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Edited by

W. T. EDMONDSON

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Third Conference on Marine Biology

PREFACE

This book contains a revised transcript of a three day conference by a group of about 20 biologists of different background who had been assembled to discuss a field of marine biology to which their varied experience was related. Recently there has been some rather strong criticism of this type of publication. In the face of the publication explosion, we must certainly examine rather critically the methods that are in use, not only for transmitting knowledge, but for recording it. Despite the vast bulk of printed matter appearing now, do we have time and space to record the way in which such a conference as this developed? Is the conventional journal article, review or book the only effective and permissible way to publish?

While one could obtain much of the information in the present book by reading published papers, many of the summaries here present new information or new viewpoints, or organize existing information toward new questions in an illuminating way that seems to me well worth communicating to other people who are thinking and working with the same problems. Some of the discussions resulted from ambiguity or incompleteness in the literature. These are questions that anybody might ask while doing the same reading, and here we have an opportunity to see how the thinking of the investigators proceeds in response to them.

The easiest way to accomplish the transmission of the crude information would simply have been to eliminate all the questions and to edit the answers and discussion into a continuity. However, this would have eliminated one of the useful ways in which this type of publication differs from conventional scientific papers and symposia.

I believe that it can be of value for a record of such a conference to be made publicly available, but the exact character of the record offers some problems. There is little value in presenting the raw transcript. In the present case the three day discussion was recorded in detail with all the interjected questions, half finished sentences, misunderstandings, poor jokes, laughter and all the rest. While those who took part in the conference may find the complete transcript a useful record for personal preservation, some of us may not wish to be reminded of our inability to respond to challenging questions or to evaluate new ideas on the spot, and much of this material is not worth publishing.

An editor then has the problem of trying to develop from the literal transcript a record that will preserve the values of the conference; therefore this transcript has been very heavily edited. Large sections of repartee have been totally eliminated or substituted by editorial summaries. In some cases a rather extensive exchange has been summarized in such a way to preserve

only the essential points made. It has been my intention in all of these condensations to leave an indication of the reasons for which the discussion developed in the way that it did.

The conference proceeded according to the following general pattern. Each major topic was introduced by a discussion leader who had prepared a statement. Generally this led to a rather wide discussion of questions which were brought up by the discussion leader. In some cases participants had prepared statements about specific problems which they made at appropriate times at the request of a discussion leader, but most of the time was taken up with spontaneous questioning and discussion.

To some extent the organization of the conference developed as it went along, and part of the discussion on the final day had its real origin in discussions that took place early in the conference. In order to make a more useful organization for reading, these sections have been brought forward in the published record and associated with the material to which they are more closely related. Nevertheless, some material pertaining to a given topic is separated.

Some of the exchanges of questions and answers are rather more worth preserving than others. These are ones which indicate directions of new work which some participants feel would be worthwhile or indicate places where more theoretical work or thinking about existing information needs to be done.

The conference brought together people working in fields which have widely different demands for techniques of gathering data, processing data and elaboration of hypothetical constructs. To a large extent the conference dealt with problems that can be developed only by applying a wide array of techniques and thinking. I have tried to preserve the kind of discussion that exposed these situations. It may be of distinct value to have this record to show what kinds of questions are generated in the mind of an experienced investigator when he hears a description of problems in a field which is foreign to his experience, but to which his experience could contribute heavily. Many of these exchanges have been shortened and simplified and any consequential incongruities or illogical development can be attributed to me.

W. T. Edmondson

I. SAMPLING ORGANISMS AND RELATED PROBLEMS

Discussion leader:
JOHN D. H. STRICKLAND
Institute of Marine Resources
University of California
La Jolla, Calif.

STRICKLAND: Methodology is, I think, subject to discussion because it underlies almost everything we are going to talk about, so I suggest that we discuss methodology when there are specific pieces of information of general interest. Any very particular methodology arising out of particular problems can probably best be discussed when these subjects are raised later on.

We have, I suppose, broadly speaking, sampling problems both in the pelagic and the benthic environment, and these are centered around the sampling of organisms of a specific size and at a specific depth, and obtaining information about the total biomass and the biomass of individual species. Many persons are equally interested in obtaining information about contagion and the patchiness of organisms. A very similar set of problems faces us in both the pelagic and benthic realms.

In methodology, I think we can discuss biomass determinations and the determination of energy contents by calorimetry and metabolic rates. Biomass can be expressed as wet weight, dry weight, ash-free weight, carbon, nitrogen, or specific metabolites. It strikes me that the most important problem in estimating the biomass of zooplankton is how to cope with the netfull of jelly so often encountered.

There are the problems of determining energy contents (calorimetry), and various studies of metabolism which mostly center around methods for determining oxygen, carbon dioxide and, possibly, excretion products.

Obviously, in metabolic rates we have a lot of very specialized studies of organs and organisms, but, roughly speaking, most work centers around the determination of oxygen and carbon dioxide; and then, of course, technically the session should be concerned about sampling and methodology associated with feeding, and this of course is an enormous problem. I think we should leave this until we discuss other aspects of feeding. Another thing that might be worth discussing, if people are so inclined,

is how to express feeding rates in the zooplankton. Should we continue with filtering rates or should we try to use some other method of expressing feeding.

This is all I have sketched out. Does anybody have anything to say about the first topics on the schedule?

CONOVER: I can make a few remarks about some of our attempts to try to get at the specific size of particulate organic matter including the microzooplankton in the Gulf of Maine. Largely through the efforts of Doctor Michael Mullin, then a graduate student at Harvard, a fractionating column for particulate matter was devised (FIGURE 1). We started out with a series of glass funnels. The stems were cut off the funnels and in place of the stem a suitable grade of nylon bolting cloth was cemented on with an epoxy glue. These things were stacked together from coarse to fine in a pile, each separated by a gasket of modeling clay or, in later versions, an O ring. The bottom funnel was not modified but was attached directly to a vacuum system. We started out with about 16 or 20 liters of water which were passed through the whole column, fractionating particles rather crudely in a number of different size categories. Material on the individual filters was then washed off onto glass filter paper on which the analysis was performed.

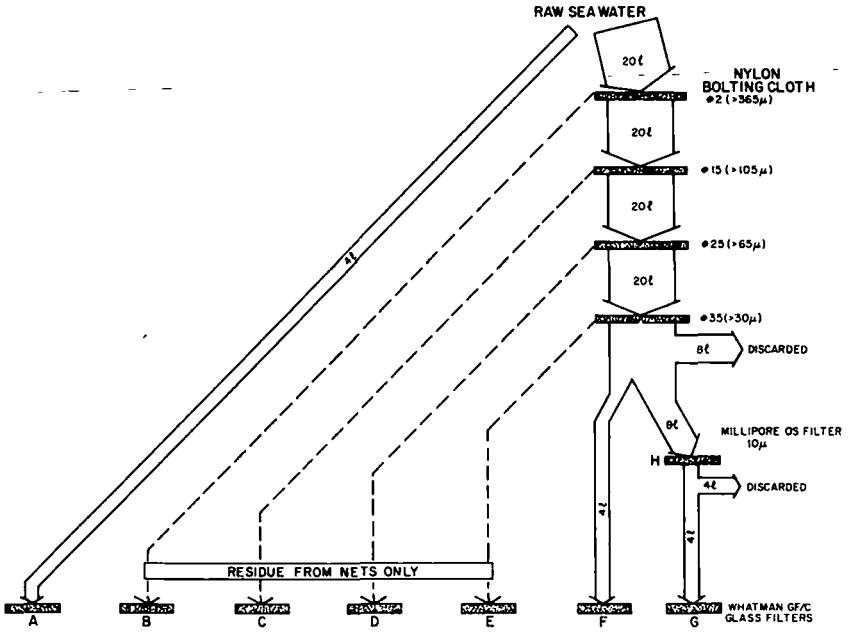

FIGURE 1. Flow diagram showing procedure for partitioning particles into several different size categories by differential filtration.

FREMONT-SMITH: What are the volumes involved?

CONOVER: Initially, the sample is 16 to 20 liters. The volume on the individual filters is, of course, very small. The following Table (TABLE 1)

TABLE 1

PARTICLE SIZE DISTRIBUTION OF CARBON AND CHLOROPHYLL *a* AT 10 M. IN WILKINSON BASIN AS DETERMINED BY FRACTIONAL FILTRATION [1]

Cruise, date, no. of samples	Effective particle diameter, in μ	Chloro-phyll mg./m.^{3}	% of total chloro-phyll	Carbon mg./m.^{3}	% of total C
Gosnold 5	365 (#2 net)	0*	0%	5.6	4%
I/3–6/63	105–365 (#15 net)	0.023	8	4.9	3
10 samples	65–105 (#25 net)	0.089	31	16.6	11
	35– 65 (#35 net)				
	10– 35 (OS Millipore)	0.065	23	66.1	43
	<10 (GF/C filter)	0.108	38	61.5	40
	Total	0.285		154.7	
Crawford 77	365 (#2 net)	0*	0%	22.5	9%
	105–365 (#15 net)				
	65–105 (#25 net)			13.4	5
	35– 65 (#35 net)			18.7	8
	10– 35 (OS Millipore)	0.079	9	34.4	14
	<10 (GF/C filter)	0.787	91	161.0	64
	Total	0.866		250.0	
Gosnold 14	365 (#2 net)	0*	0%	22.0	8%
V/22–23/63	105–365 (#15 Net)	0.072	8	33.4	13
3 samples	65–105 (#25 Net)	0.040	5	16.4	6
	35– 65 (#35 net)	0 061	7	23.3	9
	10– 35 (OS Millipore)	0.125	14	31.5	12
	<10 (GF/C filter)	0.591	66	138.7	52
	Total	0.889		265.3	
Crawford 94	365 (#2 net)	0.076*	29%	6.7	3%
VI/26–28/63	105–365 (#15 net)			15.7	8
9 samples	65–105 (#25 net)	0.022	8	12.1	6
	35– 65 (#35 net)	0.006	2	6.7	3
	10– 35 (OS Millipore)	0.038	15	16.0	8
	<10 (GF/C filter)	0.119	46	148.0	72
	Total	0.261		205.2	
Crawford 83	365 (#2 net)	0*	0%	16.2	9%
VIII/11–13/62	105–365 (#15 net)				
13 samples	65–105 (#25 net)			8.9	5
	35– 65 (#35 net)			9.9	5
	10– 35 (OS Millipore)	0.053	11	29.3	15
	<10 (GF/C filter)	0.438	89	126.3	66
	Total	0.491		190.6	

* Estimated by difference between other samples rather than measured directly.

taken from Mullin(1) summarizes some of our differential filtration results. As expected, the largest fraction of carbon and chlorophyll usually is found in the less than 10 μ category. On the other hand, quite a high percentage of the total biomass is found on the nets and this fraction may contain a higher proportion of chlorophyll than smaller-size categories(1).

We have also examined the vertical distribution of certain fractions. The portion of carbon greater than 35 μ is compared with the total carbon (FIGURE 2). There is one point on the total carbon curve point at 150 meters which must be in error and which doubtless accounts for the low total carbon in the water column. During the same sampling period, other

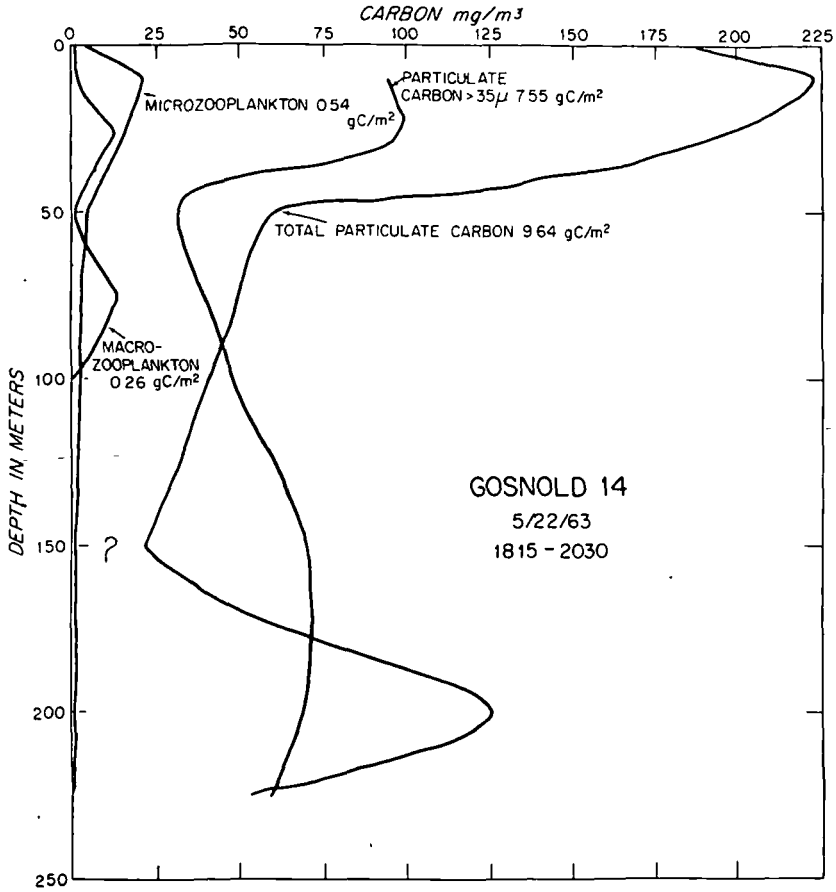

FIGURE 2. The vertical distribution of total particulate carbon, total particulate carbon retained by a filter with 35 μ apertures and that fraction of the carbon attributable to microzooplankton and macrozooplankton elements. Station in Wilkinson Basin of the Gulf of Maine, 42°50'N, 69°50'W, May 22, 1963.

casts, not fractionated, gave an average of 25.0g./m.^{2} total particulate carbon.

I also counted the microzooplankton and the larger zooplankton on the #35 net filter and weighed a representative group of these organisms. If carbon is assumed to be about 40 per cent of the dry weight, only a relatively small amount of the particulate carbon on this filter was actually in the bodies of microzooplankton. On the filter there was also a considerable quantity of "macrophytoplankton." Preliminary analysis suggests that the *Ceratium* alone may contribute more carbon than all the microzooplankton. There was much unidentifiable detritus in all of the samples, particularly in the deeper one, and from 1 to 7×10^5 recognizable fecal pellets per m^3.

STRICKLAND: What was the next size up?

CONOVER: In this particular case we eliminated the stack down to 35 μ so we took everything, including microzooplankton here.

KANWISHER: Should you not add up the 50 meters and equalize them?

CONOVER: That would be hoped for. It has been our experience that they usually do not. A couple of times we ran statistical comparisons and sometimes we got no significant difference and other times we have. I do not know what the source of the error is, but apparently the method is slightly sloppy. In this particular graph you would not expect the curves to add up since the size categories less than 35 μ are not shown.

STRICKLAND: Are you determining carbon or just estimating it?

CONOVER: We are determining carbon, using the Fox, Isaacs and Corcoran(2) method, somewhat similar to what you use except we are actually titrating.

STRICKLAND: How do you separate the phytoplankton from the microzooplankton?

CONOVER: In this particular graph, the separation was done simply by counting the organisms, weighing representative organisms and assuming 40 per cent carbon in the dry weight.

HUTCHINSON: When you continue the process, without eliminating filters so that you are measuring the smallest categories, is there any evidence that you get to a point where there is practically nothing smaller, or is it that the smaller the objects, the more of them there are found?

CONOVER: Our filtering system now consists of four grades of bolting cloth, then the O.S. type Millipore® filter, which is not really very fine (10 ± 3 μ) and, finally, Whatman GF/C glass filter paper.

Actually, we are interested here primarily in food for zooplankton and I was hoping to get some information about the relative abundance of particles in the larger size categories. We have some calculations here, derived from this work, that perhaps can be used in another discussion.

SCHMIDT-NIELSEN: How do you do carbon on filter paper?

CONOVER: The samples are always filtered onto glass-fiber filter paper, which is wet combusted with appropriate blanks.

FAGER: What do you do about clogging and the effect this would have on the sizes of the things you are separating?

CONOVER: This may be one of our difficulties. We changed our filters every time and we try to wash them as carefully between samples as we can. There is probably some reduction in pore size during the course of a cruise or run.

PROVASOLI: But in the first 20 liters, you do not find any clogging.

CONOVER: There was no serious clogging to the point where we had any difficulty getting the water through.

PROVASOLI: But even a partial clogging would reduce the size.

CONOVER: That is right, and it is possible that we are getting some size reduction, but you will generally find, if you examine what is on the filter, that you get a pretty good breakdown of organisms. For example, just looking at the organisms which are the most easily identified, you will find you almost invariably come out with *Ceratium* on the No. 15 bolting cloth.

EDMONDSON: What is the behavior of a population of sausage-shaped objects on a filter? Some fraction goes through?

CONOVER: Undoubtedly some fraction goes through.

SLOBODKIN: Would that not be true only if the filter consisted of a single net? If you have a whole series of nets underneath each other . . .

CONOVER: Some get through. The long, thin organisms tend to orient along laminar flow lines. Generally speaking, there is sufficient turbulence so not very much laminar flow occurs on the filters.

SCHMIDT-NIELSEN: What do you mean by laminar and nonlaminar flow in a filter with essentially two-dimensional holes?

CONOVER: The flow is relatively so rapid that you get a bubbling, swirling flow through the filter when you put suction on it. On the other hand, if you have a system, say, where you are running a continuous flow at relatively slow speed down a tube or something of that sort, you will get laminar flow rather than turbulent flow and most of your long objects, like the long chains of diatoms will orient along the axis of flow. If you had a filter at the end, presumably some of these might go through.

SCHMIDT-NIELSON: You do have essentially two-dimensional holes here?

CONOVER: That is right, but the way things hit the filter, they have an equal chance of hitting with any orientation.

SCHMIDT-NIELSEN: So this is partly independent of your speed of suction or your speed of movement?

CONOVER: Yes, it depends on slow speed and boundary conditions; i.e. diameter of tube, roughness of surface, etc.

FAGER: Are there any seasonal changes in proportion?

CONOVER: Not as great as we expected, at least so far. One of the things which is concerning us is that we have not yet gotten data from the height of the spring flowering period, which we strongly hope to get. One thing that has come out of this work on carbon is that there is little seasonal variation in carbon. There is some variation in the vertical distribution of it, but the total carbon in the water column varies by only maybe 40 or 50 per cent.

FOGG: This is total particulate carbon?

CONOVER: Total particulate carbon, yes. The chlorophyll, on the other hand, varies an order of magnitude.

FAGER: A 40 to 50 per cent variation seems small for a seasonal change. What is the spatial distribution of this carbon? It sounds like the sort of variation one might get if samples were taken some distance apart.

CONOVER: This could be; we have not gone into the statistics of it. We know we have not been looking at the same water all the time. We know this from hydrographic information. However, the basin that we are working on is a fairly stable one, and the water below 100 m. is pretty well isolated from other points in the Gulf of Maine. In addition, the whole Gulf of Maine is an eddy. On the other hand, water movements do occur; changes in water masses in the basin do take place at least annually. I think we could get 40 or 50 per cent variation.

PROVASOLI: Due to patchiness?

CONOVER: Due to regional differences over various sections of the Gulf.

PROVASOLI: That is why it is very important to have several stations at the very beginning to find out how much is patchiness.

CONOVER: I don't consider that a 40 to 50 per cent seasonal difference is very great. The biomass is about the same the year around, but it does change. Yet, the changes are not greater than might be attributed to "patchiness" or water movements.

HUTCHINSON: When you use the word "biomass" do you really mean biomass, or carbon?

CONOVER: Well, particularly carbon.

PEARSE: How does this look qualitatively over a period of time? Does it seem to change?

CONOVER: Unfortunately, I have very little qualitative information as yet. That is the only station to date on which I have the qualitative infor-

mation. Qualitative information comes more slowly. The samples are being worked on.

