "inside out" via analysis of the stomach contents, preliminary sampling of epibenthic and neritic plankton communities was also attempted in order to relate the spectrum of prey organisms consumed to those "available" in the nearshore environment at the time of migration.

The purposes of this paper are briefly to describe 1) the techniques we find optimum in sampling juvenile salmonids during their early marine residence, 2) an epibenthic suction pump which we utilized to sample epibenthic plankton, 3) the prey organisms consumed by these fish during their migration along the northern Hood Canal shoreline, and 4) the composition of the shallow sublittoral epibenthic and neritic plankton assemblages as sampled by the epibenthic pump.

MATERIALS AND METHODS

Predator Collection

Two methods were necessary in our juvenile salmonid collections--beach seining and tow netting. These methods enabled us to capture both schooled early resident fish in the 40-60-mm size range during daylight when they migrated through the shoreline shallows, and larger fish in the 70-100-mm size range which occupy the neritic waters farther offshore at night.

The beach seine is the same one used in the Institute's north Puget Sound and Strait of Juan de Fuca baseline studies: 37 m (120 ft) long, equipped with 18-m (59-ft) long, 3-mm (1-1/8-inch) mesh wings, and a 0.6-m x 2.4-m x 2.3-m bag of 6-mm (1/4-inch) mesh. The net as used in the juvenile salmonid studies is equipped with flotation sufficient to keep the net fishing along the surface. The nets were set by small boat during daylight low slack tide, 50 m away from and parallel to the beach, and were retrieved to the beach by hand at approximately 10 m/min. The lines attached to the poles at the end of each wing were initially hauled from positions 40 m distant until 20 m of line had been retrieved; the net was then closed down to a 12-m opening and retrieval to the beach completed. This net could sample all shoreline habitats except those characterized by very dense eelgrass or kelp or with large boulders.

Tow net collections were made with a 3-m x 6-m (10-ft x 20-ft) surface trawl, with mesh sizes grading from 76 mm (3 inches) at the mouth to 6 mm (1/4 inch) at the cod end. This net is towed at night between 2 vessels at approximately 4 km/hr for 10-minute tows along established transect lines, both parallel to shore (approximately along the -6 m depth contour) and in zigzag transects across the canal.

Fish destined for stomach contents analyses were retained in anesthetic and preserved in 10% buffered formalin with the abdominal wall slit.

Prey Organism Collection

Earlier preliminary studies of the diets of juvenile salmonids in North Hood Canal (Kaczynski, et al., 1973; Feller and Kaczynski, 1975; Simenstad, in press) had indicated the importance of epibenthic plankton, especially crustaceans. Unfortunately, there is little information on the epibenthic plankton communities of the shallow sublittoral regions of Puget Sound. They cannot be effectively sampled with traditional sampling techniques such as plankton net tows or with intertidal transect cores or quadrant sampling; nor do more appropriate epibenthic samplers such as the several developed epibenthic sledges (Holme, 1971) appear to be efficient gears when used in shallow waters.

After the success of an epibenthic pump sampler used by Feller and Kaczynski (1975), a suction pump utilized for sampling nearshore plankton in the Aleutian Islands (Burgner, et al., 1969) was modified to sample shallow sublittoral epibenthic plankton. The advantage of this type of sampler is that the researcher can sample in almost any habitat (it does not have to be towed

over the benthos) and substrate (e.g., gravel, cobble, and rock unavailable to corers). Also, it can sample at any position in the water column (unlike a sledge) and can provide an accurate measure of the quantity of water strained.

The pump system (Fig. 1) consisted of a self-priming, gasoline-powered, 5.1-cm (2-inch) centrifugal pump which draws water and associated plankters through a 25.4-cm (10-inch) conical expander into a 5.1-cm flexible plastic hose. Once through the pump, the water sample passes through a sealed-register, totalizing flowmeter into a double stainless steel cylinder in which 2 nested conical nets were suspended. The nets were of 505- μ and 206- μ mesh sizes with area/aspect ratios of 1:2.54 and 1:5.3, respectively. The epibenthic organisms were retained in standard net buckets with window screen of appropriate mesh size.

The pumping system was operated from aboard a 26-ft boat maneuvered within about 15 m of the beach and anchored. SCUBA-equipped divers then proceeded to survey the bottom and to place at random a 1-m diameter metal hoop (3.14 m² area) over a representative area. The pump was started and the suction hose end was passed to the divers who moved to the chosen sampling location. Upon a signal from the boat, the divers began to move the expander cone about 10 cm off the surface of the benthos within the sampling area, "vacuuming" the epibenthic region. Four projecting bolts on the expander were used to stir the very surface layer of the benthos. Several seconds after the diver had initiated the suction sampling, the 2 nested nets were dropped into place within the steel cylinder. This lag time ensured that the water and organisms within the pumping system at the starting time had passed through before the nets were in place and filtering. One hundred gallons was pumped through the nets before the nets were removed and the divers signalled to stop sampling. Organisms were removed from the plankton net cups and preserved in 5% buffered formalin in labeled PUC jars.

The sampling process was repeated for 3 replicates, the sampling hoop being moved to a new area of similar substrate for each sample.

In the laboratory the epibenthic plankton samples were transferred to 70% isopropyl alcohol and stained with rose bengal dye, stirred, and allowed to sit for at least a week so that organisms would be completely stained. The organisms were then separated from the sediment and detritus in the sample, sorted to the lowest taxonomic level possible by examination through a 30X dissecting microscope, and total counts and weights (to nearest 0.01 g) were obtained for each taxon.

Stomach Analyses

Stomach contents of the juvenile salmonids were analyzed according to a systematic, standardized, quantitative procedure, described in detail by Cathy Terry earlier in the course of this workshop. This method provides the numerical and gravimetric composition of prey organisms contained in the stomach, the degree of fullness of the stomach, and the state of digestion of its contents.