SANCHEZ: When you say "particulate carbon," you mean organic molecules?

CONOVER: I mean carbon-containing particles that can be retained by the feeding apparatus of various-sized organisms.

BARKER-JØRGENSEN: What was the level of particulate carbon?

CONOVER: In that particular section, the total particulate carbon came out to be about 10 grams per meter, squared, and this is approximately a 200-meter water column. That was low; actually, rather lower than a lot of other observations that we made. It was lower than another vertical series that we did at that particular station within 24 hours of the time that this one was run. Unfortunately, on the other run, we did not partition the sample for the microzooplankton material. I am sure that the main difficulty with the total amount of carbon we have here is that one, very low point at 150 meters. That point does not belong there.

BARKER-JØRGENSEN: You said you had found very little variation. Could you give a rough value of the variation?

CONOVER: What we usually get is between 20 and about 35 grams of carbon per m(2), again assuming approximately a 200-meter water column.

BARKER-JØRGENSEN: There was some variation with depth?

CONOVER: The vertical distribution with depth does seem to be seasonal. You have an appreciably greater proportion of your carbon in the deeper water as you might expect at times of low productivity in the late fall and winter. In the spring, a much greater proportion is in the upper 50 meters.

BARKER-JØRGENSEN: And the minimum particle size for retention was about what?

CONOVER: The minimum particle size would be, I would suppose, of the order of 1 micron or slightly less.

PROVASOLI: How is the water collected? A pump?

CONOVER: In this vertical series, we used a large volume water sampler, a 20 liter sampler. In most of our horizontal sampling, it is done with a pump.

PROVASOLI: What are the chances of fast zooplankton escaping?

CONOVER: They are considerable. If you compare the microzooplankton numbers that I have here(FIGURE 2) with vertical net zooplankton tows, I would say this is roughly 50 per cent, perhaps a little less.

STRICKLAND: How big is macro?

CONOVER: In this case, retained on a No. 2 bolting cloth, which is about 100 meshes to the inch—roughly 300 μ.

HUTCHINSON: Is this the standard attitude to macroplankton in oceanography at the moment?

CONOVER: I do not know that there is a standard attitude.

HUTCHINSON: I had the occasion to try to discuss this terminological problem in a manuscript that is going to press next week(3). I discovered that megaloplankton is plankton that you can see from the deck of the vessel, and it has, of course, very different connotations from a rowboat and from a large sea going ship.

FAGER: I have three sorts of observations on nonrandom distributions that should be considered when one does sampling.

Early in our diving program we sampled the plankton as well as the benthic organisms. Two of us did this by holding a 40-cm. diameter net between us and swimming as fast as we could along a line for a measured 20 meters. One day we took a sample, came up to the boat and put it in and then went back down. While taking the sample we had not noticed many mysids; a later count of the sample yielded only three individuals. However, when we went back down along the line where the sample had been taken, the density of mysids was so great that you could not see your hand an arm's length away. After a number of experiences like this, I decided that the benthic organisms were perhaps a little more stable as far as position was concerned and that I would, for the time being, ignore the planktonic organisms. I have done so ever since.

FREMONT-SMITH: Had you stirred them up, you think, by swimming?

FAGER: No, we have often sat in one place and watched swarms of them come by. I am convinced that the same sort of sampling problems are presented by zooplankton in the deep sea. Unfortunately, this is not always recognized because you see it dramatically only if you get under water and look at it.

The second observation concerns selective sampling by another of our early sampling devices, a hand dredge. This was a semicircle about half a meter in diameter with a set of teeth on the straight side that went down into the sand, a pair of skids that kept us from digging in too deeply, and a net with a changeable cod end on it. We pushed this along for a measured distance beside an aluminum rod laid on the bottom. We found that there was some variation in catches depending on who was pushing the net, apparently because some people could push it faster than others. This variation was, however, relatively small. Just as a check, to be sure we were getting a good sample of the active animals living on and near the sand surface, we took some sand cores, pushing aluminum tubes 5 cm. into the bottom and transferring the sand samples into jars in a manner

that appears to lose very few of the animals. The cores were taken adjacent to the dredge run.

We were quite startled to find that this nice dredge which was stirring up the bottom and, we thought, chasing the animals up into the water so that they would get into the net, gave estimates of populations of the more abundant crustacea in the sand that were lower than the estimates obtained from the cores by factors that ran all the way from 4 to 90. Furthermore, we got a very strange impression of what the fauna in the sand was because the species that were most common in the dredge samples were, in fact, most of them, relatively uncommon in the cores. As a result we no longer use the dredge for population estimates.

There is, however, an interesting relation between the dredge and a natural collector. One of my students, R. F. Ford, is working on a small flatfish, *Citharichthys stigmaeus,* which is the commonest fish on the bottom, in shallow water. It's stomach contents indicate that the flatfish operates as a dredge and not as a sand corer. In other words, those amphipods, cumaceans, etc. which pop up out of the sand or live on the surface are caught by both the dredge and the flatfish. The latter is, therefore, living on food organisms which are relatively uncommon and is not taking advantage of the amphipods which the cores show to be certainly the most abundant ones.

SCHMIDT-NIELSEN: Is it because the flatfish eat them that they are less abundant?

FAGER: I doubt it because the flatfish and the organisms it eats are both much more abundant in deeper water; deeper than 10 meters. In the case of the crustacea that live on the surface of the sand, this may be due to reduced water movement. At depths less than 10 meters, the surge problem is very serious. Most of the time you have to fight to stay in one place.

CONOVER: A flatfish can cover a lot of territory, however. It is not restricted. Is there any territoriality in these flatfish?

FAGER: There does not seem to be, but we have not developed a good way of marking them yet.

CONOVER: It probably can swim better than it can dig.

FAGER: I am sure of that. The third observation, based on the core samples, concerns the distributions of the more abundant infaunal species, almost all of which are highly contagious—that is, they are very patchy. We have taken layered cores and we find that 80 to 90 per cent of the populations that we are interested in are in the top two centimeters, so five centimeters is safe. The major components of the fauna are amphipods and polychaetes. Although this is a clean sand bottom, there are very few large pelecypods in it.

FREMONT-SMITH: Are the two terms equivalent, patchy and contagious?

FAGER: Yes. To be more precise, spatial contagion means that if you find an individual of a particular species you are more likely than not to find a second individual of the same species in the near vicinity.

FREMONT-SMITH: "Contagious" means contiguous?

STRICKLAND: No, it means the chance of catching an individual is catching.

FOGG: Is it any different from saying that distribution is nonrandom?

FAGER: Yes, because the individuals could be evenly spaced which is also nonrandom, but in the opposite direction. A contagious distribution implies that you will find several individuals together and then you will not find any for some distance, and then you will find another patch.

SCHMIDT-NIELSEN: Do you know anything about the reasons for this patchiness? Would that be an important problem?

FAGER: I think it is an important problem and I am trying to do something with, but I have not yet been able to do much. Although you can see things as small as these animals underwater, it is difficult to make extensive observations because most of them are under the sand.

YONGE: These are what, exactly?

FAGER: I am talking almost entirely about amphipods and polychaetes. These make up the bulk of the organisms in the sand in this particular location.

HUTCHINSON: Can you see whether a patch of sand looks different?

FAGER: There is no evident patchiness.

HUTCHINSON: You know it does not? You can not see any chemical differences?

FAGER: No. The sand is almost uniform from the surf out to 130 feet depth; the median grain size ranging only from 0.1 to 0.2 mm. The bottom slopes all the way out at a constant 1 to 2 per cent. It is as uniform a location as I think one is likely to find and yet the animals are neither uniformly nor randomly distributed(4).

HUTCHINSON: Do you have mathematical treatment of the contagion? Do you know what sort of distribution is involved, if at all?

FAGER: They fit a Thomas distribution fairly well. The Thomas distribution(5) assumes that the distribution of patches is random (Poisson) —and we have independent evidence of this—and that the numbers of individuals per patch follow a Poisson distribution. In other words, it is a double Poisson. From the fitted distribution, one can estimate two parameters, average patch size and average number of patches per sample. For one of the amphipods that we have looked at, the average patch size is estimated as three individuals. This raises the interesting question: Are there two females and one male per patch or the reverse?

CONOVER: You ought to be able to sex the animals.

FAGER: We can sex them but the estimated average patches are much smaller than the 35-square-centimeter samples we have used up to now, and so we do not have the individuals from single patches. We are now starting to take smaller samples, down to a centimeter across. There is still evidence of patchiness at this size.

FREMONT-SMITH: What would be the range of numbers within a patch, from three up to what?

FAGER: With a Poisson with a mean of three, you have about a 20 per cent chance of finding one, and less than a five per cent chance of a patch larger than six.

SLOBODKIN: There is always a note of surprise when something is not randomly distributed.

FAGER: I am not surprised.

SLOBODKIN: No, but I would like to underline that to say animals are randomly distributed in space is making a very special set of assumptions about them. It means every place they come to in your sampling area is quite equal to them and that they do not care whether any other animals of the same kind or any other kind are around. You would assume either patchiness or regular distribution. I do not think anyone really has found a random distribution, has he?

FAGER: We have one species, a burrowing anemone *(Harenactis attenuata),* which appears to be randomly distributed. This is true for all the techniques we have used: fitting number of individuals per sample to a Poisson; distance to nearest neighbor; change in the variance/mean ratio as successively larger samples were formed by combining adjacent samples taken in a line; and counting runs of like sign where we put down a plus if one or more animals occurred in a 10-cm. interval along a line, and a minus if the species was absent.

SLOBODKIN: And this is not a question of your sampling error randomizing another distribution?

FAGER: I do not believe so because we have used so many different sampling techniques and they all agree.

SLOBODKIN: I believe this is the main source of so-called random distribution.

FAGER: I would agree that this was a good explanation.

SANCHEZ: Would you not expect that in a given area, but not a very big area, for a given organism the factors that determine distribution might be homogeneous?

SLOBODKIN: If they are homogeneous, really homogeneous, you would get the randomness.

SANCHEZ: You do not mean every factor is homogeneous, only those that are pertinent?

SLOBODKIN: Only those that matter.

SANCHEZ: Perhaps that would happen in a different area, at a different time.

MCLAREN: Doctor Fager told us he chose the area with that in mind.

FAGER: I chose it so that it was as uniform, at least visually, as one could get.

HUTCHINSON: Do you not need a dynamic randomization all the time? Isotropically turbulent water would give you a random type of distribution for any organism that was planktonic in the original sense of the word of being at the mercy of the forces that were impinging on it. The moment it could do anything about them, Doctor Slobodkin's point probably would be relevant. I would not expect anything else to be random. In your sandbed, the sand grains are not buzzing around in a Brownian movement, pushing the organisms around.

FAGER: Not in a Brownian movement, but they are buzzing around a good bit.

SLOBODKIN: This is what surprised me about the anemone—that it is fairly large, it does have active movement, and it is random.

FAGER: There are a number of other, equally large, organisms which appear to live in much the same way and they are all very patchy.

HUTCHINSON: Is there anything with less of a nervous system than the anemone—are there any sponges or plants?

FAGER: There are no macroscopic plants or sponges.

HUTCHINSON: So, there is always behavior?

FAGER: Yes, but the two other abundant coelenterates, the colonial *Renilla köllikeri,* and the small anemone, *Zaolutus actius,* are definitely patchy.

YOUNG: But does one anemone move about and the other one appear to stay stationary?

FAGER: The smaller one, *Zaolutus,* which is patchy, does move distances of a few centimeters; *Harenactis* does not seem to. Some individuals that we first saw in 1957 are still in the same location, within a centimeter, which is the precision of our sampling techniques. This is in the face of sand changes which can be as great as a 25-centimeter deposition in three days.

KANWISHER: Are they fighting their way to the top during that time?

FAGER: When we get that much sand deposition our stakes disappear, so we do not know what happens. With less deposition, we do find the anemones. In fact, we usually see somewhere between 70 and 90 per cent of the animals.

STRICKLAND: Do you mark them?

FAGER: I do not know how to mark an anemone.

STRICKLAND: I was wondering how you identified individuals.

FAGER: We have a series of stations, each marked by two quarter-inch-diameter brass rods approximately two meters apart. When we want to do a census, we use a template that fits over the two rods and in the center of which there is a brass circle with an area of ¼ m^2. A fixed rod crossing the center of the circle is marked off in centimeters as is a moveable arm at right angles to it. With these two scales, we can locate a particular anemone by observing the two coordinates and noting whether it is in the inshore or offshore half of the circle. Because of problems of parallax and movement of the diver, the best we can do is plus or minus a centimeter.

In the case of many individual anemones, we have repeated sightings, all within an area which is 2×2 cm, from 1957 until the present. Even though I have not tagged the organism, I am convinced that it is the same anemone. Given the density of the species, it is highly improbable, that one would always see an anemone there and not elsewhere if, in fact, it were not the same anemone.

SLOBODKIN: That is a matter of the spatial scale of your observations. If you have a patchy group of organisms, you either find within a patch a random or an infradispersed distribution. What you mean when you say you do not get infradispersed organisms is that within each patch you have randomness.

FAGER: That is the situation.

YONGE: In these patches where you get three, four, or five individuals, what would you say (and I would not expect a very explicit answer here), keeps them together? Is it the forces of the environment pushing them together or is it some mutual attraction?

FAGER: There do not appear to be any forces in the environment here which would tend to push things together. This is supported by the appearance of the sand surface; it is uniform and there are no patches of things on it.

My present guess would be either that there is some attraction between individuals and this tends to keep them together; or that there are some forces which we have not recognized, which lead to patchiness of food. The infauna, mostly amphipods and polychaetes, feed largely on the mixture of diatoms, bacteria and organic scum, etc., that collects on the surface of the sand grains. What we are starting to do now is to take centimeter-diameter samples, count the number of amphipods and polychaetes in them, and then determine the organic content of the sand. If the organic content turns out to be patchy and if its patchiness agrees

with the patchiness of the organisms, then I think we may start to get someplace.

CONOVER: What about the movement of the sand? It seems that you could find out what the sand is doing. Have you looked at this? There are methods of dyeing sand grains.

FAGER: At the depths where we have done most work(6)—5–10 meters—the top half centimeter is almost continuously in suspension on all but 1 or 2 per cent of the days. These animals are living in a constant sand storm.

KANWISHER: Are these the particles that they are sucking on, the ones that are in suspension?

FAGER: At least partly so. The feeding of a similar group of amphipods is described in the literature. They pick up a sand grain and treat it much as we might treat a cob of corn; sort of turn it around and chew the stuff off.

GONOR: Wolfgang Wieser(7) studied certain cumacea in the Seattle area that fed precisely that way; they were very particular about the sand grains, which they picked up individually to lick off the bacterial scum.

KANWISHER: How do you visualize any lateral homogeneity in the organic material remaining in sand particles if they are in such rapid, violent motion?

FAGER: I do not know. This is why I want to look at the distribution of the organic material. If it turns out to be randomly distributed, I will have to look for something else.

SCHMIDT-NIELSEN: Is it not true that once you have as little as one single organism in a uniform physical environment, the environment is no more uniform and can never be uniform again?

FAGER: One could argue that way, but unless there were attraction between individuals, the effect would probably be very small because the density of these organisms is low—about 0.1 organism per cm^3.

PEARCE: I have kept some amphipods in sand at Woods Hole and I have noticed that they are in constant movement and that you can actually observe them burrowing through the sand. Would this be fortuitous, finding these three or so together?

EDMONDSON: Suppose you created a random distribution of these things and suppose they moved around randomly until they came somewhere close together and this slowed them down so they stopped moving around. Is this not a mechanism adequate to account for the development of patchiness, and in that case, does not the frequency distribution tell you something about it?—Can you use that kind of information?

BAYLOR: What is the environmental barrier that slows them down?

EDMONDSON: The presence of the other animals; the fact that there is somebody within range of detection.

SLOBODKIN: There are, unfortunately, too many ways of getting at it. That is one hypothesis that would work. There are perhaps several dozen others which would give the same kind of distribution, ranging from being born in one place and staying near there, seasonal sex attraction of some sort, inhomogeneity in the environment, and eddies in the water. All of these will give precisely the same effect.

EDMONDSON: But we are developing a picture of an environment so much in motion that you cannot use inhomogeneity as a very persuasive clue. With all the sand milling around, the one constant thing here is that the animal can detect, within a centimeter, that there is another one there, and they stay together while there is a flow, and everything else moves around them.

YONGE: It seems to me that it is interesting that you get the same end result where you are dealing with a polychaete which has a pelagic life history or with these amphipods where the young emerge from the brood pouch and stay with the parent.

FAGER: We count a female with young in the brood pouch as a single individual, so the patchiness is not due to that.

CONOVER: Are these amphipods, tube dwellers?

FAGER: No. They are free-living burrowers, mostly oedocercids and haustorids. This type of animal is characteristic of this kind of sand environment.

MCLAREN: To get back to the random anemone, which was an exception, it seems to have a particularly high survivorship.

FAGER: It does, and a very low reproductive rate, at least in terms of young settling out on the bottom.

MCLAREN: Does anybody eat it?

FAGER: I have never seen anything attacking it.

MCLAREN: I heard of some work out of Rhode Island last fall in which it was suggested that you could impose a good deal of patchiness on an originally random distribution of young clams by selective feeding. They tend to stop and feed in one spot, clean it out and move to another spot.

COSTLOW: Is it possible to distribute the anemones artificially within a small area, and if so, what happens to their distribution after this?

FAGER: The answer so far is no, because we have not succeeded in digging them up uninjured. They have a sort of anchor bulb and these nearly always break off when you try to dig them out.

MCLAREN: How long are they?

FAGER: An anemone is as long as it wants to be.

SANCHEZ: Is it impossible to dig it up with the sand?

FAGER: We have not succeeded in doing this yet.

FREMONT-SMITH: How many millimeters, roughly speaking, do they go down?

FAGER: I do not know how deep it is when the anemone is undisturbed, but you can dig down until your arm up to the elbow is in the sand and you still seldom get them out uninjured.

SANCHEZ: But they probably would regenerate.

FAGER: I do not know what would happen in the field. If you bring them into the laboratory with the anchor bulb broken off, they refuse to eat and slowly die.

SANCHEZ: I think the suggestion of experimentally putting them in a different place, even if the bottom end is cut, could work because a certain number of them might regenerate there in nature.

SLOBODKIN: We have some material on movement of hydra which might be relevant. Tom Griffing, who is working with me, is studying the population dynamics of hydra in a lake. What we decided to do to get around the sampling problem was to put down an artificial substrate and have the hydra settle on it. We used dowel sticks of various kinds of wood and various thicknesses, which we planted them in the lake, but the hydra paid no attention to them. There were hydra all over the place, a veritable fur of hydra, but nothing on the dowels, so we decided there was something wrong with them. We then took a fishing line with a weight on it and a small cork that was not quite enough to lift it, and attached vertical strands of artificial plants, and still the hydra paid absolutely no attention until the hydra population itself became very dense and the fur got quite thick, and then all of our substrates were abundantly loaded with hydra.

How this works I am not sure, but apparently the hydra like to stay where they are unless there is some good reason to move elsewhere. If there are rather dense populations, the new buds simply do not settle near the parent but march off to another location. This is quite seasonal, so that for a matter of many months, all through spring and summer, the dowel sticks remain completely bare of hydra and in the late fall, just before the hydra population begins to vanish (we will get to a mechanism of vanishing later) all substrates become occupied. So I suspect that animals, at least conceivably, tend to stay where they are unless something pushes.

FAGER: I am sure these anemones stay where they are at least for a period of six years.

HUTCHINSON: They have a really effective anchor.

COSTLOW: You say that in the laboratory, regeneration rarely takes place?

FAGER: We have not seen it take place when they are broken off at the bottom.

SANCHEZ: That is not so surprising. In my experience marine animals never regenerate well in the laboratory.

GONOR: Doctor Fager, were they planted in the sand head up, or were they lying on the sand?

FAGER: They were planted in the sand head up.

KANWISHER: This is probably also true in deeper water. When the atomic submarine went down off Cape Cod last year, there was a stirring of activity to find the remainder of it as well as some clues as to what had happened. There were many ships with underwater cameras positioned by sound just off the bottom for many months taking many thousands of pictures. Doctor Hershey at Woods Hole recently put these together, and we now have overlapping pictures, all in very good focus, of the bottom, a track that is many kilometers long and many meters wide. This is a mile and a half deep, 8000 feet, and one has the simple-minded view that in water that deep the organisms remain in a very uniform environment. But only a few minutes of glancing at these photographs, without any serious statistical analysis, shows that there is, again, a grossly nonrandom distribution of a few flatfish here, a few sea urchins there, and two worms in another place, with large areas in between. One can see only the larger animals, but these are positioned in much the way you have described.

SANCHEZ: Are the polychaetes in your population tube-dwelling species?

FAGER: There are three tube dwellers, *Owenia fusiformis, Pectinaria californiensis,* and *Diopatra splendidissima. Owenia* is quite common, the other two are uncommon. The rest of the polychaetes do not build permanent tubes though some of them make a temporary mucus tube as they go through the sand.

EDMONDSON: How much of a problem is this going to give when you get around to making the analysis of organic matter you mentioned, these tube remnants where the animals were?

FAGER: Because the sand is almost uniform in size, we can use a netting which will allow about 90 per cent of it to go through, but which will stop the larger tube remnants.

HUTCHINSON: Sand which has been part of the tube will have some sort of glue on it?

FAGER: That is true. A very preliminary analysis (qualitative) suggests

that these tubes may be primarily proteinaceous material. If this is true, it is probably pretty good food.

HUTCHINSON: Still, being a former tube, it would immediately give a nonrandom type of distribution as to where the food was. It would tell you where the tubes had been.

KANWISHER: You mean they are eating themselves over and over?

HUTCHINSON: Worms have to bring something into the system.

STRICKLAND: Suppose you have three little beasts together; do these three beasts keep together and move around a bit, or do you not know?

FAGER: The idea of three beasts together arises only because the numbers of individuals per sample fit the Thomas distribution very well, and from this one can get an estimate of the average patch size. But this does not say, and I must emphasize this, that, in fact, there are patches of three. There are certainly other distributions that the data would also fit. In general, estimates of parameters obtained by fitting data to theoretical distributions are useful only as indicators of interesting things to look into further. It takes direct observation to determine whether they have any real biological meaning.

STRICKLAND: But does a patch of three or four, whatever it is, stay as a patch and move around as a patch, or do they redistribute themselves?

FAGER: I do not see any way of finding out about that in the field because there is no present way to tag these 2–5-mm.-long amphipods.

SLOBODKIN: In a patch, you say you have four individuals and you know the relative sizes of the individuals. If you find a patch in the same area, do you get roughly the same relative sizes, or cannot you tell?

FAGER: That method might be used except that the animals are buried and cannot be seen in the field. In order to separate them from the sand we have to take the sample into the laboratory and, therefore, that patch is destroyed.

SANCHEZ: Does the Poisson curve refer to one species?

FAGER: Yes. We have been looking at one species at a time.

SANCHEZ: How does it look when you take the total number of organisms?

FAGER: The distribution of total animals is also patchy. There is some evidence for contagion between the distributions of polychaetes and amphipods. This is another reason for looking at the distribution of organic material on the sand which might serve as food for both.

COSTLOW: Back to the anemones; can you comment on the evolution of a patch? Does it start with one and the next time there are two and then up to a certain number?

FAGER: If it started out with five *Harenactis* it stayed at five for six years; if with one, it stayed at one for six years. We have ten permanent

stations, a total area of 2½ m². In six years we have seen only seven *Harenactis* settle on this area. While this is not a very large area, the observations agree with those based on many samples taken throughout the habitat. The average density has been constant at about five per square meter and there have been no increases suggesting appreciable settlement.

BARKER-JØRGENSEN: How far down does this patchiness go? Are the foraminifera also patchy, or the nematodes?—If the distribution were correlated with organic matter on the sand grains, you should expect patchiness to go further down.

FAGER: We have done nothing with the nematodes and foraminifera. The latter have been looked at to some extent by one of the students of Doctor F. B. Phleger, and they appear to be patchy also.

PEARCE: What forams did you consider? What did you consider in analysing the samples for forams? Do you draw a line anywhere?

FAGER: We draw a line just above the nematodes, although the mesh we use (0.15 mm.) does retain many of them.

PEARCE: What about some of the very small polychaetes? I frequently find such worms with the smaller nematodes. This is particularly true for the polychaete larvae.

FAGER: We have looked for larvae but have not seen any great numbers of them. Perhaps we missed them.

SANCHEZ: Do you know anything about the reproduction of these anemones, their habits?

FAGER: *Harenactis* is supposed to have a planktonic planula stage, but I am not certain that anybody has actually observed it.

SANCHEZ: This particular species? Also, I do not know if this was mentioned at the beginning of this discussion, but in what different times of the year are you sampling?

FAGER: All year long.

SANCHEZ: That means that at the reproductive stage of the different species, they are remaining the same as—

FAGER: Yes. The population density of *Harenactis* does not vary seasonally nor did it vary appreciably over the six years of observation.

SANCHEZ: And the polychaetes and amphipods?

FAGER: In the polychaetes, amphipods and nearly all other species examined, we get a different situation. I will use *Renilla* as an example. During the period between August and November, there is a set of young colonies, 3 mm. across and with as few as two or three polyps. (Adult colonies are 6–7 cm. across). This often doubles the numbers of colonies of *Renilla* per m². Yet the numbers quickly return to the original level and have stayed essentially at that level for six years, with relatively little variation.

SANCHEZ: This took place once?

FAGER: No, every year. Every year from August to October we get tremendous numbers of small *Renilla.* We do not at any time get tremendous numbers of small *Haranactis attenuata.*

EDMONDSON: Do you know what the mortality is?

FAGER: I have seen two things eat *Renilla.* One of them is *Pleurophyllidia californica,* a sand-dwelling opisthobranch. It has seldom been observed except when there were large numbers of young *Renilla* present. Adult *Renilla* are very frequently eaten by the starfish, *Astropecten armatus.* You commonly find them with a *Renilla* peduncle sticking out of their mouth.

SANCHEZ: You have not given us any data on asteroids, sea stars?

FAGER: There is only the one sea star at this depth, *Astropecten armatus,* but it is not abundant. We see it at every dive, but we very seldom get it in the quarter-square-meter circles that we drop "randomly" or haphazardly to get density estimates of the epifauna. We have found an *Astropecten* in a circle only six times out of 672 samples.

SANCHEZ: You got one within the circle, you mean? But you see more of them around. Could you mark them, or tag them?

FAGER: Yes, I think we could tag them.

SANCHEZ: It is quite unlikely your instrument would fall on top of them.

FAGER: It depends on the relation between their density and the size of the sample. Our sample size is too small for efficiently sampling a species with such a low density.

BAYLOR: Suppose you take a sample of this sand and try to extract all this organic matter off the sand and then combust it to see how much carbon is left; can you get an estimate of what the available chemical energy is on the sand grains?

FAGER: I do not understand what you mean by extract it all off?

BAYLOR: You are a chemist, so I would leave the method of extracting or eluting the material from the surface of the sand grains to you. Is it possible to do this?

FAGER: I am going to burn it on the surface.

BAYLOR: That is right.

FAGER: What I intend to do is sieve the sand as we do now, obtain counts on the animals and then determine how much organic material is on or mixed in with the sand.

STRICKLAND: Is it conceivable that with the enormous amount of turbulence and sandstorming, you could possibly get any patchy distribution of organic matter?

FAGER: One would not think so but you do get a patchy distribution of the small organisms that live in the top 1–2 cm.

BAYLOR: Do you get wave patterns in the sand on the bottom?

FAGER: You get ripples.

BAYLOR: This indicates some kind of a nonrandomness.

FAGER: That is right, but we have taken samples on the crests of the ripples, on the seaward slopes, on the shoreward slopes and in the troughs and, statistically, we find no difference between the distribution of animals in these four locations.

YONGE: Your environment is the same; you are dealing with one type of bottom substance?

FAGER: Yes. The median grain size is about 0.2 mm. in the surf zone and about 0.1 mm. at 30 m. depth; the change in size is gradual.

YONGE: But only a change in size, no other obvious change?

FAGER: There is no other obvious change in the substrate. There is an obvious break in the amount of sand movement at a depth of about ten meters. The average period of the waves approaching the shore is such that they start to "feel the bottom" at a depth of about ten meters. At this point there is a break in the fauna; seaward of this depth there are more longlegged amphipods and other organisms that probably live on the sand surface; shoreward, there are essentially only burrowers.

Doctor D. L. Inman(8) at Scripps has followed the change in the sand level over the year at various depths. On the beach there may be a change in sand level of as much as two meters over a year. The maximum change per year decreases seaward, slowly at first and then quite rapidly. At and beyond 10 meters depth the maximum change over the year is about 2 cm. At about 5 meters depth, the maximum annual change, although still relatively large, is less than it is for some distance seaward or shoreward. The tentative explanation is(9) that the particular relationship of wave period and turbulence makes this essentially a center of oscillation. While sand here moves a great deal, there is less net change in level because deposition and removal more nearly balance. Another faunal break is correlated with this.

SCHMIDT-NIELSEN: Could one part be due to wave action and the other part to currents?

FAGER: No, in both cases, the major cause of the sand movement is wave action. There are currents, but they are not consistent in direction and they are not strong.

HUTCHINSON: Is your sea anemone the only thing which is anchored?

FAGER: The tube-building worms are anchored, and they are patchily distributed.

HUTCHINSON: As strongly as the anemone?

FAGER: Yes.

SCHMIDT-NIELSEN: How do the tube-building worms manage when there is deposition or movement of sand?

FAGER: *Owenia* is able to twist the tube and move up and down in the sand. I have seen it do this in the laboratory. It appears that it can move down more easily than it can move up.

SCHMIDT-NIELSON: With or without the tube?

FAGER: With the tube.

FREMONT-SMITH: Does it move the tube or build a different one? I thought you said the tube and the worm move together. It is not a question of rebuilding?

FAGER: This is not a question of rebuilding, although *Owenia* does apparently continue to build the tube.

SCHMIDT-NIELSEN: If a tube is going to be moved, there must be some force exerted between the tube and the environment.

FAGER: That is right.

SCHMIDT-NIELSEN: What is the vector of that?

FAGER: The tube is a proteinaceous cylinder shingled with flat particles such as mica, shell fragments, etc. The particles are attached by their lower portion so the tube is imbricated upwards. This gives it a good deal of purchase on the environment.

SCHMIDT-NIELSEN: The force would be from inside the tube, then?

FAGER: Yes. The worm is able to twist and turn itself and the tube, and move in the sand by doing this. On the upper part of the worm there are chaetae which are so arranged that they could pierce opposite sides of the tube and thus allow the worm to turn the tube with its body.

SLOBODKIN: Is the tube relatively flexible?

FAGER: Yes, it is quite flexible.

SLOBODKIN: You can imagine the worm swelling out to grip the sides of the tube with its body, turning, exerting a torque on the tube, leaving part of the tube still, and this would give motion.

BAYLOR: If the worm has a peristaltic wave of swelling that moves down the tube it will inevitably move the setae like oars and if there is some elasticity to the tube, this will pull the oars back in and automatically force the worm downwards.

FAGER: It actually turns, though.

CONOVER: It is not threaded?

SLOBODKIN: Yes, it is.

HUTCHINSON: Worms have to keep on turning—

FAGER: I do not know.

HUTCHINSON: Yes, that is it.

SLOBODKIN: This is analogous to the gruesome story of the movement

of porcupine quills through muscles. If you get stuck with a porcupine quill it will eventually emerge, but it goes in its own direction. The miscellaneous muscle movements can only push it one way.

REEVE: How about *Renilla;* is that animal anchored?

FAGER: Not in the same sense as *Harenactis. Renilla* is more or less heart-shaped, with a peduncle. In the field, the latter is buried in the sand and acts as a very effective anchor. On rough days when the surge was heavy, throwing us back and forth ten feet or more, we have seen *Renilla* capping a hummock of sand that was at least five centimeters above the general sand level, and very successfully, at least for the time we watched it, holding that sand against the surge.

We thought at first that certainly *Renilla* would be anchored and stay in position because if you kicked one out with your flippers the surge picked it up and rolled it over and over, moving it inshore toward the surf zone where, presumably, it would be tossed up on the beach. On the other hand, we seldom saw them rolling along the bottom unless we had kicked them out. Furthermore, they are practically never found along the beach. As they are common animals, these observations mean that they are rarely displaced from the sand.

However, as soon as we started looking at the permanent stations, it became evident that *Renilla* does not stay in place. It apparently moves continuously. You may find a colony in one spot on one day but the next day there will be three colonies in new locations but none in the original spot. I still do not understand how, in the presence of the constant surge, it can possibly do this and keep from being uprooted.

STRICKLAND: Where is the sand?

FAGER: In the laboratory, we have watched it move. What it does is start a wave of contraction at the apex of the "heart" which goes back progressively on the sides to the lobes, near the point of attachment of the peduncle. The animal then sort of hunches forward. It can move at the rate of about a centimeter in five minutes. When it moves in the laboratory, the peduncle trails out behind it. If it did this in the field it would soon be cast up on the beach.

HUTCHINSON: Does it show a Thomas distribution?

FAGER: The distribution of individuals per sample does not fit anywhere near as well as that of some of the amphipods.

YONGE: *Renilla* is a pennatulid adapted for life in the surf zone. All such animals can move by means of the swollen basal region, probably never very much but they will reerect themselves if removed.

FAGER: I still do not understand how it can move because if it once got that peduncle out of the bottom, I think it would be lost.

YONGE: It keeps it in, does it not?

FAGER: I suppose so, but I do not know how it moves with it in the sand.

YONGE: This fits in with behavior in the mole crabs and other inhabitants of exposed sandy beaches.

FAGER: This is at a depth of five to ten meters, further out than they occur. We have found *Renilla* considerably deeper, but our general impression (this is only an impression and I do not know how to measure it) is that the ones that are out deeper are not very healthy. The ones in the 5–10 m. depth range are in good condition.

BARKER-JØRGENSEN: If you take *Renilla* out of the bottom in the sea, will it not be able to get back into the bottom again?

FAGER: Not under the usual conditions of surge.

BARKER-JØRGENSEN: This is an aquarium experiment, is it not?

FAGER: Yes, the observations on movement were made in an aquarium experiment.

PEARCE: Does this "leaf" possibly act in an "aerodynamic" way in order to utilize the currents in some manner so that it maintains its position and orients itself within or to the flow of water?

Comment from the floor: The leaf is horizontal.

SLOBODKIN: He is referring to the surface of a flat body being in a current which, by a very slight muscular movement, is flying downward, planing down.

FAGER: It might hold itself down, but the only thing we have ever seen is that when they get torn up, they just roll over and over and disappear shoreward.

COSTLOW: Are the movements pulsed or could they select the time of movement according to the surge?

FAGER: They might be able to select times when the surge was absent or much reduced but we never seem to be out there then!

COSTLOW: When you kick them out that is not of their own volition. They are caught off guard.

FAGER: You might say this. I do not know.

MCLAREN: Doctor Pearce has something to say on this subject.*

PEARCE: I have only recently initiated an investigation in the field of epibenthic ecology. Most of my efforts are presently expended in trying to determine the limitations of the available collecting gear and the tech-

* This discussion actually took place on the third day of the Conference, but has been brought forward here because it is closely related to the discussion of sampling and in part took its origin from the earlier discussion.

niques to be used. I have been working with a relatively simple sampling instrument, the Smith-McIntyre quantitative grab. The locale in which I am working is Quick's Hole, a passage through the Elizabeth Islands that connects Buzzards Bay and Vineyard Sound. These islands extend south of Woods Hole. There is in this passage a benthic or sublittoral mussel population which I would like to sample over a period of two or three years or longer. I would like to try to determine what changes may occur, how the community is established and develops, and how recruitment of the associated species occurs.

A preliminary investigation indicates that the population of mussels (*Mytilus edulis*) is rapidly being depleted by sea star predation (principally *Asteria forbesi*), and at such a rate that one might suspect that by springtime there may not be any mussel population to work with!

One wonders how this occurs? Loosanoff and Galtsoff's former studies(10) might lead one to believe that the population of mussels is initially recruited when the number of *Asterias* is at a low ebb due to a poor larval "set" or because of possible migratory activity by the sea stars. Later, after the benthic mussel beds have become established, the stars return to their present numbers and prey heavily upon the now mature, fully grown (70–80 mm.) mussels. The fact that the mussels are of one year class, probably three years old, and that there has been no recruitment during the past year indicates that this may be true.*

In talking with Doctor Fager I learned that this mussel community adjoins a pure sand substrate similar to that in which he is presently working. From results obtained in the preliminary investigation it appears that the amphipod species, which are established in the pure sand (without an overlying mussel association) are also found in the substrate underlying the mussel beds. He thought that this was of interest and of some significance. In other words, the amphipods are constant in their distribution, with the epibenthic mussel association secondarily established over the underlying infauna populations.

This is essentially what I have been doing. I have done some preliminary work comparing the Smith-McIntyre grab with the van Veen, Petersen, and Knudsen grabs (these are all collecting devices primarily developed by the Scandinavian school of benthic research). For the use I wish to put it to, the Smith-McIntyre seems to be the most efficient instrument.

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* *Addendum:* In January of 1964 an exceedingly heavy set of spat occurred. It originally numbered more than 100,000 spat per square meter. By mid-February it had decreased to one-tenth the original number.

The Knudsen sampler is somewhat better, however, for sampling the deep-dwelling infauna. It is in essence a large coring tube!

STRICKLAND: Can you give us a vague idea of what the Smith-McIntyre grab is like?

PEARCE: The Smith-McIntyre is simply a set of symmetrical jaws actuated by a spring mechanism and closing by virtue of the release of the spring. The van Veen grab closes by pressure applied on rather long arms, which gives it leverage and allows it to bite into the substrate. The Petersen grab has much less of a mechanical advantage. It depends primarily upon its own weight to dig into the bottom.

As previously stated, the Knudsen grab, which was developed in Denmark, is a large coring tube. It is lowered to the surface of the substrate. There is a pump within the grab which is actuated by reeling the line back up on the deck winch. The grab sits on the bottom and as the water is pumped out of it, the weight of the overlying column of water forces the grab into the substrate. It is then a matter of pulling it out. If the vessel is sufficiently large and the winch strong enough it can be done. This is why I have not used it. I understand that the Danes no longer use it, or at least not to any great extent. They broke several lines and lost the grabs.

It is, however, being widely used at the Millport (Scotland) laboratory by Doctor Peter Barnett. He is sampling an area surrounding the new atomic power plant on the Clyde. He wants to get a life history for a number of bivalve species that are present in this environment. This is being done in order to determine the ultimate effect of the heated cooling waters which leave the station on the benthic populations. He uses the Knudsen with success but he uses it from the R. V. *Calanus* which is a rather large vessel, perhaps 75 feet in length.*

As I said, I have been using the Smith-McIntyre. If you run repetitive samples, i.e., take a series of samples in the same general area, they tend to be comparative. This indicates to me that if one collects and screens the samples in a consistent manner, consistent and valid results will be obtained.

STRICKLAND: How deep can you go?

PEARCE: Maximally, it can bite to a depth of 14 centimeters. In actual practice, however, it usually digs to a depth of six to nine centimeters.

STRICKLAND: How deep down are the things you are sampling for?