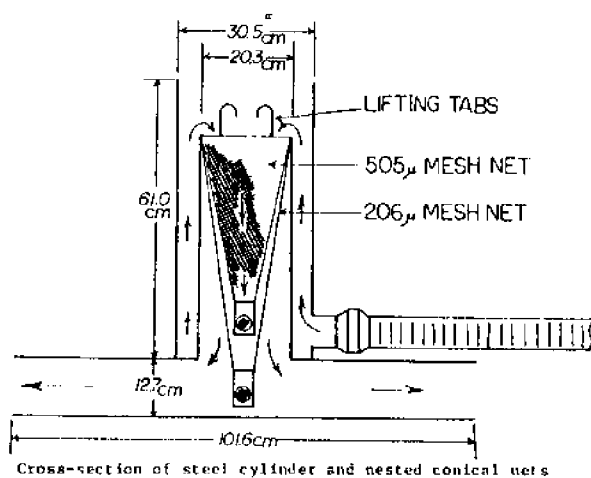
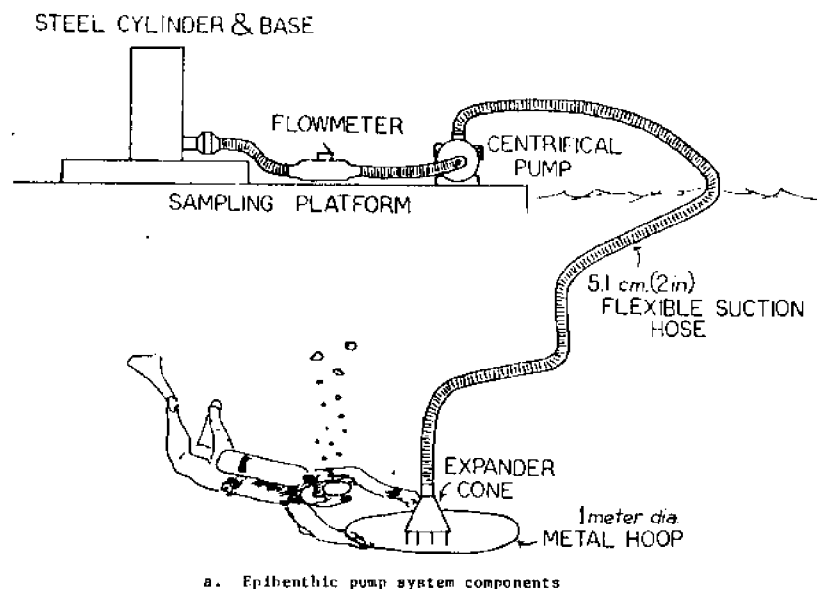


Figure 1. Overall system design and construction detail of epibenthic pump sampling system

Sampling Sites

During peak migration period (March-May), beach seine collections, from which juvenile salmonids were retained for stomach analysis, were made approximately monthly at 5 sites in the north Hood Canal area. Tow net collections were conducted biweekly along 6 general transect lines (Fig. 2). Epibenthic plankton samples were taken from shallow sublittoral areas at the beach seine sampling sites and from the neritic zone at an offshore piling adjacent to one tow net transect line.

RESULTS AND DISCUSSION

Prey Organisms of Juvenile Salmonids

As indicated earlier in Simonstad (in press) and in the limited literature discussing Puget Sound juvenile chum and pink salmon food habits (Kaczynski, et al., 1973; Feller and Kaczynski, 1975), in the daylight period of their early marine migration juvenile pinks and chums prey mainly upon epibenthic crustaceans, later in the migration period shifting to insects and some planktonic organisms, depending upon the nearshore habitat in which they are feeding. Larger chums and pinks found in neritic waters offshore at night were consuming larger pelagic prey, principally gammarid amphipods, calanoid copepods, and fish and macroinvertebrate larvae.

The prey spectra illustrated in Figure 3 are representative of the data from the past year's collections and support the earlier information. Both chums and pink juveniles in the 35-45-mm range concentrated their feeding upon shallow sublittoral populations of epibenthic crustaceans and their eggs—principally harpacticoid copepods, gammarid amphipods, mysids, cumaceans, and leptostracans, and harpacticoid and gammarid eggs. Larger prey such as gammarid amphipods and mysids provided higher biomass contributions to the diets, but smaller organisms such as harpacticoids and their eggs tend to dominate the diet numerically.

One major question is the source of the gammarid and harpacticoid eggs in juvenile salmonid stomachs. The source of these eggs or egg cases may be in consuming ovigerous females and the separation of eggs from the adults in the stomach, which is probably the case with harpacticoid copepods. In many instances, however, the abundance of eggs is far out of proportion to the number of adults in the stomach, suggesting that the eggs are consumed as separate food items. The data indicate that this may indeed be the case with gammarid amphipod eggs. Many of these organisms may be too large or difficult for small juvenile salmonids to handle, and in attempting to do so, the salmonids may cause the amphipods to release the eggs from the brood pouch. Thereupon, the predator could consume the free eggs. Such feeding behavior should be tested in laboratory experiments to substantiate whether or not this is an actual feeding strategy.

There was considerable overlap in diet between juvenile chum and pink salmon early in their concurrent marine residence, but divergence in diet with time and size. The pinks eventually shifted much more to gammarid amphipod eggs,

calanoid copepods, and leptostracans as they got larger, while the chums appeared to continue their feeding preference for harpacticoids, although leptostracans had also increased in importance in the chum diet.

Nighttime tow net catches indicate that larger juvenile salmonids occupy the neritic waters off the Hood Canal shoreline, although not in dense schools as found along the shallow sublittoral during the day. Neritic-occurring juvenile chums and pinks were more catholic in their diet and tended to concentrate upon larger pelagic organisms. There still was considerable contribution by harpacticoid copepods and gammarid amphipods but they may have been a remnant of daytime feeding in the shallow sublittoral, depending upon when the fish samples were obtained. Clupeid larvae were important in the diets of neritic chum and pink salmon in April, typically dominating the prey composition by biomass. Approximately a month later, decapod and cirriped larvae, insects, and calanoid copepods had replaced the fish larvae as the most important prey organisms. At this time the diets of neritic chums and pinks had become slightly more divergent, with chums consuming a greater percentage biomass of calanoid copepods and decapod larvae while pinks had consumed more cirriped larvae.

Epibenthic Plankton Populations

Preliminary sampling of shallow sublittoral epibenthic plankton with a modified suction pump indicates that, with some improvements, this system may provide a valuable source of quantitative information about the composition of prey organisms available to juvenile salmonids. As a tool for sampling neritic plankton, however, it may need further reconsideration or some modifications in sampling design.

Table 1 illustrates the numerical and gravimetric composition of epipelagic plankton at 2 shallow sublittoral sites and 1 neritic site at Hood Canal, March-May 1976. The abundance of organisms is shown for both the 206- μ and the 505- μ mesh samples, and for the larger organisms retained by the 505- μ mesh net, biomass is indicated where possible.

The composition of our samples taken at the Trident base was similar to the composition found by Feller and Kaczynski (1975) in their epibenthic sampling of Dabob Bay, Hood Canal.

Total numbers of organisms sampled by the epibenthic pump are within reasonable variation (< 50% of mean) over the 3 replicate samples taken at each site. Values for the total biomass of organisms retained by the 505- μ mesh net are considerably more variable, which may be due to the lack of precision of the weighing instruments when very low weights are involved.

Principal salmonid prey organisms are effectively sampled and, in some cases, have acceptable values of variability about the sample mean abundance values. Values for many organisms, however, have coefficients of variation over 100% of the mean. Whether this is a fault in the sampling technique, or is genuinely descriptive of the spatial distribution of clustered populations of organisms is not clear at this time. We intend to make further modifications to the sampling design in order to reduce variability attributable to the sampling technique.

Harpacticoid copepods, gammarid amphipods, and their eggs are all sampled with the pump, though with a wide range in variability. As with the incidence of these crustacean eggs in the predator's stomach, the occurrence of separate eggs and egg cases in the pump samples poses a problem. Either the pumping process is separating the eggs from the ovigerous females or these eggs are much more freely available in the environment than we assumed.