PEARCE: I have found about the same thing that Doctor Fager has in sand. Animal life tends to occur in the top two or three centimeters of

* P. Barnett, Personal communication.

substrate. The Smith-McIntyre consistently digs down to around six centimeters.

STRICKLAND: How much water is above the bottom?

PEARCE: The depth that I am working in? At present this varies from the immediate sublittoral (1.5–2 meters) to a depth of 20 meters. I must convert from feet to meters since the precision depth recorder being used records in feet.

SANCHEZ: Can you not see this better by diving?

PEARCE: I have considered this. I am not a diver, I would like to learn, however. At the present time the Marine Biological Laboratory does not permit diving, so I cannot do it under the auspices of the laboratory.

There are other problems as well. The area in which I am working has rather treacherous currents; up to three miles per hour. This means that observations must be conducted during slack tides and these periods last only between 15 and 20 minutes. Diving would be a fine adjunct but it would not, in itself, solve all benthic sampling problems. To carry out the type of sampling which we are considering here one must dive and use a coring tube or some other sampling device. Doctor Fager mentioned using direct visual observations, i.e., lowering a ring or quadrate and making a count of the organisms within the perimeter of the device. It is, however, difficult, when you have a benthic fauna, particularly an epibenthic fauna, which is distributed over an irregular surface, to lower something down and then get a visual count. A number of animals which live on the bottom tend to be highly motile, particularly crabs, fish, and so forth. These forms are probably missed as soon as the diver's presence is noted!

Actually, I have collected rather large sculpins, cling-fish, eels, and similar bottomfish in the Smith-McIntyre. It seems to be a "quick" grab. When it is lowered quite rapidly, it is capable of collecting motile forms.

SANCHEZ: What sort of information are you after?

PEARCE: First, I am interested in determining what organisms are found there at the present and throughout the year. Second, Professor Thorson has initiated a program in Denmark, a long-range sampling program, in which the annual recruitment and survival can be determined. It is a program involving the collection of plankton from the water overlying a particular substrate as well as a benthic survey of the latter. The larval forms in the plankton can then be compared with the organisms that are settling out. Through such a study, a long-range view of "larval-wastage," survival, etc., may be had.

I am working largely by myself so I am unable to have as ambitious

a program as this. However, I do want to see how this community or association is oriented at a particular time. In other words, I am interested in the biological interrelationships within the association and in how the latter may change over a period of time.

I had an opportunity, while I was in Europe last year, to work in several Scandinavian and British marine environments. These included waters surrounding the Isle of Lohm, Finland (the University of Turku's Marine Station is there), the Varangarfjord, a large fjord ancillary to the Barents Sea, and the Danish Øresund. Epibenthic mussel associations were found in all three locales. It was noted that while some of the species found in the associations appeared to be different, there were similarities regardless of the area observed. If one goes to Puget Sound the same thing can be found; the epibenthic *Modiolus* association seen there is similar to the *Mytilus* associations found in the Scandinavian waters or in Quick's Hole. These associations or communities, regardless of where they appear, seem to be similar and they are comprised of comparable niches occupied by the same sort of animals. I am interested in seeing how this thing is established. Actually, mussels seem to determine a community much as a holdfast of an alga would determine a community. Doctor Fager, I understand, has a student working on the latter now. The holdfast of attached algae and the byssal mass of the mussels both seem to provide an environment for a unique association; so I am interested in studying this.

SANCHEZ: In the substrate?

PEARCE: Yes. I am interested in the pinnotherid crabs, and their symbiosis, i.e., the relationship between the crabs and their hosts, in the present case the mussels. The presence of the pinnotherid crab, *Pinnotheres maculatus,* may make the host mussel more subject to predation. It may weaken the mussel in some way. Evidence from a previous study indicates that this may be true(11).* I am interested in these relationships and their study complements the community investigations. Again, I hesitate to use the word "community" since some people do not believe in the community concept. I do, however.

SANCHEZ: Can I go back a moment with respect to the method of study of communities at this level? Has photography not been used?

PEARCE: Yes, Doctor Howard Sander's group as well as others at Woods Hole have used this approach. Vevers(12) has also photographed the benthos. Doctor Barnes of the Millport, Scotland, station has used TV with some success(13).

* *Op. cit.,* p. 336.

SANCHEZ: For this particular level where you are, a few meters below the horizon, I should think it could be used.

PEARCE: I do not think underwater photographs give a true picture of what or how much is really there. I think that Doctor Fager, in diving and observing the area within a survey ring, found this to be true. He put the ring down and made visual counts. Later, in sampling this substrate, he found a much higher percentage of individuals then he had sighted visually. If accurate visual counts are difficult to make I am sure that it would be even harder to interpret a photograph. I think that Doctor Sanders has found this to be so.

SANCHEZ: Is this rocky bottom?

PEARCE: No, this is a sandy bottom. However, a rocky bottom might be even more difficult to observe.

SANCHEZ: What mussel is this?

PEARCE: *Mytilus edulis.* It appears quite different when it grows in a benthic situation rather than in the intertidal. It is larger, has a more sturdy shell, and apparently a greater rate of growth.

SANCHEZ: What does it attach to?

PEARCE: It looks to me as though it is attaching to previous mussel shells.

SANCHEZ: A piling operation?

PEARCE: You see the same thing in San Juan Channel, in Puget Sound. It is definite that there they build up over generations. Actually, I have never used a quantitative instrument there, but in dredging, when the mussels are brought to the surface, they are oriented so that the living mussels will be at the top of a complex and one may observe a "stack," five or six mussel layers deep.

SCHMIDT-NIELSEN: I want to ask a question along the same line. What species of a similar nature are in the benthic communities you investigated?

PEARCE: *Modiolus modiolus* in Puget Sound. *Mytilus edulis* and *californianus* are also found there. In the waters off Finland *Mytilus edulis* were found. The same species occurred in the Varangarfjord and Øresund. *Modiolus* was also found in the latter.

SANCHEZ: I gather from your comments that the problem of *Asterias* eating up the mollusks here has not been prevented so far—the *Asterias* predating on the mollusks has not been prevented, has not been stopped.

PEARCE: No. I know it occurs. Doctor Loosanof's original studies(10) some years ago were predicated on this complaint.

SANCHEZ: I know it is an old problem and that is why I wondered if anything had been done. Are most species of asteria predating equally?

PEARCE: Both *Asterias forbesi,* found south of the Cape, and *Asterias vulgaris* occur on the mussel beds. The latter occur south of the Cape in

only limited numbers. Earlier in the year, when I first started sampling in the area, there were relatively fewer *vulgaris*. Since the water has become cooler more *vulgaris* seem to be present. This is a matter of 20 or 25 samples.

SANCHEZ: You have no difficulty in discriminating between the two *Asterias*?

PEARCE: No, not that I know of. John Valois, who has been working in the area for some time, says that the shape of the arms as well as the color of the madreporite is indicative.

SANCHEZ: I warn you against this.

PEARCE: I am sure there are subtle differences.

SANCHEZ: I can tell you an anecdote. When I was taking the latter part of the Woods Hole course some years ago, we brought to the laboratory session a certain number of *Asterias vulgaris* and a certain number of *Asterias forbesi*. They were laid on a long sea table, one species at one end and the other at the other end, and we were told to compare the forms and note the differences; so we began doing this but by the end of the year the animals had crept all over the sea table and then nobody, not even the instructors, could tell which was which.

PEARCE: Who originally separated them? I looked into the problem because I was working in asteroids; I looked at this problem in museum collections, and so on, and it is difficult if at all possible.

STRICKLAND: I think Doctor Kanwisher may have something to tell us on recent developments in instrumentation.

KANWISHER: Lateral homogeneity, as Doctor Fager has told us, has long bothered many people. The same is true in mid-water. If one looks at a Hardy plankton record from the North Sea and sees mile-by-mile changes in characteristics of the plankton, it is upsetting. In the inshore waters, John Teal and I have been working with partial pressure of carbon dioxide, P_{CO_2}, which can be continuously monitored and recorded. We find violent variations in a half-mile to many-mile scale which we have not been able to correlate with anything yet, but it has stimulated us in an effort to find other things that we can measure to see what is causing it.

CO_2 is particularly pertinent because it exchanges slowly across the surface and is chemically combined and it is sensitive to change by biological activity. So one might like to know something about the plants and animals present that affect CO_2.*

* EDITOR'S NOTE: Here followed an extensive discussion and demonstration by Doctor Kanwisher of advances in sea-going instrumentation for the determination of population density of organisms and properties of sea water which give information about biological activity. Several small instruments were exhibited and the principles

YONGE: Have you had any experience with the Hardy continuous plankton recorder in this connection?

KANWISHER: No, I have not. I have looked at some of the recorders in Scotland.

SCHMIDT-NIELSEN: What is the Hardy recorder?

YONGE: It is a torpedo-shaped instrument of some considerable weight out of water and is towed by a metal warp behind a suitable vessel(15). It has an opening through which water enters and then flows through a continually moving band of bolting silk. This passes from one roller to another at a known speed. As the exposed surfaces pass on to the second roller, they are covered by another sheet of silk so that the plankton sample is contained, like the contents of a sandwich, between two layers of silk. It is preserved in formalin.

This is rather complicated and there were many initial problems but the majority have been solved over the years. The major trouble now is the occasional loss of a recorder but they seldom, if ever, fail to work. You get the final double roll of bolting silk with the plankton sandwich between.

SCHMIDT-NIELSEN: But there is a tremendous number of man-hours going into the analysis of this afterwards?

YONGE: Yes.

FREMONT-SMITH: This is then studied under a microscope—the sandwich is separated?

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of operation and use discussed with Boden, Pearce, Edmondson, Sanchez, Fager, Strickland, and Lasker.

The major part of the discussion concerned an instrument built on a modified Coulter counter principle in which a sensor would be pushed ahead of a ship(14). The sensor has an orifice leading into a tube containing three electrodes so connected that when a particle passes through the tube a double electrical pulse results that has convenient properties for recording. The pulse voltage varies with the size of the particle. A single orifice can give an order of magnitude of, say 0.2 to 2 mm. With a series of orifice sizes and other variations, it is possible to get information on the size spectrum of organisms and other particles. Provision of screens for keeping out the "jelly things" or for concentrating particles of a particular size range gives flexibility. By monitoring the pulses on an oscilloscope, it is possible to arrange to take samples when localized clouds of particles are encountered in order to permit identification of the particles.

For small particles such as phytoplankton, *in situ* light scattering and spectral photometric measurements are capable of giving information with a certain amount of discrimination of particle classes and pigment content.

Lasker pointed out that the bow wave in front of a vessel can interfere with sampling devices pushed in front, and referred to work with the B. C. F. Plankton pump at La Jolla in which it was necessary to pump water at a velocity faster than that of the ship to get adequate samples.

YONGE: That is right. The plankton is sorted out and each person specializes on one particular group. One person may work on copepods and another on planktonic larvae, another on this, and another on that.

PROVASOLI: The speed of the boat controls the unrolling so that you know exactly from which part of the ocean the sample was taken.

YONGE: I should say something more about this, although I have never used a recorder. This work is done at the Oceanographic Laboratory at Edinburgh which comes under the Scottish Marine Biological Association. It all stems from the work of Alister Hardy(15) in Hull in the 1930's.

Continuous records of plankton are made by this highly ingenious machine which is towed by commercial vessels running usually from British ports across the surrounding seas. This program has been extended gradually, helped by the introduction of weather ships, until it now reaches across the North Atlantic. We have here got a wide picture covering a long period of time as well as a great area. The value increases the longer the records are continued.

There is now a seasonal picture of the occurrence of the main planktonic constituents, especially around Great Britain, not for one but for a series of years and showing, for instance, the changes associated with greater or less inflow of Atlantic water around the north of Scotland. A plankton atlas is being compiled on the basis of these data. This is continually being worked up; we are seldom, I think, more than a few months behind time, if that much. In the hands of mathematically qualified people these data are proving extremely valuable.

We are beginning to get down to the basis of productivity, at any rate, to the causes of the variations in productivity in what are the main fishing areas of the west of Europe. And this is now extending far to the west.

STRICKLAND: What proportion of the trained Scottish marine biologists is tied up in that program in one way or another?

YONGE: Just the staff; we employ some thirty-odd people, I should say, of which less than half are graduates, the rest technicians, etc. Only plankton-recorder work is done. There is a close tie up with Fisheries Laboratory at Aberdeen.

STRICKLAND: The great inertia, I think, in starting a program of this sort, say, on the West Coast of the United States, would be the great difficulty of recruiting from scratch very rapidly 15 people of the right type of taxonomic background who would be willing to do it and who would be competent to do it. Several of us have wondered whether something could be done here. I realize it has evolved in this way historically in the United Kingdom but we have wondered whether the recruitment of high school children, by a few psychiatrists who picked out the ones who

have a sustaining factor and the ability to recognize shapes, could not produce the sort of people required for much of the spade-work.

FREMONT-SMITH: Do not overvalue a psychiatrist, please.

YONGE: We used to think we should find difficulty in maintaining a suitable staff at Edinburgh whereas it would be easier at Millport with the usual facilities of a marine laboratory. But it has proved easier to get suitable people for Edinburgh. They are fascinated with our wealth of data.

FREMONT-SMITH: So, you have to have the data in hand to get the people?

YONGE: Right. Now we are cashing in on 20 years of data-collecting.

FREMONT-SMITH: We need 20 more years.

STRICKLAND: Do these mathematicians you get look at the tapes?

YONGE: Yes, everybody looks at the tapes.

SANCHEZ: Does the usefulness of this information require that the organisms be identified down to species?

YONGE: It can be.

SANCHEZ: But it does not require it?

YONGE: Yes, you would hope to distinguish between *Calanus finmarchicus* and *Calanus helgolandicus,* for example.

PEARCE: I talked to Steve Geiger, who is with the group now. He says it necessitates learning a whole new system of taxonomics because most of the animals are squashed so you have to be able to identify animals that have been stepped on—but they have evidently been able to do this.

YONGE: When this started, one wondered about all this, about the mass of data that was accumulating and about the nature of the material when it came to be examined. But this has not proved an insuperable problem. The plankton survey has been an undoubted success.

But I agree, it does depend so much on the amount of data, while I think we have been most fortunate in getting the right kind of people. They have found the work fascinating.

RAY: I think you have given a good reason for getting people of high caliber now who are interested in this remarkable collection of information and can do something with it, but how did you get people for the last 20 years to do the collecting? They must not have been mathematicians, and so on.

YONGE: No, they were not.

RAY: What type of person did you have 10 years ago, or 15 years ago?

YONGE: You have to go back to before the war when Alister Hardy started it at Hull. It is hard to answer that. There have been a few people, I suppose, who have not been so good, but there have been a lot of

people who have been extremely good, people who have reconstructed things amazingly often from the fragments of plankton.

RAY: Has there been a setup to train the people there, to take people who are relatively untrained?

YONGE: I think R. Glover, who is now in charge of the laboratory, would say it takes about twelve months after appointment before the person really pulls his weight. Of course, we now have a scheme under ONR, which a number of you may know about, and we have two people from this country at present with the group at Edinburgh.

FREMONT-SMITH: You are training a nucleus for us so that we may have them back, hopefully, to start our collection?

YONGE: That is the hope.

FAGER: This very rich source of data, some of which has been published is, I think, some of the strongest evidence for the whole problem about which John and I have been talking, namely, patchiness in the sea(16). One of my students took "samples" at 20-mile intervals from the continuous record made on a trip across the North Sea from Hull to Bremen. He looked particularly at *Biddulphia sinensis*. The Hardy recorder showed five distinct peaks of abundance of the species. If he started his sampling 20 miles out of Hull, he found evidence for two large patches and an average density over the run greater than was actually present. If he started sampling 30 miles out of Hull, he found an almost constant density throughout the run, with an average much below the actual. In fact, depending on where you placed your first station, he found you could get almost any picture you wanted of the average density and the variation in density of this species across the North Sea. Other species gave similar results.

As most oceanographic cruises do take samples at definite intervals of this magnitude or greater, this has led me to wonder just exactly what oceanographic sampling, as it is now done, means in terms of the actual density of phytoplankton, and probably zooplankton, populations.

YONGE: Yes, you have to have a continuous record to get over the phytoplankton patchiness.

BAYLOR: Does not the impression of patchiness that your student achieved depend on the periodicity of sampling?

FAGER: He imposed a 20-mile periodicity. The actual sampling was continuous.

BAYLOR: It depends on the periodicity of sampling he used.

FAGER: He used just one period and varied the starting position.

BAYLOR: This says that the data are periodic also, to some extent.

FAGER: Probably, to some extent.

BAYLOR: And that you are aliasing the data.

FAGER: I don't understand what you mean by "aliasing the data."

BAYLOR: Aliasing the data is the sort of thing that happens—if, for example, you sample a sine wave and you always sample it at its peak then you do not know it has valleys. Or, alternatively, if you always sample in the valleys you do not know it has peaks, so if you sample periodically, at a frequency slightly greater than the first harmonic, for example, you can therefore believe that the data have a long period to them, when, in point of fact, they do not. They have a short period.

FAGER: That is exactly what happened here. By using sampling intervals that were reasonable in terms of what oceanographic expeditions do, he got a tremendous range of estimates because he was, as you say, aliasing the data. I did not know the term, but it describes what was happening precisely.

FREMONT-SMITH: Is it good or bad?

BAYLOR: Oh, it is very bad to alias data.

PROVASOLI: Is there any hope that electronically, by projecting shapes, one can go through and create a Hardy plankton recorder that would eliminate the taxonomist? I pose the question to the electronics man.

KANWISHER: The electronics pulse triggered by a particle going through a tiny orifice can be used to trigger a flash which will take a picture on a single frame of an 8 mm. movie camera.

MCLAREN: That seems to be no advantage over identifying organisms in a net.

CONOVER: I think it would be harder.

FAGER: In answer to Provasoli's question, Riedel, a micropaleontologist at Scripps, has talked to electronic experts about a machine to identify radiolarians. These are relatively much simpler in terms of shape. Such a machine is apparently feasible, but it will cost a great deal of money and this has not been forthcoming.

COSTLOW: Are we going to hit a problem with this patchiness? We are concerned about photographing or identifying the things that we catch, and yet it has been mentioned several times now that the sampling techniques themselves are still quite crude, so that any attempt at statistical analysis of the occurrence of these things does not mean a thing. Even the identification is not going to mean much else than that you could say this species does happen to be there.

STRICKLAND: I think you can still begin to develop the techniques one stage at a time.

KANWISHER: Strickland has show very clearly in deep water off British Columbia, for instance, that apparently phytoplankton is limited by grazing. This means that predator relationships or grazing relationships are

so important that one would like some way of assessing them in spatial continuity.

STRICKLAND: Yes, but I think the point here, though, is to what extent you concentrate on the sampling problem before you concentrate on the methods, and to what extent you concentrate on the methods before the sampling. The answer is, that I suppose both have to go together and there tend to be periods of imbalance. I think most of us would agree that, on the whole, we are badly imbalanced, we have neither good sampling nor good methods, but we are probably worse off in sampling than with methods, once we have the sample.

COSTLOW: What can electronics do for sampling?

KANWISHER: It cannot do much. I have not any hope to offer. The situation looks pretty grim.

BAYLOR: I disagree with you. I think you do have hope to offer here, because your device has considerably smaller spatial resolution than the Hardy plankton sampler and will eventually give us a much better idea of what the small-scale patchiness looks like than we can ever get from the Hardy plankton sampler.

STRICKLAND: I think you can speed up the Hardy plankton recorder.

BAYLOR: In point of fact, you do not do it.

YONGE: There are various ways in which it might be improved. One of the most important is to get it to undulate, to go up and down in the water. At present, it operates at one level only and it would obviously be better if it sampled a series of layers. This would reduce the effect of patchiness at any particular level.