These pump samples also indicate that it may be feasible to detect the changing abundances of epibenthic plankters with time and season as well as illustrate definite interhabitat differences in available epibenthic prey. The pump samples can also provide intact specimens necessary for evaluating the life histories of many of the more important plankters.

Plankton pump samples from neritic waters are definitely more diverse than from the shallow sublittoral, though not necessarily more variable. Whether or not it samples many of the larger, more mobile components of the neritic plankton available to juvenile salmonids is the question. For instance, fish larvae and some decapod larvae may not be represented in the samples in proportion to their occurrence in the environment, or perhaps not at all. Again, this may be a function more of the patchy distribution of these plankton than of the sampler itself.

Juvenile Salmonid Diets and "Available" Prey Organisms

A preliminary comparison of juvenile chum and pink salmon prey organisms with the overall spectrum of epibenthic and neritic plankton available for consumption (Fig 4) suggests some interesting aspects of juvenile salmonid feeding behavior. In the shallow sublittoral, juvenile salmonids preferentially consume the smaller, less abundant harpacticoid copepods rather than the larger, more abundant gammarid amphipods. Although the incidence of gammarid eggs suggests that the salmon may attempt to prey upon adult gammarids, they may not be able to ingest them because of the amphipod's size or activity. Despite the fact that the epibenthic pump samples did not illustrate a great abundance of leptostracans, these small crustaceans also formed a large percentage of the plankters consumed in the shallow sublittoral.

Neritic-feeding juvenile salmonids consumed several organisms which either were not abundant components of the neritic plankton or were not effectively sampled by the pump--e.g., cirriped larvae, clupeid larvae and insects. Almost all the important prey in this feeding realm are larger than those in the shallow sublittoral, which may be because of the larger sizes of the neritic salmon and nighttime feeding behavior in limited light conditions.

Summary

Juvenile chum and pink salmon during their early marine residence in Hood Canal rely heavily upon shallow sublittoral epibenthic plankton, especially small crustaceans such as harpacticoid copepods. Larger salmon, greater than 50-55 mm, are prone to feed in neritic waters upon larger plankters including fish larvae. An epibenthic pump sampler has been shown to provide

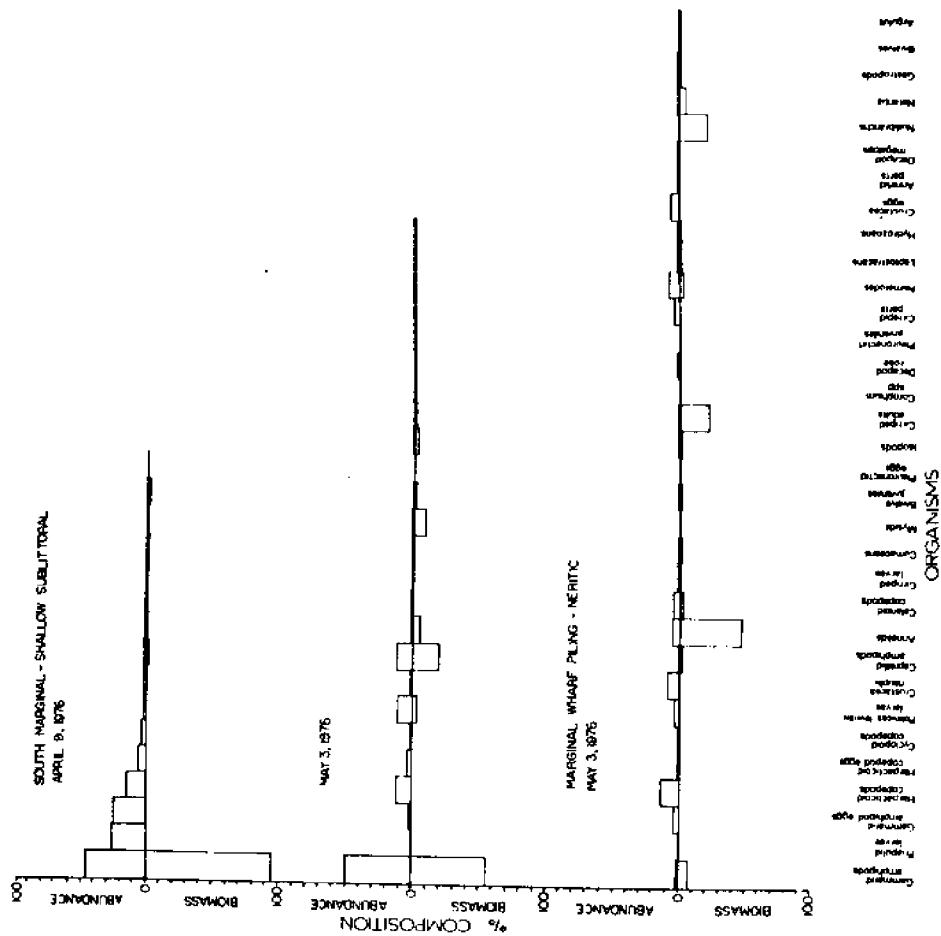


Figure 4. Composition of shallow sublittoral and neritic plankton assemblages at two sites on Hood Canal, Washington, April-May, 1976.

a reasonable quantitative sample of the available epibenthic plankton assemblage in the shallow sublittoral feeding environs of the juvenile salmonids. Neritic plankton samples tended to be less representative of the spectrum of prey organisms available to neritic-feeding salmon. Comparison of salmonid prey composition with epibenthic and neritic plankton composition suggests that smaller daytime-feeding salmon are preferentially, or functionally, consuming the larger organisms in the prey spectrum. Further sampling, and more detailed, must be performed to elucidate some of the factors involved in this apparent selectivity and to evaluate better the relative availability of the different prey organisms with time.

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Table 1. Taxa composition of epibenthic plankton sampled by epibenthic pump at three sites in Hood Canal, March-May 1976. Values are per 100 gallons pumped.