KANWISHER: I have a tremendous respect for the Hardy plankton recorder device. It has not been used in America and this is to our shame and discredit. It was my original inspection of the Hardy plankton records that brought upon me a greater consciousness of the inhomogeneity of these factors we have been mentioning.

SANCHEZ: I do not have much experience in this field but from what I know of the merits of the work of the Hardy plankton recorder as done by the British biologists, it would seem to me that Doctor Kanwisher's instrument could fit in very well to solve some of the problems. As I see it, there is quantitative and qualitative information coming from the Hardy plankton recorder and, for one thing, the quantitative information could very well be solved with an instrument of the type Doctor Kanwisher spoke of.

PROVASOLI: Or as a means of cross-checking.

SANCHEZ: Quite. If you get information on the number of organisms and the size of organisms, you get a good amount of usable information for certain types of ecological work, and if one can do the sampling of

the species involved at certain intervals, one can get the more statistically significant organisms present. You would probably skip a few of the unimportant species, but then you could sample occasionally every so many miles or so, get a small sample, and fill in. You do not need a continuous recording for that. What you are looking for is really significant organisms, organisms which make up the larger bulk.

PROVASOLI: This is the kind of discussion I hoped would develop. There is a fundamental difference between what we are doing in America and what is being done in other countries. We tend to take biomass or other measurements which give us the number of certain-size organisms, their carbon content and so on, but we do not specify what species we are dealing with. Since animals are eating only certain species and not others, we do not collect the useful data that the plankton recorder gives us.

STRICKLAND: Except that it possibly can get a large amount of that type of data more conveniently than the other type.

PROVASOLI: That is quite true.

STRICKLAND: Both are needed.

FREMONT-SMITH: Are both not needed in some areas, and is there not something that can be done about this? Is this a very expensive instrument?

YONGE: I would not be able to answer that. About £500, I think.

PROVASOLI: The expensive part is the personnel.

HUTCHINSON: There is a very basic problem involved here. The biomass approach, which I once, I think, called hological, i.e., a discourse on whole things, involves, obviously, losing a lot of information. The question arises whether this information is scientifically so valuable that you must not lose it, and that seems to me to depend upon what the fundamental explanation is of having a lot of different kinds of things in the system. I have taken, perhaps ad nauseam, many hours at many meetings trying to discuss this problem, mainly coming to the conclusion that at least so far as most of the phytoplankton goes, we have not the remotest idea.

We cannot at the moment, I think, tell whether the loss of information in lumping everything together is throwing out nearly everything we want or only a small part of it, because we do not have any respectable set of ideas as to what the diversity means.

I think, in the zooplankton, we could come to the conclusion that there are a good many different kinds of foods and that a good many different kinds of things ate them, but when we get to the phytoplankton it does not make any sense in terms of any theoretical concepts that I know of. So we simply have to accept that we do not know whether this lack of

knowledge about species is a fundamental or a rather unimportant defect in those methods that lump everything together.

STRICKLAND: Even if you know something about species, you must also eventually get some idea of the mass of edible material tied up in a given species. You still have to know something better than numbers. Mr. Glover gave me a reel from the Hardy recorder two years ago. This reel was marked off in sections, each corresponding to some distance. For taxonomic work they do not read every section so one can cut off every other one, say, with scissors, get a wash bottle and wash most of the animal matter off the silk and do a Kjeldahl nitrogen test. Even with the thing set up as it stands, we can get a quantitative estimate of the amount of particulate nitrogen in the sea above a certain size. I think the answer is to try to do both taxonomy and nitrogen biomass at this stage until we find out, as Doctor Hutchinson says, which is the most important. I think they are both important.

EDMONDSON: I just want to follow up what you said. In practice one cannot always do everything one knows how to do. One has to make choices.

Can one not sometimes decide in terms of the specific questions one is investigating which is most useful? I can well imagine that there are situations in which the fact that the *Calanus* patch is *hyperboreus* or *finmarchicus* is relatively inconsequential. Does it make a difference to a whale, or whoever eats these things?

On the other hand, if you are considering the effect of these animals on their own food supply, perhaps there is a bigger difference, if there is any difference, in selection of food species or digestion. Perhaps one has to look at it from time to time in this way: What is the question? One can perhaps suggest that it does not matter if the particles in a given range are this species or another, except when it does turn out that, for example, two species may be different in food value for other animals. You have to determine whether or not it makes a difference because surely there are species that are essentially the same as far as their supply value goes.

There is another aspect. Some of the questions one asks are like where is the nitrogen? What demand is being put upon the nitrogen cycle, so to speak, by the organisms? Here, I think, the lumping together approach not only is useful, but necessary. There are aspects here where you have to do this in order to make progress.

YONGE: I think you are bound to need a knowledge of your species until such time as the chemists can determine the origin of water masses chemically.

The chemists can tell us nothing about the differences between At-

lantic and coastal waters but a biologist can tell quite clearly as soon as he looks at the plankton where the water came from, and this is a fundamental matter where productivity is concerned. As soon as the chemists can take their analyses a stage further and say, "This is coastal water and that is Atlantic water," then the plankton indicators cease to be of such great importance.

FREMONT-SMITH: I think Doctor Edmondson put his finger on it. It depends upon the question (and we have had this kind of discussion come up in many conferences). Which is the most important method? And the answer is nearly always that they are both *the* most important, but one is most important to answer question A, and the other to answer question B. So, if we would be a little more specific as to what question we are putting to nature, it would clarify which is the most important method, and then a method, of course, obviously, may be more important in one period than another. But I think this discussion has gone around a circle.

PROVASOLI: I think, we might also say that the real goal is to know all about the sea environment. We have started to work on the sea only recently and we have the gigantic task to telescope what has been done on land in the different periods of development in science. In the 19th century we were mostly interested in morphology and life-cycles, later on in evolution, genetics, physiology, and biochemistry. All this has still to be done on most animals and plants of the sea. We need the so-called old-fashioned zoology and botany as well as the most advanced methods of today's science.

FREMONT-SMITH: We have to specify the subgoals under your very big goal, because if we just fix our minds on the big goal and say, "What is more important than this?" we get caught in this discussion; but if we specify a series of subgoals, then we can say, "What do we need to answer to fulfill this subgoal?"

EDMONDSON: The "hololological" approach generally has consisted of putting together the pieces. The pieces were measured separately and put together. Now everybody is trying to find an easier way to do it, by measuring the whole to begin with.

SLOBODKIN: I have a feeling I was here two years ago in almost the same spot, almost the same chair. The same argument came up of, What is the best way to do something without anybody ever even mentioning the "something" and Doctor Fremont-Smith pointed out that, well, let me put it in my way: You can say that this is the best method, and then someone asks, "The best method to do what?" and that is embarrassing. Then Provasoli said that we have styles in science, and so we must follow some sort of historical determinism in the style in which we handle ocean-

ography, which I desperately resent. I have no particular way to refute it. I simply resent it and want that recorded.

I do not like to think of the progress of science being historically deterministic.

PROVASOLI: I was just mentioning what has happened on land and the possibility we have had to cover different aspects in different times, so that we know fairly well what most of the plants and animals are and what they do. But in the sea we still have to do the job that was done on land from the time of primitive man to now, of knowing what are the species, and to assess what quantities are involved and what the productivity of the system is.

Besides all that, we want to utilize these resources, to manage them, and to start cultivation. All this means, getting down to brass tacks, studying species, life-cycles, food chains, and so on.

FAGER: I think it might be pointed out that perhaps only a marine biologist would say we know what is happening on land.

SLOBODKIN: I have a terrible sensation that we are dealing with a "Five-year Plan of Oceanography," that we have set up the national goal and we march onward and upward to it on a utilitarian basis. I would prefer to think, and in fact do think—I can not do anything about it—that the process of trying to find things out is in a sense an esthetic and personal one. If there were a well-organized science of, say, ecology, with clearcut goals and clear plays for each man, I would be doing something else.

PROVASOLI: Hear! Hear!

FREMONT-SMITH: I do not think there is very much danger in the forseeable future of this happening.

STRICKLAND: To take up Doctor Fager's remark about the marine biologist's knowing what is happening on land, I was going to ask whether anybody has ever solved the insect problem of contagion? How do people go around deciding the number of gnats around a lake, or does not anybody do this?

EDMONDSON: You count the larvae in the lake.

HUTCHINSON: This is strictly true.

STRICKLAND: I was wondering if anybody could tell us how one gets the aerial distribution of insects.

KANWISHER: This was seriously being done by one Briton working in the grass lands in West Africa a decade ago, by taking a Land Rover with nets hung by the wheel and going across the savannah, and periodically collecting what came out the tail end of the net.

STRICKLAND: He had his problems too, I guess.

KANWISHER: I asked him what the average weight of mosquitoes was and he said, "About the same as that of elephants."

SLOBODKIN: There are some data by Url Lanham * on the old field in Michigan that the micro arthropod fauna below the ground surface is essentially equal in weight to the deer and small mammal population above the ground surface.

STRICKLAND: Was this done with an impeccable sampling system?

SLOBODKIN: Impeccable only in spots.

FAGER: The same sampling problems appear in both places, but in the sea we have three dimensions to work with rather than two. On land there are three only if you are talking about flying insects, but they do not fly very high.

HUTCHINSON: It has been suggested deductively by Lack(17), that there must be a bird to eat them, but since it would be transparent it would never be observed (Hardy's Swift).

MCLAREN: On the question of methodology, I think that while there appears to be a dichotomy between Doctor Kanwisher and the Hardy approach, really there is more in common between these approaches than one might think at first glance. Both are attempts to discover pattern or lack of pattern in the sea, in biomass, or in individual organisms. In fact, there is an entirely different approach, and that is to decide upon a pattern beforehand or to discover one, such as Cushing(18) has done, for example, in picking out a plankton patch and then working out the relationships within that pattern, the dynamics.

The second approach seems to me to be probably a great deal more fruitful for understanding the question of productivity and feeding, and so forth.

STRICKLAND: You have first to find your patch, and I think Cushing(18) was probably quite lucky.

MCLAREN: There are other simplified situations such as the lake I am studying in Baffin Island which is, in fact, a marine microcosm. These are the sorts of natural experimental situations which, I think, are enormously revealing if you can exploit them.

CONOVER: With regard to patches, this is essentially what we have been doing in the Gulf of Maine, tagging patches with parachute drogues and eventually radio-beacons to float around, we hope, with the patch. The system at the moment is to use a large cargo parachute, and aluminum pipe and some inner tubes as a buoy; the relative drag of the surface buoy is quite limited. To this we attach a trailer which has a sampling

* Url Lanham, Museum of Zoology, University of Colorado, Boulder, Colorado, personal communication.

hose and periodically we come out, weather permitting, attach to the hose, and take our samples.

STRICKLAND: How do you know the drogue stays with the patch?

CONOVER: For this we have only limited evidence. We have thrown out dye and have been able to detect the dye over the period of our sampling, about 56 hours. However, the diffusion, or whatever it is that is causing the dye to disperse, is very considerable and although we are able to detect the dye, the dye is by no means as concentrated. It is only about ten^{-3} of its original concentration.

FREMONT-SMITH: Does the dye diffuse faster than the patch?

CONOVER: The patch, of course, is something that we do not know is there. We are essentially choosing a hunk of ocean and making a patch.

STRICKLAND: When you lower six parachute drogues, each one ten meters below the other, you may find that four of them go in one direction and two of them take off in the opposite direction which makes it a bit difficult to know what has happened to a "patch."

CONOVER: We have put them at different depths in the environment we are working at. In general, they do have a net movement in the same general direction. They may diverge sometimes, for brief periods, and go in different directions, but in the environment in which we are working under usual conditions, the water mass appears to be a single water mass from surface to bottom.

FAGER: This brings up some work that John McGowan has been doing at Scripps. What he did was put down a parachute drogue and follow it and take samples near it every four hours over a period of five days.

At the same time, another ship held a position close to the location where the drogue was initially put in. Samples were taken every four hours over the same five-day period. In both sets of samples, he looked at the variability in zooplankton, both in numbers of individuals and in species content. He found nearly as much variation in samples presumably taken in a single patch which he was following with the drogue as he did in those taken in one place where patches were probably flowing by.

His conclusion was that the only way he could really follow a patch was to get a drogue that would do vertical migration. This is technically a little difficult, but can be done. I am convinced that the situation is even more complex, that patches are, at least in zooplankton, to some extent ephemeral, and that they do not necessarily follow water movements. What I am saying, I guess, is that the word "plankton" in its original meaning is nonsense for most of these things we are working with.

HUTCHINSON: Was he working with all plankton?

FAGER: No, this was only zooplankton.

HUTCHINSON: It seems to me that the phytoplankton, at least in the limited sense of your discussion then, would provide a fairly good control.

FAGER: At the time there was no one to look at the phytoplankton.

YONGE: But surely the phytoplankton is also very patchy?

FAGER: Yes.

STRICKLAND: A little less contagious, perhaps. Is the implication that the zooplankton is possibly nonplanktonic in a teleological sense, because it actually wants to move? In other words, the smaller and less mobile the plankton, the more likely it is to be followable by a drogue. Is this it?

FAGER: That is what I would guess. I think one has to bring in the question of purposeful behavior on the part of the zooplankton—to what purpose, I do not know—because it apparently does not just drift with the water.

CONOVER: Zooplankton forms a beastly problem, there is no question about it. The carbon elements and the chlorophyll sampled with our drogue program are somewhat better behaved. We are not at all convinced that this is the ultimate way of doing things, but we hope that by using radio buoys, which we can leave out for a period of weeks in a water mass, we will get around some of these problems. We assume that the patches are relatively small, and that in the larger body of water which contains the patches there is movement in one direction or the other which we may be able to follow.

HUTCHINSON: Do you not think one needs a lot more information about the small-scale physical oceanography of such a patch? This is a very real limitation on all aspects of the sampling problem or anything connected with it.

BAYLOR: I certainly agree with this. We have been addressing some efforts in this direction for some time. We are by no means the first people to make such observations. Bary(19) has a paper on stained water, and McNaught and Hasler(20) have shown, for example, that the *Daphnia* in Lake Mendota do collect in windrows of what appears to be either Langmuir circulation or some modification of the Langmuir circulation pattern.

I regret very much that we do not have the computer analysis completed on our data on this kind of distribution of plankton in the ocean. However, we have the analysis of one set partially completed which we feel is not our best data so I will describe how we think Langmuir circulation influences plankton distribution.

To collect our data on the distribution of abundance of plankton we have used Kanwisher's and Maddox's plankton sampler which is pushed ahead of the boat through the water to sample the water for the presence of plankton. As each of these organisms (or possibly it may be an inert

particle) goes through the orifice of this device, it gives rise to an electrical pulse that we record on magnetic tape. The magnetic tape in turn is turned into digitalized paper tape which is suitable for feeding to a computer and eventually you can analyse the data for periodicity.

In one particular case that we recorded in Buzzard's Bay, when you analyse the data for the relative frequency of cold downwelling currents (presumably of Langmuir circulation), or the distances between the abundances of plankton, you get a frequency distribution polygon which has a single prominent peak. This peak corresponds to a distance of 24 feet between centers of plankton abundance and between the locations of cold downwelling currents of Langmuir circulation.

SLOBODKIN: This is twenty-four feet between the center of one dense patch and the center of the next?

BAYLOR: Yes, and with very few plankters in between. The ones that occur in between centers of abundance appear to be nonrandomly distributed and not even Poisson-distributed.

FAGER: Is this distance of twenty-four feet a function of your method?

BAYLOR: For example, in this particular case we decided that where we had as many as ten plankters together within a period of a second, this was the minimum abundance of plankton that we would agree was a center of abundance and hence was a place to start measuring from, to find the distance to the next center of abundance. So, every time we had at least ten or more within a period of a second, we would use this as a place to start counting off the distance from.

FAGER: What is a second in distance?

BAYLOR: We assumed that the boat was travelling through the water at a uniform speed, which is, of course, not true, but for our purposes you can regard it as almost true.

FAGER: What I am getting at is, that 24 feet may be an artifact in the sense that if you increased the distance in steps, it may be the closest that your analysis could come to the true value.

SLOBODKIN: Have you aliased your data?

BAYLOR: Let us say plus or minus four feet.

FOGG: This twenty-four feet applies to one particular time and one particular situation? It is nothing general?

BAYLOR: Yes, that is very true. The next record had a periodicity of about thirty-six feet and I do not like the ways these are going up by multiples. I think it is possibly misleading. Worse yet, the next one was 48 feet.

We ran a power spectrum analysis of the data and felt that such nice harmonics were grounds for suspicion. You, too, can be very suspicious of these data. That is why we decided at this point in the data analysis that

we did not think our results were good. At this time we have finally got a program complete for analysing the data and we have analysed what we believe to be one random sample. This random sample was taken by pushing the transducer ahead of the boat which was put hard over into as small a turn as the boat could possibly make, so that you were sort of continuously travelling in your own wake and stirring up the water. In that case, we did get nice, completely random results, but we have not yet had an opportunity to analyse the remainder of the data.

Incidentally, we also measure the temperature as we go along and it looks as though, from a preliminary study of the data, that there probably will be some correlation between the periodic changes in temperature and the periodic changes in the abundance in plankton.

SCHMIDT-NIELSEN: You mean the temperature is patchy?

BAYLOR: Yes.

SCHMIDT-NIELSEN: Good!

BAYLOR: We have some theoretical basis to explain patchiness in the surface-water circulation that is presented by Langmuir circulation, in the ocean, estuaries, or lakes. If you consider a cubical volume of ocean with wind blowing uniformly across the surface, the water is set into motion, in effect, as a series of rotating cylinders, each of which rotates in the opposite sense to its nearest neighbor, as in a train of gears. The axes of the cylinders are parallel to the wind. So, there will be lines with converging circulation and downwelling alternating with diverging circulation. This means that if there is evaporation at the surface, the water which comes down in the downwelling area will have a cooler temperature than the water, say, in the middle of the cylinder so that for every downwelling there is a steep drop in the temperature and this shows clearly in a continuous record of the temperature. We believe that it is at these places that one can find an abundance of organisms. So far, it appears that the organisms are not so much underneath as that they are located on either side of the steep temperature gradients.

We think that there is possibly a behavior pattern that can help to explain this a little bit. It goes back to some experiments by Harder(21) in which he set up a graduated cylinder with sea water in it, so that the top half was warm and the bottom half was cold, and he discovered that on releasing plankton into this, the plankton would all gather at the temperature gradient.

STRICKLAND: What plankton?

BAYLOR: Just about everything. You pull a net through the water as you walk down the pier and whatever comes up, it does not matter—cope-

pods, crab larvae, jellyfish, what-have-you—all of them will gather at this particular interface.

SCHMIDT-NIELSEN: What are the dimensions in the width of these cylinders and the magnitude of the temperature differences?

BAYLOR: According to Woodcock(22) (and our data would substantiate it), first of all they are different in size, every other one being a large one or a small one, and this appears to have something to do with the direction of the wind. In general, from one of these down-welling areas to the next varies from about 20 feet to 100 feet, and this seems to depend to a great extent on the wind speed.

SCHMIDT-NIELSEN: Is this not also the depth of the thermocline?

BAYLOR: Approximately.

FOGG: Can it occur in a much smaller scale? I have a slide (FIGURE 3) which seems to show the same sort of thing with the lines about 5 cm. apart.

KANWISHER: Is this from above the surface?

FOGG: Yes, this is from above the surface.

BAYLOR: This goes a long way to explain Cassie's patchiness(23) that he finds on a scale of centimeters, does it not?

SCHMIDT-NIELSEN: Could you have something similar in the ripples in your beach, in your sand?

FAGER: We took samples on the tops of the ripples, in the trough

FIGURE 3. A bloom of *Gloeotrichia echinulata* in Lake Erken, Sweden, September 1957. The colonies have become aligned in stripes about 5 cm. apart in the direction of wave movement. This figure also appeared in G. E. Fogg. 1965. Algal Cultures and Phytoplankton Ecology. University of Wisconsin Press. Madison, Wis.

and on both sides of the ripples, and we found no significant differences.

EDMONDSON: That is, lined up with the waves of the water, but in your sand you should look transverse to the ripples.

FAGER: We have done that also.

BAYLOR: To finish this up quickly, there is another experiment on behavior of organisms. Take an ordinary aquarium, fill it up with sea water, and take a small glass tube which you run just at the surface of the water all the way across, and now pump cold water through the glass tube. The effect of this is to cool the surface water and cause a cold curtain of water to fall from the glass tube, which then runs out across the bottom.

In this case, the experiment is to liberate plankton in one end and to chase it over toward the other end with a light. In this case, you find again that they gather in the discontinuity of gradients, in the curtain of cold water that is tumbling down from the surface. They will go through it and come back. They just gather there.

If they are strongly phototactic positively and you have a light over here, a few of them come over to the lighted end of the aquarium, but most of them will stay.

FAGER: This implies that when we dive through a thermocline—and one can easily feel the temperature difference—we should see concentrations of zooplankton. Yet, in my experience, you see them in not more than 10 per cent of the cases. When you do see them, they are quite striking.

HUTCHINSON: Is that not partly because after a bit of time in the very stable situation of the thermocline there are all sorts of adaptation reactions that occur, so that usually the situation is different from what it would be in an experiment?

SCHMIDT-NIELSEN: In these two systems you have a steep gradient, of course, and does this not depend on whether or not you have these particular animals within their temperature preference, within that very narrow gradient?

BAYLOR: I do not think I can answer that. All I can say is that we have simply towed a net alongside the dock and taken whatever came up and tossed it into the aquarium.

SCHMIDT-NIELSEN: But if the one does not like the warm and another does not like the cold, they had better stay in the gradient.

BAYLOR: Perhaps that is the way it works. As a matter of fact, if you look at their behavior, you discover that organisms that are away from the temperature gradient have a long horizontal vector to their movement and only a short vertical vector. Only the ones that are in the gradient

have a relatively short vertical vector and almost no horizontal vector to their motion. This is essentially what keeps them in one place.

KANWISHER: Have you tried hot water to see if they would fly to the other side?

BAYLOR: No. You have to put a line source of heat in the bottom to set up a convection current that would give rise to a warm curtain of water rising through the aquarium. The behavior is similar to what Smith and I(24) once described as color dances that, we found, were probably associated with the absorption spectrum of chlorophyll in the water, and we think it is rather interesting that there may be some parallel here between laboratory imitation of downwelling and the downwelling in Langmuir circulation in which phytoplankton may be adsorbed to bubbles from breaking waves; these organisms adsorbed to bubbles in turn are brought to the surface and then carried on the surface to the downwelling area where they are then carried downward through the water.

So, this mechanism provides some kind of an adaptive value for having the sort of behavior pattern Smith and I described(24). Additionally, the organic materials in solution in the sea water which are surface-active also adsorb to the bubbles and are brought to the surface, where they, too, are released as a surface film which is then transported to the converging circulation area where it is collapsed and turned into particles which will support the growth of plankton.

BARKER-JØRGENSEN: I should like to ask whether it is the temperature gradient which is attracting the zooplankton or whether it is the density discontinuity. Harder(21) recently made experiments where he investigated the distribution of plankton in relation to physical gradients, and he found it was the density discontinuities and not the temperature gradients which determined the distribution.

BAYLOR: I neglected to say, in describing Harder's experiment(21) originally, that he has also done this with sugar and found that the plankton does collect in the density-discontinuity gradient.

HUTCHINSON: Were these all marine organisms he worked with or did he use any fresh-water organisms?

BAYLOR: I do not know whether he used any fresh-water organisms or not.

SANCHEZ: What were the temperatures in the natural experiments, in the lake?

BAYLOR: The ambient temperature at the time that experiment was done was about 15°C, and I would guess that the gradient probably amounted to a tenth to half a degree.

RAY: Although this is quite a different kind of organism, there has

been shown in the migrating pseudoplasmodium of *Acrasia,* particularly *dictyostelium,* sensitivity to as little as .001 of a degree.

SANCHEZ: But this is probably in a stable environment, not while it was turning over to fight against the turbulence.

STRICKLAND: I think the question of energy content might come in here. Would you say that you now can burn off everything that you want to, Doctor Slobodkin? Do we know how much we have to burn off, or whether we do not have to burn off anything?

SLOBODKIN: I am very happy that Lasker is here to yell "Foul." The idea is to determine energetic content of organisms by direct calorimetry. I should point out that this is simply a free-energy determination and if entropy matters, I would not know it. I have reason to think that it does not matter too much for the kinds of statements one would like to make.

When you take a blind collection of organisms, you find that the overall range that animals take up in number of calories per ash-free gram is relatively low, from approximately 5100 calories to approximately 7100 calories. This is a blind collection of animals representing as much taxonomic diversity as you can get—not random, but simply getting what came handy.

If an animal takes up more than approximately 5800 or 5900 calories per ash-free gram, there is always a sound biological reason for this; that is, it is always an animal that is at the end of its feeding season or has been raised in some situation in the laboratory in which food is coming in so rapidly that it cannot grow or reproduce enough to keep up with it and begins to lay down fat. The fattest organisms that we have found, or that anyone has found, are some of Conover's *Calanus hyperboreus* right after their annual meal, and Marshall and Orr sent me some of their determinations on *Calanus finmarchicus* after its annual meal; I believe the meals end at different seasons.*

CONOVER: It depends on the area, certainly.

SLOBODKIN: Also, premigratory small birds have from 7300 to 7500 calories per ash-free gram.

STRICKLAND: Does not some of this depend on how you dry these things? You do not have to retain much water to alter the ash-free content.

SLOBODKIN: This is true. Let me state what I think I have got. There

* The material discussed here and the discussion of efficiencies is published in reference 25.

is a family of difficulties and I think some of you will have some familiarity with some of these. The hottest thing one finds is a bird egg, or the yolk of a bird's egg, and it turns out that per ash-free gram of bird's egg there are 8100 calories. I make no stipulations about taxonomy because they are unnecessary. You get this from a humming bird's egg yolk up through to a rhea's egg yolk. We started off with brush turkeys and chickens and they turned out to be alike, and maybe a dozen or so other species. Reptile eggs, as far as we have gone (there are a few taxonomic diversities), all seem to be alike too, all running around 6500 to 6600 calories per gram.

Biochemically, one could go from approximately 4100 or 4200 calories for a thing that is high in carbohydrate up to around 9000 for something which is high in fat. As a point of fact, animals under ordinary circumstances stay within around 600 calories of 5500 calories per ash-free gram.

We are using this as a technique to determine the degree to which energy limitation matters to a population in the field. For example, dealing with fairy shrimp, collected by Tom Griffing, my laboratory assistant, the preliminary data indicate that a fairy shrimp population appears and then disappears seasonally. Does it disappear because someone ate it, does it disappear because it is starving to death, or does it disappear because something peculiar happened in the water? If someone ate it, if it was destroyed by a carnivore, it would be anticipated that the food supply for the few surviving fairy shrimp would go up and that the caloric value per ash-free gram of fairy shrimp tissue would increase with time or, in any case, not decrease.

If the fairy shrimp is eliminated, by a chemical change in the water, you would expect no particular change one way or the other in the caloric content. What one usually finds is that the new young fairy shrimp are running around 4800 or 4900 calories per gram; that the prereproductive animals are at 5800 or 5900 calories per gram, and just before the fairy shrimp disappears from the pond, the latest samples run around 5100 down to 4900. They hatch out with an energy supply in their yolk. They use it up rather quickly, but while they are growing up, the food supply is increasing around them. There is a fairly abundant food supply and then they are out-competed, if you will.

STRICKLAND: What about the quantity of refined water which is not removed at the temperature you dry them at before you combust them?

SLOBODKIN: Alright, let us look at the problems. There is the water problem. There is also the problem that in burning these things, the combustion in the calorimeter is not quite complete and you must get secondary combustion in a muffle furnace to get the ash value. Paine has a paper coming out in *Ecology*(26) in which he shows that very slight differ-

ences in the temperature of the muffle furnace will cause differences in vaporization of various of the salts making up the animals.

In particular, this is a nuisance with marine organisms. The ctenophores are preadapted to resist burning and if you dry a ctenophore you find it is 90-something per cent water and the remaining 5 per cent of material is at least 85 per cent salt. You make a tablet of this and put it in the calorimeter and ignite it, and you get a slightly singed salt tablet and it is a little depressing.

But given these problems we are still left with a very narrow range. If the drying method really mattered much, I would expect some taxonomic component in caloric value—that is, a certain kind of tissue is more dryable than others. This is not necessarily true, but it would seem to make certain sense. There is no taxonomic component, as far as I can tell, for whole organisms, and this goes from protozoa through to small fish.

KANWISHER: You mean the whole fish or the whole humming bird?

SLOBODKIN: I did not do the birds. My machine deals only with samples around 50 mg. If I went above 100 mg., it might burst.

KANVISHER: If you do parts of them, do you include things like seal blubber and whale blubber?

SLOBODKIN: I am dealing with whole organisms.

FAGER: And in the case of the bird, you throw it in a Waring blender, and dry and use the resulting bird soup?

SLOBODKIN: That's right.

KANWISHER: It is not the fatty tissue *per se?* It is the overall organism?

SLOBODKIN: Yes.

HUTCHINSON: What about the jelly?

SLOBODKIN: Jelly is, by and large, salt, if you refer to the kind of jelly that clogs plankton nets.

STRICKLAND; It is the bit that is not primarily water that is interesting.

HUTCHINSON: Its ash-free calorific value is relatively small relative to the whole organism.

SLOBODKIN: That's right. Curl* has made the determination on *Mnemiopsis,* using a great deal of benzoic acid so that he could get combustion, and he came up with 5500 calories per gram, so it is sitting right where we sit. Philipson has repeated my burnings on around ten to fifteen different species and they check out completely.† I had material in the desiccator which I gave to him. He redried them, presumably at home, used a different kind of calorimeter, a much better kind in the sense of simplicity and reliability, but his data were essentially identical with mine.

* Herbert Curl, Jr., Oregon State University, personal communication.

† John Philipson, University of Durham, England, personal communication.

STRICKLAND: How do you dry them?

SLOBODKIN: I dry them in a vacuum room of approximately 60°C. for approximately 24 to 48 hours, keeping the temperature low to avoid vaporization.

LASKER: I would like to comment on this. Bob Paine * was working in my laboratory for a while, where he investigated some of the factors affecting calorimetry. One of the things he found was that the inclusion of salt in the tissue being analyzed, particularly hydrated calcium carbonate, causes a much lower caloric value than the true one. It is impossible to dehydrate calcium carbonate even in an oven at 100°C.

SLOBODKIN: You do find 'way out values, but we assume this is the kind of thing we are dealing with. There is a danger in this which is the sort of danger associated with Frazer's *Golden Bough.* Once having decided a King was sacrificed, he spent the rest of his life collecting data to show it; but since he decided in advance, the data did not show anything.

In the same sense, we had a series of initial determinations, actually on seventeen or eighteen species, and then it occurred to us why we were getting this distribution. From then on we could not make a blind sample. So, confining my discussion now to material selected before I developed any hypotheses on the subject, you do get a skew normal distribution with an occasional outrider.

Glottidia was a perfect nuisance. You make pills out of it, put it in the bomb and they sputter and splatter and leave brown scum on the surface of the bomb and grayish floc in the pan, and so on. And at this point you just give up. I am using the burnings that appear to be clean and uncluttered, and we have some faith in them.

CONOVER: What are the various aids to burning that you are using? I understand benzoic acid is one.

SLOBODKIN: We only use benzoic acid. Our bomb is a little sort of Franklin stove arrangement, a platinum saucer in which we set a pill on its own little platinum dish and this is held in place by a fuse wire which acts as a spring pressing the pill against the bottom of the pan, and then it comes out and connects on the other electrode. We are dealing only with solid pills of material and a lid is necessary. If the lid is not there when the combustion starts, soot appears on the roof of the bomb and you can mirror the edge of a displaced lid in the soot pattern on the top of the bomb, so you apparently need this to confine the

* Robert Paine, Zoology Dept., University of Washington, Seattle, personal communication.

actual flame. It is simply a matter of burning the thing at 30 atmospheres of oxygen.

Other people have used other procedures. Comita(27) has been wrapping animals in filter paper and burning the filter paper, animal and all. For certain purposes this may be alright, but we have not done this.

The pill itself must be a tight homogenous pill. With certain organisms, when you grind them in a mortar and form a pill, you end up with something almost the texture of vermiculite. When you set fire to this, it apparently develops bubbles internally and sputters and the material flies in all directions. We hope that a different grinding procedure might help with that. We have not got it so far.

But we do have this consistent distribution. The inference from it, which we may get into later, is that energy is generally in short supply for organisms. Going very quickly through the arguments which I have published in a number of places(25,28), if this were not the case we would anticipate taxonomic differences in calories per gram just as we have taxonomic differences in aluminum per gram or molybdenum per gram in organisms. If this were biochemically limited, we would never expect to find an organism running at 7300 calories per gram. We do find that, biochemically, it is possible to become a bit tubby, but organisms usually do not; when you have extra energy you immediately use it for growth and reproduction.

CONOVER: Not copepods.

SLOBODKIN: Or you have a hard season coming up and have to, in a sense, carry your lunch. You carry your energy about with you.

CONOVER: Incidentally, the fat that these animals store has a caloric content of something better than 10,000 calories per gram. We had a good biochemist do the extraction for us. I presume it consists of quite a lot of long-chain unsaturated fatty acids, judging from the few analyses that have been done, but more than that, I do not know.*

LASKER: Is there any natural oil that has 10,000 calories?

CONOVER: Copepod oil has.

LASKER: I think Nujol, which is the finest mineral oil you can get, has only 11,000.

STRICKLAND: I do not think gasoline is that high.

CONOVER: Nujol is a good high-energy standard. The thing I am interested in at the moment is getting a good relatively low energy liquid standard, and if anybody has any ideas along these lines we would be happy to hear about them. Has anyone tried to experiment along these lines?

* It also contains as much as 5 per cent pristane, a branch chain hydrocarbon possibly derived from phytol(29).

SLOBODKIN: I would like to ask a question. Does this check out with the kinds of thing you are finding?

LASKER: Yes, it does, almost completely. Just to show the usefulness of this caloric information, I can show some information on the embryological development of a fish embryo. I think you will be able to see from TABLE 2 that with an initial caloric value of .3 calorie, you can follow the embryological development and utilization of energy by following the yolk diminution in volume; we measure catabolic calories by indirect calorimetry (oxygen consumption), and by using the standard conversion factors it is possible to construct an energy balance. The abscissa gives the time scale for the embryological development of this larval fish, which happens to be the Pacific sardine. You can measure the volume quite accurately with a microscope. Knowing the initial caloric value of the larval yolk, you then can convert volume to calories(30).

SLOBODKIN: At what hours do they start swimming?

LASKER: They hatch out at 72 hours.

SLOBODKIN: And presumably they move inside the egg before that?

LASKER: Oh, yes, they are moving around inside the egg. Before, you mentioned their efficiency. For the whole period of time here, which was 180 hours or about seven and one-half days, a figure of 79 per cent efficiency was obtained; therefore the sardine embryos are using up very little energy as far as I could see.

HUTCHINSON: What does this mean? It is conversion of yolk into what?

TABLE 2

AVERAGE YOLK UTILIZATION BY SARDINE EMBRYOS AND LARVAE AT 14°C EXPRESSED AS DIMINISHING VOLUME AND CALORIC UPTAKE. THE CATABOLIC CALORIES ARE BASED ON MEAN RESPIRATORY FIGURES. A CALCULATION FOR PERCENTAGE EFFICIENCY OF YOLK CONVERSION TO TISSUE IS INCLUDED BELOW [AFTER LASKER.(30)]

Elapsed hours from spawning	Yolk volume (mm^3)	Calories remaining	Catabolic calories
0	0.56	0.300	0
42	0.48	0.260	0.0063
71	0.29	0.160	0.0096
80	0.25	0.130	0.0040
100	0.16	0.085	0.0088
120	0.09	0.048	0.0088
140	0.04	0.021	0.0088
160	0.01	0.005	0.0088
180	0	0	0.0088
			Total = 0.064

$$\text{Percentage efficiency} = 100 \times \frac{0.300-0.064}{0.30} = 78.7\%$$

LASKER: Animal tissue.

HUTCHINSON: How are the catabolic calories measured?

LASKER: By oxygen consumption.

SLOBODKIN: Is 78 per cent equivalent to saying that 78 per cent of the energy that was in the egg initially is still in the embryo?

LASKER: That is right.

SLOBODKIN: In tadpoles, this is approximately 96 per cent. The difference is in a sense meaningless. This is being repeated, but I pass it on for what it is worth now.

What we decided to do, since we have this lovely machine, is to see how much energy it takes to transform a fertilized frog egg into a tadpole. FIGURE 4 shows hours of development and the calories per single embryo for *Rana pipiens*. Two different seasons; I is the normal breeding season and II is an off season—only embryologists use it.

The shape stays the same. These are the data of Jill Clarridge.* What happens is rather startling because the calories per embryo actually go up to some degree, regardless of season, approximately 5 per cent between fertilization and 60 to 70 hours. These are embryos raised in their jelly coats. After the appropriate number of hours, they are removed from their jelly coat and burned.

If you very carefully strip the embryos out of their jelly coats and raise them in isolation, the energy in the embryo goes down, as it should, but it only goes down possibly 5 to 6 per cent. Notice the scale is highly condensed.

This is being repeated, but 90 per cent constant levels are indicated by the vertical line. Notice this is peculiar. Toward the end, some of the embryos have hatched or are in the process of hatching. Others have not, and when you strip them clean of jelly, in some cases you get the membrane immediately around the embryo with the enclosed fluid in your sample, and in others you do not. We did them separately.

If you include the fluid around the embryo you get a slightly higher value. The point of this is that, first, it is an illustration of what calorimetry can do; second, there is the general point of metabolic cost or energetic cost to being complex or to developing, and I would like to suggest that energy is dissipated by imparting acceleration to something in biological systems. Energy is dissipated by doing work and work is measured in the normal physical sense.

If an embryo is simply changing its shape internally, it is not really doing work on anything. It is when it starts pumping blood through its system or starts swimming about that it is really doing work and energy

* L. B. Slobodkin, Patricia Stocking and Jill Clarridge, unpublished data.