	Marginal wharf piling (neritic) 5-3-76		
	206- μ mesh net	505- μ mesh net	
	Abundance	Abundance	Biomass (g)
Gammarid amphipods	0.3 \pm 0.6	4.0 \pm 3.6	0.01 \pm 0.02
Gammarid amphipod eggs	10.0 \pm 4.4	0.7 \pm 1.2	*
Amphipod		0.7 \pm 0.6	*
Caprellid amphipods		0.3 \pm 0.6	*
Harpacticoid copepods	31.7 \pm 25.3		
Harpacticoid eggs	2.7 \pm 2.5		
Calanoid copepods	8.0 \pm 5.6	4.3 \pm 2.9	*
Cyclopoid copepods	3.3 \pm 2.1		
Leptostracans	1.3 \pm 1.5	1.3 \pm 1.5	*
Cumaceans		1.0 \pm 1.0	*
Isopods		0.3 \pm 0.6	*
Annelids		13.3 \pm 7.5	0.07 \pm 0.02
Annelida parts		3.3 \pm 4.2	*
Nematodes	0.7 \pm 0.6	15.7 \pm 21.1	0.01 \pm 0.01
Decapod larvae		0.7 \pm 1.2	*
Decapod zoea		4.0 \pm 4.4	*
Decapod megalops		1.0 \pm 1.0	*
Decapod nauplius	8.3 \pm 14.4		
Crustacea nauplius	11.3 \pm 12.7		
Crustacea eggs	15.3 \pm 26.6		
Cirripedia		1.7 \pm 2.1	0.02 \pm 0.03
Cirripedia larvae	1.3 \pm 1.2	0.3 \pm 0.6	*
Cirripedia juveniles		0.7 \pm 1.2	*
Cirripedia parts		8.3 \pm 6.8	*
Natantia		0.3 \pm 0.6	0.01 \pm 0.02
Priapulid eggs	61.0 \pm 105.7		
Gastropods		0.3 \pm 0.6	*
Nudibranchs		0.7 \pm 0.6	0.04 \pm 0.06
Bivalvia		1.3 \pm 2.3	*
Bivalvia juveniles		0.3 \pm 0.6	*
<i>Polinices lewisi</i> juv.	4.7 \pm 1.5	4.7 \pm 2.9	*
<i>Argulus</i>		0.7 \pm 0.6	*
Hydrozoans		0.3 \pm 0.6	*
Sample Mean	344.0 \pm 126.4	167.7 \pm 47.4	0.17 \pm 0.06

*Negligible weight, < 0.01 g.

	South Marginal (shallow sublittoral)					
	4-9-76		5-3-76		5-3-76	
	206- μ mesh net	505- μ mesh net	206- μ mesh net	505- μ mesh net	206- μ mesh net	505- μ mesh net
Abundance	Abundance	Biomass (g)	Abundance	Abundance	Biomass (g)	Biomass (g)
Gammarid Amphipods						
<i>Corophium</i> sp.						
Gammarid amphipod eggs	44.7 \pm 23.7					
Caprellid amphipods		0.3 \pm 0.6	*			
Harpacticoid copepods	27.0 \pm 13.3	1.7 \pm 2.9	*			
Harpacticoid copepod eggs	9.3 \pm 10.1					
Calanoid copepods	0.7 \pm 0.6		*			
Cyclopoid copepods	4.0 \pm 5.3					
Leptostracans						
Mysids		0.3 \pm 0.6	*			
Cumaceans		1.0 \pm 1.0	*			
Isopods						
Annelids		1.3 \pm 1.5	*			
Annelid parts						
Nematodes						
Decapod larvae						
Decapod zoea						
Decapod megalops						
Crustacea nauplius	3.0 \pm 3.0					
Cirripedia						
Cirripedia parts						
Cirripedia larvae						
Bivalvia						
Bivalvia juveniles						
<i>Polinices lewisi</i> larvae						
<i>P. lewisi</i> juveniles						
Ophiuroids						
Pleuronectid juvenile						
Pleuronectid eggs						
Hydrozoans						
Sample mean	215.0 \pm 65.6	206.7 \pm 109.7	0.15 \pm 0.17	0.5 \pm 0.7	208.0 \pm 171.1	1083.3 \pm 520.6
						0.65 \pm 0.40

*Negligible weight, < 0.01 g.

	North Carlson (shallow sublittoral)			
	3-29-76		4-16-76	
	206- μ mesh net Abundance	505- μ mesh net Abundance	206- μ mesh net Abundance	505- μ mesh net Abundance
Gammarid amphipods	0.7 \pm 1.2	59.7 \pm 40.9	0.3 \pm 0.6	46.7 \pm 25.6
<i>Corophium</i> sp.		0.7 \pm 1.2		0.3 \pm 0.6
Gammarid amphipod eggs	7.0 \pm 5.0	0.7 \pm 0.6	15.7 \pm 10.6	
Haracticoid copepods	12.0 \pm 12.5	0.3 \pm 0.6	14.3 \pm 7.5	
Haracticoid copepod eggs	11.7 \pm 1.5		6.7 \pm 3.5	
Calanoid copepods	6.3 \pm 7.8	15.3 \pm 8.4	4.0 \pm 1.7	12.3 \pm 4.0
Cyclopoid copepods	1.7 \pm 2.1		7.3 \pm 11.0	0.01 \pm 0.00
Caprellid amphipods		3.7 \pm 6.4	0.3 \pm 0.6	0.01 \pm 0.02
Leptostracans	0.3 \pm 0.6		0.3 \pm 0.6	
Kysids		0.7 \pm 1.2		
Cumaceans		1.3 \pm 1.5		4.3 \pm 4.0
Isopods		1.3 \pm 1.5		11.7 \pm 13.6
Annelids		6.7 \pm 9.9		2.7 \pm 10.0
Annelid parts	0.7 \pm 1.2		0.3 \pm 0.6	
Nematodes	0.7 \pm 1.2		0.3 \pm 0.6	0.01 \pm 0.01
Decapod larvae	0.7 \pm 1.2		0.7 \pm 0.6	0.06 \pm 0.06
Decapod roea		2.0 \pm 3.5		
Decapod megalops		5.7 \pm 9.0	0.3 \pm 0.6	50.3 \pm 61.5
Crustacea nauplius	1.3 \pm 2.3			13.3 \pm 16.4
Cirripedia larvae	1.0 \pm 1.7		4.0 \pm 3.6	
Bivalvia		0.3 \pm 0.6	0.7 \pm 1.2	
Polychaetes lewisi adults			0.3 \pm 0.6	1.3 \pm 1.5
<i>P. lewisi</i> larvae				5.3 \pm 9.2
<i>P. lewisi</i> juveniles	0.7 \pm 1.2	1.0 \pm 1.7		2.0 \pm 3.5
Reptantia				0.7 \pm 1.2
Reptantia roea		5.3 \pm 9.2		0.3 \pm 0.6
Gastropoda larvae				0.3 \pm 0.6
Insecta parts	0.3 \pm 0.6			
Caligoid copepods	0.3 \pm 0.6			
Sample mean	98.3 \pm 36.6	223.7 \pm 114.7	0.20 \pm 0.18	300.0 \pm 194.3

*Negligible weight, < 0.01 g.

IMPORTANT ASPECTS OF FORAGING BEHAVIOR AND FEEDING MORPHOLOGY IN RESOURCE PARTITIONING STUDIES OF FISHES

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The range of food items that a fish can potentially eat is largely determined by its foraging behavior and feeding morphology. Resource partitioning among most coexisting species of demersal fishes in southern California appears to be the result of differences in foraging behavior and feeding morphology (Allen, 1974). A description of the foraging behavior of many species, however, does not occur in the literature, perhaps because this behavior may seem obvious or unimportant. The objective of this paper is to emphasize the importance of foraging behavior and feeding morphology in resource partitioning studies and to describe the types of behavioral and morphological information that might apply to these studies. The information I have included in this paper appears to account for the coexistence of species in southern California fish communities and is further elaborated in "A resource partitioning model of southern California demersal fish communities" (Allen, manuscript).

After examining the species that coexist in recurrent groups (Fager 1957, 1963) formed from different sets of data and at different levels of association (SCOWRP 1973), I believe that differences among species in foraging behavior (including vertical space and time foraged) or in morphology that allows selection of food particles with different qualities (sizes, hardness, etc.) generally result in sufficient food differences to allow them to coexist. Foraging behavior of deepwater fishes, however, is often difficult to observe directly and must often be inferred from the morphology of the fish and from its stomach contents. I assume that most fishes are rather opportunistic in their choice of food particles, generally taking anything edible that they encounter (although preferences no doubt occur when sufficient food is available). Species that forage in the same manner but in different places may eat different species of food items because different food items may be found at each location. Conversely, two species may feed on many of the same species of food items although locating them in different places (i.e. one species may capture prey species while they are in the water column while another may capture many of the same species while they are hiding on the bottom). Stomach contents alone, then, may not clearly

represent the foraging behavior of a fish relative to that of other coexisting or similar species. The morphology of an organism, on the other hand, places limits upon its behavior and therefore often determines the behavior for which the species is best adapted. As most species are in some way morphologically different from each other, the important differences are those which allow a given species a foraging behavior that is different from that of other coexisting species (slight morphological differences among spatially separated species may be of less importance than the spatial separation itself).

When two species occur together very frequently, they generally are very different from each other in morphology. The most basic morphological differences among frequently coexisting demersal species are related to the orientation of the species with respect to the bottom while foraging for food. Species that very frequently occur together generally represent one of the following combinations: 1) a bottom-living species that forages in the water column and a water-column species that forages on the bottom; 2) a bottom-living species that forages on the bottom and a water-column species that forages in the water column; 3) a bottom-living species that forages in the water column and a bottom-living species that forages on the bottom; and 4) a water-column species that forages in the water column and a water-column species that forages on the bottom. In general, bottom feeders usually have well-developed lips and often have mouths oriented in a way so as to easily feed on the bottom (ventrally asymmetric jaws in bottom-feeding flatfish, ventroterminal mouths in some sclaenids, sharks, and all rays, or downward protrusible jaws in species such as combfish). Species that feed in the water column generally have poor lip development and terminal or dorsoterminal mouths. Types of food organisms that are most useful for estimating the orientation of the fish with respect to the bottom are those species that live entirely on the bottom or in the water column.

The orientation of a species with respect to the bottom is often associated with its search-and-capture behavior. The major types of search-and-capture behavior found among demersal fishes include the following: 1) ambushing; 2) stalking; 3) pursuing; and 4) searching. To *ambush* means to lie in wait for prey. An ambusher expends relatively little energy searching for prey and relies on the prey coming near enough to be captured. For this reason, most prey organisms are rather active. To *stalk* means to approach a prey organism near enough for pursuit or ambush. A stalker has to expend energy searching for prey that, once located, is quite capable of escape, either by flight or retreat to cover (as in tubicolous polychaetes). To *pursue* means to overtake and capture. This behavior is related to stalking and generally involves a prey organism that may escape by flight. To *search* means to look for prey organisms. A searcher often expends much energy looking for food organisms that, once located, are not likely to escape. Often these organisms are hidden or have body structures (i.e. shells) that may make them inedible to most species. In general, searchers are oriented toward the bottom when foraging for food (particularly utilizing sessile and infaunal prey organisms), while the others are oriented toward the water-column (utilizing planktonic and nektonic prey) or to both the water column and the bottom (utilizing epifauna, nekton, and plankton).

The diel time of foraging is also important in determining the range of food items encountered by a fish. Two spatially coexisting species that forage in a similar manner would encounter different food organisms if one species forages during the day and one species forages at night. The time of day that a species forages is determined in part by the sense organs that it uses to locate prey and by the activity patterns of the prey organisms that it is best adapted to eat. Species that forage at night (or in deeper water) may have either larger or smaller eyes (depending upon whether they locate their food by sight or not) than closely related diurnal (or shallow-water) species. Nocturnal or deepwater species that feed on active items nonvisually may locate them with lateral line organs. Species that have other well-developed sense organs (i.e. olfaction, touch, or taste) often have an advantage over visual feeders in locating prey at night and may therefore be nocturnally active; many of these species, however, are also capable of locating concealed prey during the day and may be diurnally active. Species that feed primarily on crabs and other epibenthic crustaceans which are active over soft-bottoms at night (Hobson, 1968) are also generally more active at night.

Differences in the size of the area foraged can also allow species that feed on similar food items to coexist; wide-ranging species may forage over a larger area although less thoroughly than sedentary species. The amount of food taken by an individual of a wide-ranging species from the home range of several individuals of a sedentary species may be rather small, resulting in the wide-ranging species having little impact on the food available to the sedentary species. Wide-ranging species are often more elongate (if bottom-living) or fusiform than sedentary species, or possess swimbladders that allow them a greater mobility than species without swimbladders.

Occasionally species forage in a similar manner to other coexisting species; these species generally show differences in structures that allow them to eat different types of food particles. Differences in feeding structures fall into two categories: 1) structures relating to the size of the particle engulfed and 2) structures relating to the type of particle engulfed. The first category can be divided into three major feeding types: 1) filter feeders, 2) engulfers, and 3) reducers. *Filter feeders* feed primarily on food particles that are very small relative to the mouth size of the fish (i.e. anchovies). These fishes sieve the food particles out of the water by means of elongated gillrakers. *Engulfers* feed on food particles that approximate the size of the mouth. Large or small particles can be engulfed but extremely small particles cannot be separated from the water and food particles larger than the mouth usually cannot be reduced to mouth-size particles. The size of the particle engulfed generally increases as the species grows because the mouth size increases with the size of the fish; different species, however, show different rates of increase of mouth size relative to body length. *Reducers* are capable of reducing a large food particle down to a size that can be engulfed in the mouth. These species often have cutting teeth (i.e. some species of sharks) or moveable tooth plates (hagfish). The incisor-like teeth of the opaleye (*Girella nigricans*) allow it to cut off bits of sessile algae.

The second category includes specialization of the mouth and digestive tract for particular food items. This includes 1) generalists and 2) specialists

that are adapted for crushing and grinding hard items. Most species are considered to be generalists within the range of items available to them. However, hard items taken must be swallowed whole and thus these species are not as efficient at utilizing this food source as species with structures adapted for crushing these items. Crushing structures can exist in the jaw teeth (rays, some species of shark), pharyngeal teeth (pile perch, *Demalichthys vaeca*) or toothed pharyngeal sacs (*Stromateidae*). These species might forage in a similar manner as generalists but be able to use a different food resource.