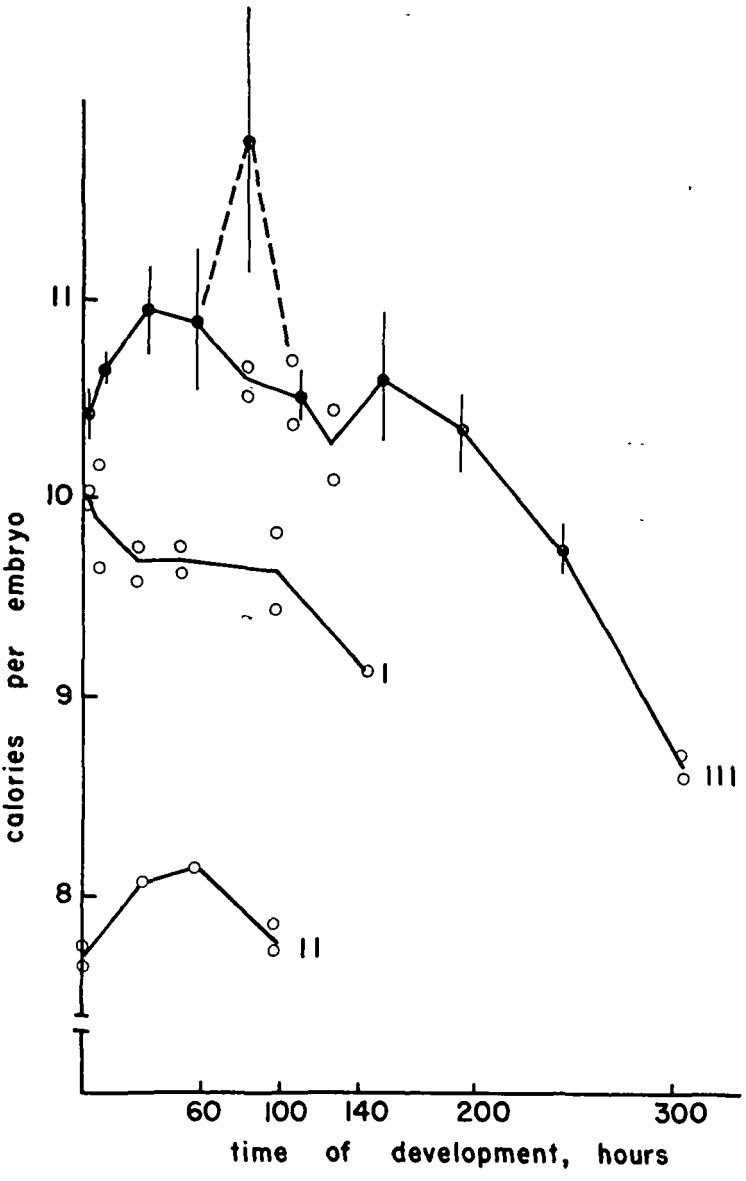

FIGURE 4. Caloric content of single embryos of *Rana pipiens* during development. Vertical lines show 90 per cent confidence limits. I, embryos without jelly. II, and III, embryos with jelly, two different seasons.

is expended. What we hope to do is repeat this and try paralyzing tadpoles in various ways to see if we can eliminate that drop.

FREMONT-SMITH: The differentiation, then, would be not doing work?

SLOBODKIN: In the normal sense of the word it is not. One has the intuitive sense that it ought to be.

HUTCHINSON: Surely, differentiation must involve a very small amount of real work. Acceleration has to be imparted to some portion in the middle of the cell to get it onto a membrane, or something of that kind.

SLOBODKIN: This we have. There is a slight drop, which is what it ought to be, and it checks out with the oxygen-determination data, assuming reasonable equivalents for oxygen-caloric conversion.

BAYLOR: Where did that extra 5 per cent come from?

SLOBODKIN: That came from the jelly; it must come in the form of carbohydrate because the energy per gram of embryo changes in such a sense that what came in must have been of relatively low caloric content per gram.

BAYLOR: This 5 per cent gain is in the embryo when you have stripped the jelly off?

SLOBODKIN: Yes, in the embryo that has been growing in a mass of jelly, after we strip the jelly off. The point of having yolk, incidentally, is rather interesting. Yolk is a carried lunch. It is not needed for development but it is there to carry the organism while it does the work involved in catching its own first meal. We are trying to repeat this work.

II. FEEDING

Discussion leader:
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BARKER-JØRGENSEN: In presenting problems for discussion, I intend to restrict myself to the suspension feeders, both because of their fundamental importance, and because it is the only group with which I have personal experience. Other participants in the conference may bring up other feeding groups for discussion. I already know that Professor Yonge is going to speak about deposit feeding in bivalves and gastropods.

Suspension feeding means the uptake of food particles that are mostly too small to be sensed and seized individually. The suspension feeders are therefore forced to extract food on a mass scale. This type of feeding will often exhibit traits of automatic and stereotyped character. We may perhaps say that, typically, undisturbed suspension feeders will feed more or less continuously and they will clear the surrounding water of particles more or less independent of the food value of these particles and at rates that are constant below certain concentrations of particles.

There is disagreement concerning the correctness of this statement within the various groups of suspension feeders and we may therefore pose a number of questions to be discussed in order to elucidate convergent and divergent adaptations within the suspension feeders. First, we may ask: To what extent is continuous feeding characteristic of suspension feeding? This is an important question because when we want to estimate feeding rates, it is necessary to know to what degree the feeding is continuous. Continuous feeding would mean that the uptake of food is not regulated by the needs of the organism.

The next question we may ask and discuss is: To what extent is it true that the surrounding water is transported to or through the feeding organs at rates that are independent of the quality of the particulate matter in suspension in the water, and also of the quantity of the concentration? Finally, the third question we may formulate is: To what extent selection of food is taking place in the various suspension feeding groups, and also which types of selection are realized?

FREMONT-SMITH: When you speak of constant feeding, are you assuming that a group is feeding constantly, or that each individual organism is feeding constantly?

BARKER-JØRGENSEN: I am speaking of the individual organism.

FREMONT-SMITH: Is there a way of making a distinction between the individual organisms and the group? Do you study the individual organism separately in the laboratory, or how can one be sure that, for instance, 30 per cent are not resting from feeding at any given time?

BARKER-JØRGENSEN: If you investigate single specimens, you may see whether feeding is continuous or not in this single specimen, and you may try to see how the length of feeding time is dependent upon various factors in the environment. In this way you may find that you can get a situation where feeding is continuous.

In nature, the rates at which food and other materials present in the surrounding water are retained and made available for ingestion are mainly determined by the rate at which water is transported to the feeding organ and the efficiency with which these various particles are retained in these feeding organs. I therefore suggest that we next discuss or consider these two factors and discuss them with special reference to the question as to how far the rate of water transport and efficiency of particle retention, that have been measured in the laboratory, also apply to conditions in nature.

We may pose one further question for discussion. This is concerned with the role played by mucus in the feeding mechanisms of many, if not most, suspension feeders. This has been stressed by many, many investigators. It may be of interest to discuss the properties of mucus that make it especially suitable for suspension feeding, such as occurrence and the structure of mucus nets and sheets in suspension feeders.

Finally, we may discuss actual feeding mechanisms. Some of the participants present may have new material to present on this subject, and I may add that we have some new observations on feeding mechanisms in appendicularians.*

This was the series of questions that I formulated, and we may now proceed to the first one. This was the question of whether feeding is continuous or discontinuous in various types of suspension feeders.

REESE: I have worked a little on *Artemia,* the brine shrimp, in which feeding is continuous. It certainly does depend on the organization of the animal. The brine shrimp is a relatively primitive crustacean which has no great specialization of appendages. The appendages which it uses for

* Editor's note. It was not until the third day of the conference that Doctor Barker-Jørgensen got back to this material. For this report the discussion has been brought forward to page 107.

gathering food are also used for moving the animal along and for gaseous exchange. This animal moves its appendages continuously and gaseous exchange takes place presumably continuously. The animal also moves along continuously and it may be observed to feed continuously because feeding, or at least gathering of particles, is an automatic function of the movement of the appendages.

This is not necessarily so in some animals that are very common suspension feeders, like copepods, which in the adult do not use their locomotive appendages for gathering food.

LASKER: Having made some observations on filter feeding euphausiid shrimps, it seems to me, at least in laboratory cultures, that if your culture is quite dense these animals fill up very rapidly with a food organism such as *Dunaliella.* Then feeding stops, although the animal continues to swim through the water and has its thoracic basket open. This would fit under your heading as one which is discontinuous, or at least one that can be made discontinuous by very heavy suspensions of phytoplankton.

STRICKLAND: This would never occur in nature, would it?

LASKER: Not the densities I have used.

SLOBODKIN: I have some very old observations on *Daphnia* where the rate of defecation seems related to the concentration of food. When the animals are put in a system where a certain suspension of algae is present so that they can eat out the medium completely, they finish the food and then, in general, defecation is not observed. The front half of the animal's gut shows a different color from the hind half; there is a dark green in the anterior portion of the gut, and the hind portion of the gut is brown or blackish. The animal can hold this two-colored system for as long as the six days that I have watched, presumably for somewhat longer.

If, at the end of that period, new algae are introduced, both feeding and defecation starts, and microscopic examination of the gut indicates that the brown and green material is shifting position in some way; that is, you find brown masses in the anterior end, and you find green material appearing in the posterior end. If, however, the animals are kept in a fairly dense suspension of algae, so that there is no period without food coming in, the gut seems to be, in essence, open at both ends and material is swallowed and passed out almost directly in a loose, flocculent, greenish fecal material rather than the somewhat brownish, or certainly not green, relatively dense feces that occur when algae is either absolutely scarce or present only at interrupted times. This is just a microscope observation.

FREMONT-SMITH: Is there a chemical change in the chlorophyll that could be part of the digestive process?

SLOBODKIN: I am sorry, all I know about it actually is the color change.

HUTCHINSON: May I ask whether you have any observations on *Daphnia* that suggest that the statement that they are very easily starved to death when they are absolutely free from food is true? There has been a great deal of highly contradictory and rather anecdotal material published. I think von Dehn(31), particularly, was very sure that *Daphnia* could be starved within 30 hours, if you really got the medium clear of particulate matter, whereas there are equally improbable statements that you can keep *Moina* in laboratory distilled water (which I have failed to do) for four or five days without anything in it. None of this has ever been properly cleared up and it would be extremely interesting to know what you have got.

SLOBODKIN: We set up parallel populations, some of which were fed every sixth day, others were fed every other day. The size of a population fed every sixth day was not very different from the size of a population fed on the average same amount of algae, but at one-day intervals, which I think is part of the answer.

I know that in the populations fed every other day, the algae, as indicated by counts of the water in the medium, were essentially gone after 12 to 14 hours. It is possible that, having a greater amount of algae at rare intervals, algae was present for as much as two days, but I would not believe it was any longer than that, and I do not believe it was that long, judging from the absence of a Tyndall beam effect in the water. That is part of it, I think. These animals certainly could go for at least four days with nothing at all.

BAYLOR: Could I add another little anecdote to this? When Smith and I(32) worked on the responses of *Daphnia* to X-rays, we went to a very early paper published about 1885 in which a gentleman said that it was possible to evacuate the gastrointestinal tract of these animals by giving them Epsom salts. We did this in order to make sure that there was no material left in the gut that could fluoresce and give the animals a clue when they were exposed to X-ray. After subjecting them to Epsom salts, which actually was very successful in evacuating them, we then gradually put them into distilled water by multiple changes of more and more distilled water and less and less pond water, so that they were able to adjust their osmotic systems successfully to this, and finally we felt that we had them absolutely food-free and, what was more important, this procedure made sure that there were no feces in the water which would fluoresce. When we got to the point that we could no longer see fluorescence in the water, when we were dark-adapted, we felt that they were food-free, and at this point we began our X-ray experiments.

Such animals left in the same tank in which we had done the experi-

ments, in spite of having an enormous X-ray dosage, would live for as much as a week without any further food added.

HUTCHINSON: This was in distilled water?

BAYLORS Yes.

HUTCHINSON: Which *Daphnia* was it?

BAYLOR: *Daphnia pulex.*

SLOBODKIN: Smith* has recently shown that, depending upon the nutritive condition, the weight of an individual animal at a given time can vary by as much as a factor of 2, at least.

It is certainly true that an animal that has been starved for an extended period of time is highly transparent, the carapace is typically dented, and the color is crystalline. A well-fed animal has discrete fat droplets; the color of the ovaries in *Daphnia pulex* is an olive green whereas it is a greyish color when the animal is starved. The body has a reddish tinge, particularly in low oxygen, and it does not have this color when the animal is starved, the idea being that the animal can build up, I believe, extensive internal reserves in the form of fat, associated with the production of hemoglobin. If you took an animal which was completely transparent and about to starve to death anyway, and did something to it, it would continue to starve to death.

RAY: If I might add something here, even though it does not relate to suspension feeders it does relate to the question of starving to death, and what the animals can do. *Limnoria* can also be kept in the absence of food for long periods of time. It is easy to do because their normal food is wood and if you keep them in water without wood they do not swallow anything else. They will, under laboratory conditions, survive for six weeks on the average, in the absence of taking any particulate stuff into the gut. During this time, they are quite active and they only gradually slow down. After they become very thin and emaciated-looking or actually die from starvation, we have fixed them and made serial sections, and we have found that they are able to metabolize all of the tissues of the body. There is practically nothing that can be seen inside the skeleton at all. The only things are a few miserable little wisps of muscle fiber running down the legs which will still move, and even the entire central nervous system is utilized, so that we can no longer see the ganglia or any strands of the central nerve cord. The only thing which is not utilized in complete starving to death is the head muscles and these operate the jaws.

* F. E. Smith, Department of Zoology, University of Michigan, Ann Arbor, Michigan, personal communication.

FREMONT-SMITH: Does the central nervous system regenerate if you refeed them before they die?

RAY: I am sorry, I cannot answer that for sure because I have not figured out how to determine whether the nervous system is gone, microscopically gone, without sectioning them, and after that it is hard to revive them.

FREMONT-SMITH: You might take half of them and see.

HUTCHINSON: Can they learn anything? If they can, this is an extraordinarily important organism.

BODEN: Can I get back to Doctor Lasker's group? We have found that euphausiids that we have tried to keep stable in the laboratory for experimental work went quite blind if they were not fed. We could put an electrode into the eye and get absolutely no response at all. I suppose this is just a lack of vitamin A_1 or something, because if we did feed them, we could still get a response.

HUTCHINSON: You could reverse it?

BODEN: No, we could not reverse it; at least, we never tried that. But if we kept feeding them we could still get a response.

SANCHEZ: I have a certain number of observations along this line but I am not sure that they would not be more pertinent when we discuss nutrition further on. There are some points with respect to the presentation that Professor Barker-Jørgensen made which I would like to go back to. To start with, what observation is there to sustain the belief that some organisms do feed continuously? What organism is known to feed continuously?

BARKER-JØRGENSEN: From a perusal of the literature, it would seem that the *Porifera* are such organisms. Also the coelenterate *Aurelia* has been stated to feed continuously, as has most of the serpulimorph worms. The copepods may also come into this scheme, but not convincingly so; suspension-feeding prosobranchs and bivalves, and the ascidians probably also. However, regarding all these groups, there has been some discussion as to whether feeding is continuous or not. It means whether it is regulated by the filling of the stomach and the appetite of the animal.

In the case of the oyster it is very interesting to see that the length of feeding time has increased since the beginning of the century. In early observations, it was stated that the oyster is feeding about eight hours a day, and it actually ended up with reports showing that it is feeding more than 20 hours a day, and that is close to continuous feeding. It looks as if the question is whether the animals are disturbed or not disturbed. It means that only if they are undisturbed, they will take up food automatically. The food uptake will not be regulated by the filling of the stomach. Your experience with *Euphausia* is apparently an excep-

tion to this rule. There is another exception described by Bone(33) in Amphioxus, where he found that feeding stopped when the Amphioxus had filled its intestinal tract with food—that means algae—but not if it filled it with colloidal graphite, so apparently there was a mechanism of determining the food value of the stuff that filled the stomach.

Bone stated that Amphioxus discontinued feeding until the content was digested and the intestinal tract had been emptied.

STRICKLAND: But by definition something with its gut completely crammed full cannot feed. You mean that the actual exterior responses stop when its gut is full?

BARKER-JØRGENSEN: Yes, the feeding mechanism stops.

STRICKLAND: But even if it did not, it still could not feed.

BARKER-JØRGENSEN: It could collect food. That is the question. The general mechanism in the automatically feeding suspension feeders seems to be, that if there is no room in the gut, they would discard the food at the level of the mouth. Doctor Reeve, you spoke about this mechanism just a minute ago in *Artemia.*

REEVE: Yes, in the brine shrimp you have to separate the feeding process into food collection and food consumption. *Artemia* collects the food automatically, but as the food is passed along the food groove towards the mouth, the mouth parts are formed in such a way that they are pushing the food up to the mouth and the mandibles are ramming the food into the mouth. It appears that since the food can only go through the gut at a certain rate, if it is being presented to the mouth at a faster rate it cannot get into the mouth and is dispersed again into the medium. The food particles which are delivered to the mouth parts in greater quantities than can be consumed accumulate there as a growing mucoid blob. Eventually, this aggregate becomes entangled with the first thoracic limbs as the latter begin their backward power stroke, and so the particles are dispersed back into the surrounding medium.

MCLAREN: Is collection continuous in *Artemia,* say in an ordinary diurnal light cycle? Have you attempted to simulate natural conditions as nearly as possible in attempting to determine this?

REEVE: No, I have not.

MCLAREN: It seems to me curious, considering the generality of animals such as insects, that the suspension feeders do not have a refractory period of some sort, like everything else in creation.

BARKER-JØRGENSEN: This is the danger of suspension feeding, of course, if you do not have special mechanisms to prevent it. But, you have a number of mechanisms varying from group to group of suspension feeders that will prevent overloading of the intestinal tract, as, for instance,

mechanisms for scattering the collected food at the level of the mouth, and thus protecting against overloading of the digestive tract.

HUTCHINSON: Do you think that is fairly general among suspension feeders right through the animal kingdom, generally?

BARKER-JØRGENSEN: Yes, as far as I can tell, all suspension feeders have a mechanism of protection against overloading and this, of course, fits very well with the concept of continuous feeding. Generally, I do not think that suspension feeders are very often exposed to overloading. I think they are generally living in a very meagre environment.

HUTCHINSON: Yes, it is remarkable that they have developed some of these mechanisms in view of what they are up against.

YONGE: If I could speak about bivalve mollusks, I have looked at very many genera of bivalves since I began with *Mya* in 1922(34), and there is a constant succession of selective events. The water is drawn into the mantle cavity, the larger particles immediately drop out and are removed. Smaller particles are then caught on the gills. The larger particles on the larger mucus masses fall off on to the mantle cavity. The particles which are taken on by the gills are led between the palps and there, as a result of exposure to complex tracts of cilia which can be exposed or not, you get a third stage of selection. All particles which are not swallowed pass on to the mantle cavity, are consolidated in mucus, and pass out as pseudofeces—a very useful and all-embracing term.

SANCHEZ: This is not selection for size, is it?

YONGE: This is a purely quantitative selection, but I will qualify that remark in a minute. As far as you can see, generally speaking, it does not matter whether you give them graphite or India ink, or you give them the finest and purest cultured diatoms, they seem to react in the same way.

The material proceeds along a relatively short esophagus and into an incredibly elaborate stomach with a series of selective mechanisms, the whole thing being complicated by the fact that the revolving crystalline style is projecting right across the cavity of the stomach.

Particles are again selected here. Those of minimum size pass into the ducts of the digestive diverticula for intracellular digestion. The remainder pass into the midgut, so to the rectum, and there is probably little or no further digestive action. What does occur is a consolidation within a mucus envelope so that the true feces deposited by a bivalve can long persist. You find them in bottom deposits of considerable age(35).

You cannot divorce the feeding mechanism from the actual digestive mechanism. They are interrelated and in all suspension feeders there is always a closely associated rejection or cleansing mechanism.

All this adds up to the fact that these organisms feed quantitatively,

and yet we have the most revealing observations that Loosanoff(36) made several years ago, when he fed young oysters on a mixed suspension containing colored bacteria, and those particular organisms were definitely rejected by the palps. That revealed a real and unusual qualitative selection.

SANCHEZ: I do not know the data, but in sponges, since the ingestion of material involves the incorporation of food into the cytoplasm of the cell, there probably is a certain amount of qualitative selection of what is being brought into the chamber.

HUTCHINSON: There is a very strange observation made by Lowndes(37) many years ago on *Diaptomus* which he got from a very shallow pond full of green alga—*Kirchneriella*—and it was feeding exclusively on a benthic desmid, which was one of the rarer algae in the pond, and rejecting the common *Kirchneriella*. There must have been a great deal of filtration involved, presumably opening the maxilla and letting the wrong things through and catching the desmid.

BARKER-JØRGENSEN: What is the size of this diatom—what is the difference in size?