To adequately describe the sort of foraging behavior that allows species to coexist then requires a number of approaches including inferences from morphology and stomach analysis, when direct observation is not available. The interpretation of fish stomach contents with respect to the food habits of the fish would probably also be greatly facilitated if some effort is directed toward describing the foraging behavior of the fish.

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THE FEEDING BIOLOGY OF THE BAT RAY, *Myliobatis californica* IN TOMALES BAY, CALIFORNIA

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The bat ray, *Myliobatis californica* Gill, occurs from Oregon to the Gulf of California and is common in California bays during the spring and summer. MacGinitie (1935) observed that during its feeding activities the bat ray can dig channels up to 1 meter wide, 50 cm deep and 4.5 meters long in benthic substrates. In intertidal sand flats in Tomales Bay, California, circular pits up to 1 meter in diameter and 20 cm in depth are made by bat rays in late summer. In some areas over 50% of the sand flat surface is covered with bat ray pits. This recurrent seasonal disturbance of the substrate due to bat ray predation on benthic communities may be important in affecting their structure and faunistic composition. In preliminary studies of the effects of predation on benthic communities in Tomales Bay, we were interested in obtaining information about changes in diets of bat rays in relation to size.

Stomach contents from 422 bat rays were obtained in Tomales Bay during the annual Shark and Ray Derby on July 12-13, 1975. Data from this sample are reported here. All specimens were caught by hook and line in Tomales Bay. The rays were brought in live and weighed to the nearest half pound within 10 hours or less from the time of capture. The rays were eviscerated on arrival and stomach contents were removed and preserved in 10% formaline in seawater. After 3 days the stomach contents were transferred into 70% isopropyl alcohol. All diet items were identified within 3 weeks of the collection time. The length and width (or diameter in cylindrical organisms) of all identifiable diet items were measured to the nearest millimeter. The most commonly used bait for catching rays were frozen anchovies, squid and the echinoid, *Urechis caupo*. *U. caupo* used as bait that was found in the stomach was easily differentiated from that eaten alive by the rays. The worms used as bait were always flat, having lost their natural, rotund shape, and were also torn or punctured and much paler in color. *U. caupo* eaten alive maintained their red or bright pink coloration and live shape and never showed signs of tearing or perforation. Surprisingly, no partially digested *U. caupo* were ever observed. Many of the organisms found in the ray stomachs were so disintegrated as to preclude their identification or use in estimates of their contribution by weight or volume to the total diet. Some species,

such as the polychaetes *Neanthes brandti* and *Lumbrinereis tetraura* were often indistinguishable and their counts were combined. A few squid or squid fragments were present in some rays, but since squid were used as bait and could not be differentiated like *U. caupo*, they were not counted. The clams *Tresus nuttalli* and *Saxidomus nuttalli* were identified either from shell fragments or from siphon tips and plates and pieces of the foot. Live clams collected in Tomales Bay were examined to obtain diagnostic criteria for the soft parts. We are indebted to the Petaluma (California) Outdoorsmen's Club for their generous help in providing for the collection of this sample. Ray Richardson helped in many ways with organization and collection of samples. We also thank Pacific Marine Station graduate students who helped collect the samples.

Of the 422 rays, 285 were female and 137 were male. The weight distributions of the rays are shown in Figure 1. Only one male over 20 kg was caught, weighing 56.75 kg in comparison with the largest female which weighed 63.79 kg. Females decrease rapidly in frequency from weights of 30 kg. upwards.

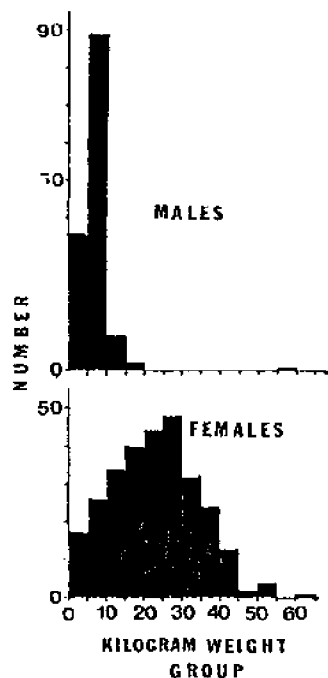


Figure 1. Weight distributions of bat rays classed in 10-kg weight groups

A total of 422 stomachs were examined, of which 149 contained 627 identifiable food items. These were in order of descending numerical importance; polychaetes (*Neanthes brandti* & *Lumbrinereis tetraura*), 214; *Urechis caupo*, 99; *Saxidomus nuttalli*, 191; *Upogebia pugettensis*, 74; *Priapulua nudus*, 65; *Tresus nuttalli*, 34; *Cancer* spp. (*C. gracilis* and *C. anthonyi*), 21; *Hemigrapsus nudus*, 12; *Listriolobus pelodes*, 3; *Macoma secta*, 2; *Macoma nasuta*, 1; and *Stylatula elongata* 1. The third edition of Light's Manual was used to identify the above Invertebrates (Smith and Carlton, 1975).

No significant correlations between prey size and ray size were found for individual species or the total suite of diet items combined. However, examination of frequency distributions of proportions of particular items in the diet of weight groups of rays or by percent of stomachs containing a particular item revealed distinct trends in bat ray diet as a function of size. The results are summarized in Figure 2. The data suggest the following trends in bat ray diets. Both *Urechis caupo* and *Tresus nuttalli* increase in importance with increasing bat ray size, while *Priapulua nudus* and polychaetes decrease in importance in larger rays. Polychaetes appear to have a maximum frequency of occurrence in rays of middle size, between 5 and 25 kg. Other trends are not clearly apparent. While the frequency by items of *Upogebia pugettensis*

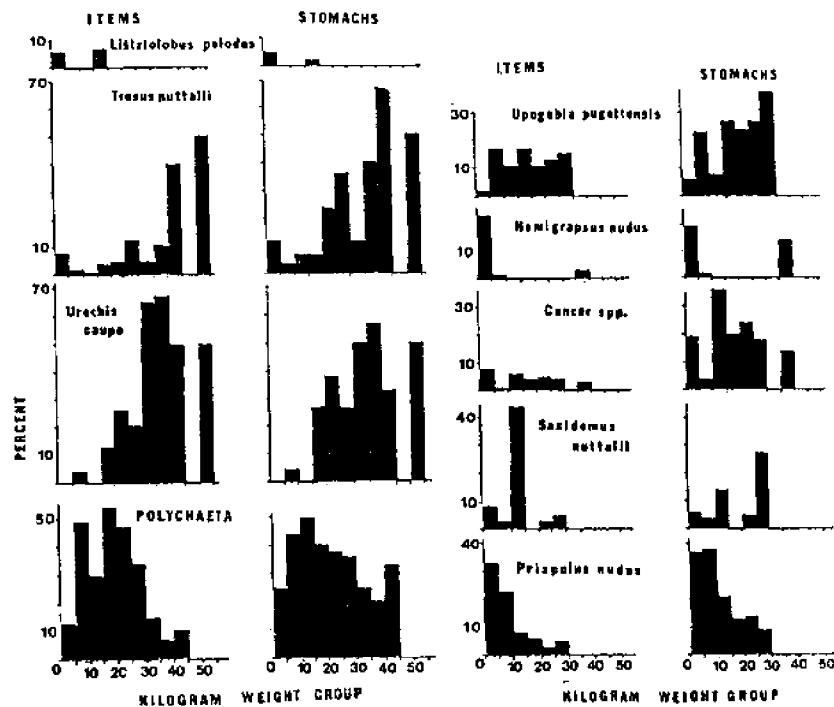


Figure 2. Proportions of food items in size groups of *Myliobatis californica*. Sizes are classed into 10-kg weight groups. Proportions of items are shown as percentages of the total number of food items found in the weight group indicated. Proportions in stomachs are shown as percentages of stomach containing particular items in the weight group indicated.

remains unchanged, its frequency in stomachs increases with size. No clear trend is apparent for *Saxidomus nuttalli* or *Cancer* spp. and the data for *Listrolobus* and *Hemigrapsus* are insufficient to indicate any trends. The data suggest that there might be a relatively abrupt change in diet in female rays above 30 kg in weight. Rays above this critical size appear to specialize in feeding on *Tresus nuttalli* and *Urechis caupo*, two of the largest and deepest burrowing organisms in Tomales Bay benthic communities.

Comparisons of male and female bat ray diets for specimens 15 kg in weight or less were made using data on the numbers of stomachs containing different diet items. The data are shown in Table 1. The items were ranked in order of decreasing abundance and a spearman rank correlation coefficient was calculated. This was not significant ($r_s = 0.29$). On the basis of this small amount of data we conclude tentatively that diets of male and female bat rays below 15 kg in weight are not different.

The foregoing information suggests that as *Myliobatis californica* increases in size, larger, deep-burrowing organisms become increasingly important in the diet. The species that become very common in rays greater than 30 kg in weight, *Urechis caupo* and *Tresus nuttalli*, are both deep-burrowing organisms. *U. caupo* occurs in U-shaped burrows down to 1 meter in depth and *T. nuttalli* is known to burrow down to 0.5 meters (Fitch, 1953). We can only speculate about the reasons for this change. Perhaps there are mechanical consequences associated with large size that permit large rays to burrow deeply and feed efficiently on larger benthic organisms.

Table 1. Frequencies of food items in stomachs of male and female *Myliobatis californica* 15 kg or less in weight

Food Species	Females	Males
<i>Listrolobus pelodes</i>	0	1
<i>Saxidomus nuttalli</i>	1	3
<i>Priapulius nudus</i>	7	21
<i>Hemigrapsus nudus</i>	5	1
<i>Upogebia pugettensis</i>	1	6
Polychaetes	25	16
<i>Urechis caupo</i>	1	1
<i>Tresus nuttalli</i>	4	1
<i>Cancer</i> spp.	7	0

In his study of bat ray diets in Tomales Bay, Ridge (1963) combined weight classes so as to have equal numbers of individuals in each weight class. Thus, his smallest size group included rays up to 1 kg in weight and the largest group combined rays between 15 and 50 kg. This precludes comparisons of our data with his findings. However, his largest size group did show an increase in occurrence of larger clams, shrimp and echinuroids. Moreover, Ridge identified over 66 species of benthic organisms in ray stomachs, with 17 species of polychaetes identifiable to genus. Our much shorter list of diet items is probably due to our using a sample taken on 2 days during the year while his samples occurred throughout the year. In addition, we were obliged to use rays kept alive up to 10 hours allowing for digestion of many items before preservation while Ridge preserved stomachs immediately after capture.

There are no estimates of the size of the feeding bay ray populations in Tomales Bay. Of 90 rays tagged at the beginning of June, 1975 in Tomales Bay, one was recaptured in the bay 2 weeks later and 2 were captured in San Francisco Bay, 40 miles south of Tomales Bay, 1 month later. These results are useless for population size estimation and suggest that high migration rates would not allow effective mark-recapture estimates of abundance. Anecdotal observations by Tomales Bay fishermen indicate that schools of rays numbering in many hundreds can sometimes be observed in shallow waters. Some believe that many tens of thousands of rays might be present in late summer. The extensive disturbance due to ray feeding in intertidal areas suggests that subtidal predation might be equally high. About 18% of our sample consisted of rays greater than 30 kg in weight. Large *M. californica* have been observed by divers off Catalina Island, California. During their feeding activities they excavate deep depressions and attract many other fish which feed on the organisms thus exposed (R. Schmitt, Department of Biology UCLA). Therefore, it is likely that bat ray feeding in Tomales Bay might also make more food available for other species of fish. During shallow water dives in Tomales Bay we observed that *Urechis caupo* burrows were frequently used hiding places for small crabs, particularly *Hemigrapsus* spp. This suggests that bat rays might also indirectly regulate abundances of small crabs by affecting the abundances of *Urechis*. These observations suggest that experimental studies of effects of bat ray predation on benthic community structure should include studies of indirect effects on other predator populations.

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DISCUSSION: SESSION 5: INTERPRETATION AND RESULTS

Immediately after Steve Obrebski's presentation, Jack Word asked about the terrebellid worm used in his studies. Obrebski said that it was *Eupolymnia crecentis* and noted that the guts of the worms were always palatable; it was either the body or tentacles that weren't palatable. And with other terrebellids, if the body is protected then only the tentacles are unpalatable, and usually it lives in a hard tube and has a very rapid escape response. Obrebski also mentioned that his response to the question, "Why in the devil doesn't something get eaten when it's very abundant?" especially if it's exposed and active, is to get some of the critters and the fish, starve the fish for 5 days, and put some of the critters in the tank; if they don't get eaten, then they are unpalatable.

Gary Smith said that, in analyses of diet overlap and potential competition, the key requirement is to look at the food supply. Thus, without a food limitation there's no competition, but the abundance and availability of food items are very difficult to measure. Obrebski replied, "I don't think that food limitation, per se, is the criterion because, as you know from looking at Ivlev's curves, the issue is the maximization of feeding efficiency. Then, if a species is feeding with a competitor that is simultaneously reducing the density of the organisms being fed upon, such that its efficiency decreases (because it is dependent on the density of the food item), then you might expect to have behavioral interactions between the species such as one or the other increasing its (feeding) efficiency by chasing the other predator out." Citing juvenile chum salmon chasing out juvenile coho salmon, he stated that "The issue is not limitation of resources but maximization of fitness, and that is a factor independent of resource limitation in a sense."

Word asked Colin Levings whether his collections of amphipods in the estuary's currents produced juveniles in both the inner and outer delta. Levings said that the data so far didn't seem to indicate any difference in the size of the animals distributed through the water column. Word replied that female amphipods don't appear to come out into the water column as males or juveniles do, although there may be transport via plant detritus.

Asked how he dug holes in sediment to duplicate those created by rays, Glenn Van Blaricom replied that he just used his hands in the same manner that the rays used their "wings." He was also asked whether swimming activity had any effect on community sampling areas. Van Blaricom replied that it definitely was a problem and worth worrying about. He tried to confine his swimming activities to certain corridors and only reach out of these in order to minimize disturbance. John Stephens asked Van Blaricom about the frequency of surge-related disturbance in that habitat. It apparently is frequent during the winter, though rare in the summer. John Ellison asked about related sand transport and Van Blaricom said that they had stakes placed in the study area and these didn't show much variation; when it did occur, it appeared to be associated with the occurrence of major storms.

Si Simenstad asked whether certain areas had higher densities of holes; Van Blaricom replied that there was no indication of any preferred areas, i.e., a relatively random activity.

Obrebski asked if there was any indication of how much of the recruitment to the disturbance sites was settlement or migration; Van Blaricom said that, although they were just generating that data, it appeared that at least for crustaceans and polychaetes, it was via migration.

The general discussion started with questions of Simenstad regarding performance of the plankton pump. John Sibert wondered how much of the pump sample came from outside the 1-m sampling ring. Simenstad said that the divers who manipulated the suction cone had observed a few animals being sucked from outside the sampling area and that they were considering going to a cylinder in order to better isolate the bottom sampling area and prevent lateral contamination. The larger question is the percentage of the total available epibenthic plankton which is sampled in a single 100 gal. 200 gal. 300 gal etc. sample and whether organisms are differentially available to the pump. Sibert also asked whether the 1-m² area sample was subsampled; Simenstad replied that three 1/10 subsamples, with replacement, were used to characterize the whole sample although it was a difficult tradeoff because you need enough to provide the necessary biomass estimates but, by that time, you've almost got too many to count.

The question was raised about the comparability of the pump samples with core samples. Simenstad said that they hadn't made any direct comparisons yet, especially since not many investigators had resorted to a sieve size as small as 200 μ . Word recommended that they not be too concerned with different penetrations of the suction "field" in various substrates because most of the organisms of concern occur in the upper few centimeters anyway.

Word also asked whether or not the pump system in operation made any noise underwater; Simenstad said that the divers could hear (or feel) the gasoline engine powering the pump so it was impossible to say if the pump itself was noisy. Robin LaBrasseur commented that they can hear their

plankton pump underwater, but that they could not detect any organism reacting to that as such. Bob Feller suggested increasing the filtering efficiency (to prevent clogging) by increasing the surface area of the mesh relative to the mouth opening.

John Ellison questioned the validity of Obrebski's use of the term "preference" to imply that the fish was, in some way, passing up one food item for another, "when considering diets of 2 different fish, you really need to look a lot closer at the benthos of the water column, wherever their food is, before you use this term . . ." He suggested that we have to be more careful in use of "preference," "selectivity" and terms of that nature. Obrebski agreed that his use of the term was imprecise. His data showed that in some instances there is similarity in food items and sometimes there is considerable dissimilarity. He went on to cite a paper on bluegill predation on *Daphnia* which was relative to this problem; the paper addressed some theories about what it is that foragers optimize, i.e. what size range of food items is being optimized. One of the points made in the paper was that these fish, when presented with a new, different size range of organisms, could almost instantaneously adapt their behavior so as to optimize their foraging in this context. This illustrated why we shouldn't really interpret anything unless we've had a chance to see the fish do something to diet items offered in a tank or, optimally, in a natural situation.

Ellison asked if it wasn't more of a question of availability. Obrebski suggested that it's undoubtedly more complex than that--it is quite possible that organisms, if they're offered alternative items, will switch to optimize both on items and size classes and their behavior will also be affected by the presence or absence of other competing species through behavioral interactions.

Along the same line, Gary Smith also wondered about the use of food composition as evidence of competition, optimization or partitioning strategies of predatory species. He thought that there was a good chance that, if food is abundant, it's just a result of chance encounters of food particles, not partitioning or selection but rather morphologies, behavior, etc. Obrebski said that, if you postulate a random encounter model to explain the abundance of a particular food or an organism, then given a fixed morphology and foraging behavior, there will still be consequences as the amount of a particular item will depend upon a variable encounter rate. Thus he suggested that once you know these things, only then can you make statements about competition. Jim Allen postulated that when food items are in very low density, then it probably is a matter of prey availability but, if you've got a large number of species, representing a variety of escape responses, then it is of some advantage to a predator species to modify its behavior such that it optimizes its predation on certain food items.

Stephens recounted his experiences observing *Rhacochilus vacca* to determine whether it was a grazer or selective feeder. Because it is one of the least active and does the most searching, a diver can actually

observe eye movements. He described how they make a number of approaches to food items before finally consuming one such that you can count bites/minute. When he eventually looked at their diet, they were largely taking small molluscs. Other species which approached food with less searching and associated eye movement were usually more generalistic in their diet.

Stephens also suggested that morphology can be deceiving. He cited the cases of tooth structures in a blenny, *Mecostomictleya sandi*, which has teeth fused into giant clipping plates, a feature absolutely foreign to that group. One would have thought that it must eat algae like a kyphosid but, surprisingly, it's a plankton feeder.

Sibert returned to a prominent theme, that we had been dropping a lot of terms like "competition," "selection," "availability" without definition. He suggested that this topic might be suitable for later workshop meetings. Sibert did add, however, that he wasn't sure "competition" has been too well defined in the ecological literature either. Healy added it was either that or overly defined.

Terry made a strong argument that you can't look at just one dimension, food, but need to include space, feeding periodicity, and so on. Obrebski described his observations of sculpins feeding on harpacticoid copepods and clam siphons in shallow water; the fish sat in one place and would suddenly dart forward and grab something. Crabs apparently do the same thing; they sit in one place and wait for a clam siphon to appear to start pumping and then the crab takes a swipe for it. These observations, Obrebski noted, made one feel that you know a whole lot more about what's going on!

Sam Bledsoe asked Stephens how he was going about putting together a large-scale picture of trophic relationships, including accounting for the high degree of variability, etc. Stephens indicated that he expected every kind of problem imaginable. They will derive approximations at each level, e.g. caloric/biomass estimates by visual observations of indicator species and extrapolate from these. Bledsoe returned to the problem of large-scale year - year, month - month variability in biomass and abundance mentioned by Stephens and suggested that either the spatial scale is too small to say anything about the particular population or that they have to extend over a much longer time scale in order to achieve some repetition. Stephens described how most of the cycles they've seen of huge increases in abundances have been occurring all over the Southern California Bight and they are catching local representations of what has been occurring. He cited examples of calico rockfish, Garibaldi, and black croaker, all of which had recently gone through huge population explosions. Stephens suggested that 7 years was way too short a time to get a handle on what was happening. He said that one of the biggest problems is the lack of life history tables, and no estimates of sources of mortality and predation.

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