HUTCHINSON: The *Kirchneriella* and the desmid would ordinarily be about the same size, would they not?

BARKER-JØRGENSEN: Yes, but what is the absolute size?

HUTCHINSON: Thirty microns.

EDMONDSON: *Ankistrodesmus* would be only about 20 to 40 μ.

YONGE: I feel that these setous feeders are more selective than the ciliary feeders. I am sure that in *Calanus* there is a selection of individual particles in a way there is not in a bivalve.

BARKER-JØRGENSEN: There is an observation by Menzel(38) that backs up the qualitative selection in the oyster. I think I found the reference in your monograph on the oyster. He observed a qualitative selection in very young transparent specimens of materials collected on the palps.

Loosanoff(36) demonstrated that qualitative selection took place but he could not tell by means of which mechanisms. In the observation of Menzel, the particulate material collected on the palps was observed to form into a small ball at the tip of the palps. Particles would continuously get loose from the ball, and if the particles were algae they would be transported up the palps to the mouth and be ingested. If they were inert, they would go back into the ball and finally the ball would be discarded. I cannot see the sensory apparatus that is at work in this.

CONOVER: I have some rather recent observations made on the selectivity by *Calanus* of a few specific particles which were big enough so that individual objects could be watched. I am working with the large *Calanus hyperboreus,* almost a centimeter long, so I can feed it quite large things,

including large *Artemia nauplii,* various eggs, and a nice diatom we have in culture, which is about 350 μ in diameter.

I had been watching the animals with a microscope hoping that I would see something eaten for some time without much luck, so finally I decided to try to force-feed them. I found this was a very easy thing to do; you could take the particle which you wished to feed the animal and place it in a position so that it could be easily handled by the appendages, and very quickly most times the material was actually brought to the mouth. Certain animals had far greater skill in handling large particles such as this diatom, a *Cosinodiscus.* It obviously gave some of them more mechanical difficulty than others; they simply could not get hold of it in a proper manner.

PROVASOLI: Was it slippery?

CONOVER: I do not know. They just seemed to have difficulty with it and it would sort of bounce around from one appendage to another.

Most interesting was that I found that these animals in some cases would reject things that they had actually brought into contact with the mouth. One of the things that I tried feeding them was their own feces, which they rejected 100 per cent of the time. But only after it came in contact with their mouth, was it discarded.

I found that the animals obviously showed some preference for what they happened to have been feeding on. In one case I had a gravid female that had laid eggs, which she was eating. I found this was her decided preference, for she would not take the large diatom even though she was able to capture it.

On the other hand, I saw another individual, when given the eggs, bring them to the mouth and then just throw them away. So, it looks as though there may be a sense of taste here, or chemical sense, or something of that sort.

STRICKLAND: The female preferred her own eggs to anything else?

CONOVER: She had been eating them. She apparently preferred them because it was what she was used to. I am supposing this.

FREMONT-SMITH: This was a single female?

CONOVER: Yes. The animal had been starving but she laid eggs in the dish and had been feeding on them. This was quite obvious.

STRICKLAND: That is Harvey's observation(39).

CONOVER: It rather looks like Harvey's thesis, that animals that have been feeding on a specific type of cells prefer that type.

FREMONT-SMITH: But she had only been feeding on it since she was starved?

CONOVER: She had only been feeding on her own eggs, I would have estimated, for about two or three hours, probably.

I think it is safe to say that no calanoid copepod that has been studied can really be considered a continuous suspension feeder. I hope that is a safe statement. It applies to any one that I know anything about, at any rate.

Because they do, to a certain extent, use their feeding appendages for swimming, I do not think it is possible by observing "feeding movements" of a copepod to tell whether it is actually in the process of feeding. Quite frequently the head appendages are apparently moving in a normal manner, that is, a normal manner for feeding, without any feeding taking place. Mullin's paper(40) gives information about this. First of all, that grazing is not a continuous process in that if you measure filtration over the first brief period of time it is a very much higher rate which you obtain than if you let the filtering continue for a longer period (FIGURE 5).

In these experiments, of course, some removal of cells is taking place, and there is an effect of concentration on the filtering rate (FIGURE 6). Filtering rate falls away quite rapidly with increasing concentration of cells.

This is, in effect, operating in a manner opposite from the previous figure; that is, if the animal were reducing the number of cells in the culture medium, its filtering rate should increase.

EDMONDSON: Does that possibly mean progressive deterioration of the animals?

CONOVER: No, I do not think that. I think they get full and stop feeding. I am reasonably certain that this is the case.

PROVASOLI: Was the cell material of the algae washed before being fed by concentration, or was it directly fed with the liquid?

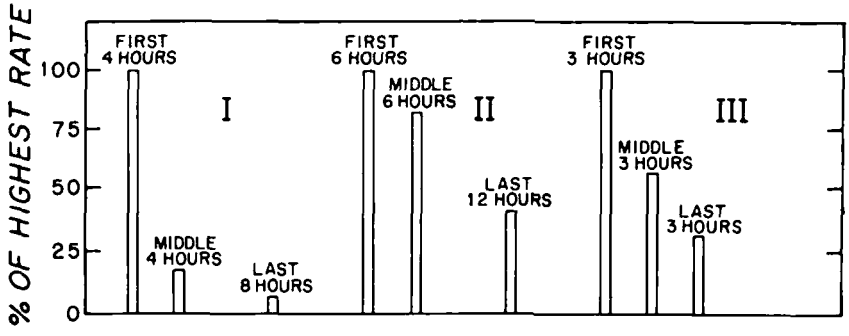

FIGURE 5. Relative grazing rates of female *Calanus helgolandicus* at various intervals during three experiments. I. 16 hr. experiment; feeding on *Asterionella;* 100%–255.6 ml./day/copepod. II. 24 hr. experiment; feeding on *Ditylum;* 100%–363.9 ml./day/copepod. III. 9 hr. experiment; feeding on *Ditylum;* 100%–246.9 ml./day/copepod.

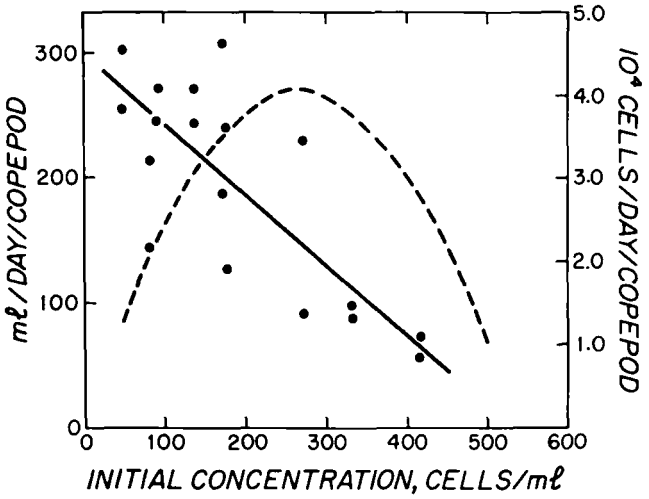

FIGURE 6. Grazing by female *Calanus hyperboreus* on various concentrations of *Ditylum brightwellii* (three experiments). Left ordinate and solid line = grazing rate. Regression equation: $\overline{Y}_x = 0.56\,x + 300$; correlation coefficient: $r = -0.791$. Right ordinate and broken line = rate of intake cells.

CONOVER: You are referring to the possibility of external metabolites?

PROVASOLI: Yes, I am.

CONOVER: This is not entirely ruled out, but they were washed. The age of the alga culture affects filtration and gives a good negative regression (FIGURE 7). I do not believe that any of the evidence for an effect of external metabolites on copepod feeding is irrefutable. What I would point out here is that, among other things, in the particular culture which we used for this experiment, the organic weight per cell increases with culture age. Whether this fact alone can account for the decline in feeding, I do not know. It may simply be food concentration; when the animal has had enough to eat, it simply stops feeding. There is, perhaps, a lot of other indirect evidence that could be brought in.

The straight line in FIGURE 6 shows the change in rate, and the curve I do not know. It may simply be food concentration; when the animal reaches saturation, as seems to be the case in *Artemia* when the cell concentration gets to be above a certain level. Possibly, its needs are more quickly satisfied and it stops feeding earlier. The same effect is shown for a different cell in FIGURE 8. This is a small one, and the other is the large cell. What this shows is that, in the case of the large cell, the feeding rate is suppressed a good deal more rapidly than in this case where the cell is quite small. The concentrations for the small cell are very much

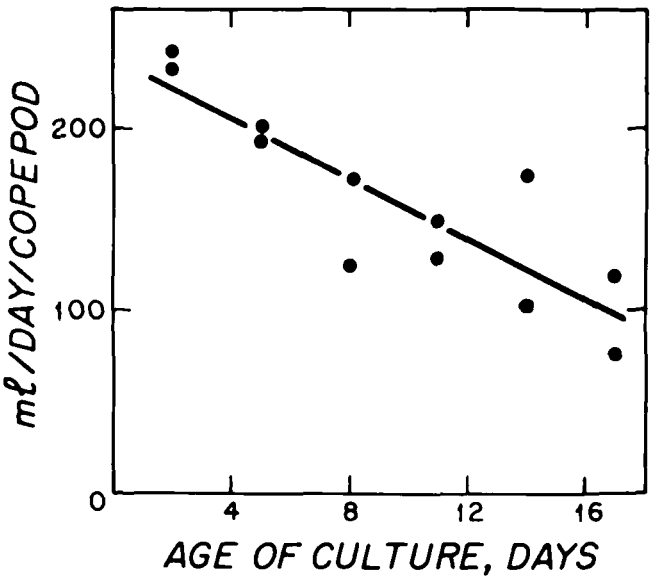

FIGURE 7. Grazing rates of female *Calanus hyperboreus* on suspensions of Thalassiosira made up with cultures of various ages (two experiments). Regression equation: $\overline{Y}_x = -8.29\ x = 240.2$; correlation coefficient: $r = -0.857$.

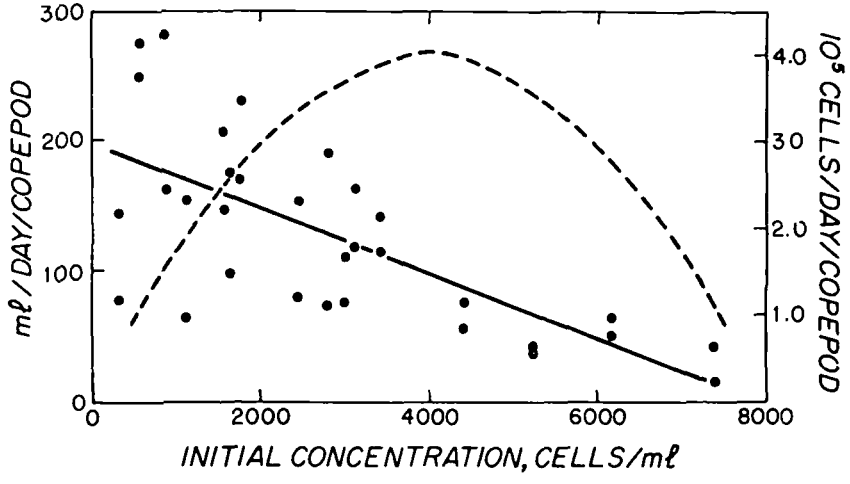

FIGURE 8. Grazing by female *Calanus hyperboreus* on various concentrations of *Thalassiosira fluviatitis* (four experiments). Left ordinate and solid line = grazing rate. Regression equation: $Y = -0.0246\ x - 197$; correlation coefficient: $r = -0.696$. Right ordinate and broken line = rate of intake of cells.

greater. This is a small *Thalassiosira.* The other is *Ditylum.* I think you will find an order of magnitude difference in volume.

SCHMIDT-NIELSEN: How do you determine these things to begin with; when the animal stops feeding, how much it is feeding, how much per day, and all this? How are these various things determined?

CONOVER: Mullin's experiments(40) were set up in a rotating wheel to keep the samples in suspension. Not only that, but he had an arrangement whereby in the bottom of his feeding vessel he had a little mounted magnet and a point on this rotating wheel where there was a stirring motor, so that there was an additional brief stirring.

SCHMIDT-NIELSEN: How do you determine how many cells per day per copepod?

CONOVER: These are simply measured by changes in concentration in the water.

SCHMIDT-NIELSEN: And the amount filtered the same way?

CONOVER: Some of this has been done with a Coulter counter.

BAYLOR: How do you keep that magnet from beating the animal to death?

CONOVER: It is a relatively short period of time that the magnet is going around and the copepod seems to be smart enough to get out of the way. They do seem to survive alright.

BARKER-JØRGENSEN: And it will not influence the feeding?

CONOVER: You get a higher filtering rate if you use this kind of system. What he found (and I have observed similar things) was that rotation alone sets up an eddy. That is, the circulation patterns inside the container are continually repeated and you do get concentration within the eddy. Particle movement is not completely random.

YONGE: How rapid is the movement?

CONOVER: In this case it is probably once or twice a minute.

YONGE: Really quite slow?

CONOVER: Yes, it is quite slow.

STRICKLAND: Were they growing?

CONOVER: These experiments were run in the dark. There can be no photosynthesis. There is a possibility that there is some cell division. You run controls and you hope that these controls are adequate. You can run this experiment for four, six, eight hours. In between, you do not need to make any observations or interfere with it.

MCLAREN: You cannot really tell whether the older cultures are good or bad for the copepod?

CONOVER: No, I cannot. I have some data on assimilation which suggest that the animals assimilate young cultures better.

BARKER-JØRGENSEN: How did the concentrations of algae compare with natural concentrations?

CONOVER: I did not do that experiment.

BARKER-JØRGENSEN: I think, as a general rule, in all suspension feeders above a certain level of concentration you will have a decline in feeding activity.

CONOVER: I think by and large in Mullin's experiments he tried to keep his concentrations relatively low. This does not necessarily mean that they are low compared to what you would perhaps find in some natural environments.

They were adjusted to about 2000 cells/ml.*, which is a substantial concentration. It is around bloom concentration, anyhow.

FOGG: Since this is a diatom, the cells will be the same size, more or less?

CONOVER: In this case, the cell is pretty uniform.

FOGG: So, the animals must be detecting the chemical difference.

CONOVER: I am not saying this: There are those who would interpret these experiments that way, yes.

BAYLOR: Are the old cultures healthy?

CONOVER: What makes a culture healthy? They are presumably growing, and if you subculture from them they take off again quite rapidly. This is a rather good diatom in that it doesn't bleach rapidly in old culture. I would say they were healthy, yes.

BAYLOR: Has anyone isolated a chemical substance from a culture of phytoplankton of any kind which will inhibit feeding, particularly looking at old cultures that are about to crash?

CONOVER: These are Ryther's experiments(41).

BAYLOR: Is there a specific compound?

CONOVER: No. It has been said that something called chlorellin will cause this phenomenon but I do not know whether this has actually been proven. Chlorellin has been found in *Chlorella* cultures and when *Chlorella* is used to feed *Daphnia,* the feeding is depressed by old cultures, so you can form your own conclusions.

BAYLOR: It is very interesting that eserin plus acetylcholine will give the same effect of inhibiting feeding and it produces a behavior pattern which is characteristic of hunger in *Daphnia.*

YONGE: To what extent do these things pass through the alimentary canal of the animal unchanged?

CONOVER: There was some discussion on this. These large cells that I have been observing are completely smashed. However, it is not uncom-

* This is equivalent to about 300μgC/1. for this cell.

mon to observe cells that appear to be in quite good condition—smaller cells. In fact, I have seen cells that looked as though they were alive. Eventually we are going to test this. We have looked at the infrared spectrum of the cells in the fecal material and you do find that there is apparently some uninjured chlorophyll in the fecal material, but this is only one observation.

BAYLOR: Whole cells or chloroplasts?

CONOVER: Not whole cells. The observation was made on this large *Coscinodiscus* that we used, and the chloroplasts are very small in this species. It was difficult to say whether the chloroplasts were intact. What we did find in the mass of material after we squashed it on the slide, was that, by and large, you get an orange fluorescence which is more characteristic of the carotenoids, but you would get here and there a little pinpoint of brilliant red light which was more characteristic of chlorophyll.

HUTCHINSON: But this has a general significance that, I think, is quite important. If you consider evolutionary pressure on a series of types of phytoplankton of about the same shape, it has often been supposed that a larger size is going to make the organism somewhat harder to handle and, therefore, large size will have the selection advantage provided it is not going to complicate things in terms of the nutrient uptake of the organism.

On the other hand, if large phytoplankters are more easily broken and the small ones can really go through and occasionally reproduce afterwards—as I think is true of some of the algae going through *Artemia*—then you have an interesting balance that would suggest that perhaps the middle to large size is the most dangerous thing to be.

STRICKLAND: That seems to be the most frequent size in the diatoms.

HUTCHINSON: Yes, that is right.

CONOVER: What would you call something that is middle-sized?

STRICKLAND: Oh, 50 to 100 μ per diatom.

CONOVER: That is large.

HUTCHINSON: That is very large by fresh water standards.

CONOVER: I would say even in the Gulf of Maine where you have got a diatom-predominant flora, that 60 per cent of the chlorophyll will go through a 10 μ filter.

STRICKLAND: This brings up one point about feeding and that is the filtration rate of an animal. This is nearly always expressed in terms of a volume per unit time. Would anything be lost by expressing it by either of two other measures: the rate by which material is consumed or, perhaps, the number of particulate organisms removed per hour? Why do we keep on with a "filtration" rate?

CONOVER: I do not know.

SLOBODKIN: There is a basic difference in the emphasis that the organism itself puts on it. Certain animals that are not particularly filter feeders, take as prey a particle which is quite large relative to themselves. In that case the number of particles per day consumed can become of peculiar interest.

The true filter feeder takes an organism as food which is effectively infinitely small, compared to itself. There are exceptional animals, as will be indicated, but these are on the borderline of no longer being filter feeders.

BARKER-JØRGENSEN: The copepods are on the borderline.

SLOBODKIN: They are. The true filter feeders really are functioning in terms of how much volume they can pass through a filter system.

BARKER-JØRGENSEN: The volume and the efficiency, those two combined, are the important factors in determining feeding rate.

EDMONDSON: There is still an interest in the volume of water which an animal can clear of its particles in a day regardless of the exact mechanism that it uses.

CONOVER: In this category, the volume filtered largely depends on a number of other factors and, taking laboratory experiments into the field, this becomes a rather difficult thing to interpret.

EDMONDSON: I am thinking of some work of Erman's(42) in Moscow, with a continuous flow apparatus, on rotifer feeding. They are not filter feeders. They throw the particles against the mouth, and suck them through the mastax. Erman subjected these rotifers to a very wide range of abundance of small algae including much denser populations than were ever encountered in nature, and the animals did not greatly vary their rate of clearing in terms of milliliters cleared per day over a wide range of concentration. Therefore, the rate of ingestion was proportional to the abundance of particles in the medium, and in the densest concentration these animals would eat five times their wet weight in a day.

CONOVER: This sounds like a fantastic organism. Even *Artemia,* which sort of eats its way through the water, does have a mechanical limitation.

BARKER-JØRGENSEN: When you are interested in the rates at which suspension feeders clear the water of various particles, it is of importance to know whether this clearance is dependent or independent of the concentration of the particles. If they are dependent you would have a spectrum of values to operate with, but if you find in laboratory experiments that the clearances are independent of the concentration of particles, then it should be fairly simple to determine rates of food uptake or particle uptake.

STRICKLAND: This might be the exception rather than the rule.

BARKER-JØRGENSEN: No, I do not think it is the exception, but I think that many laboratory experiments have operated with concentrations that have been outside the natural range, so that you are off the limit where the clearance is independent of particle concentration. I think the rule is true, for instance, in the sponges, in the bivalves and in the ascidians, and apparently also in the rotifers that Doctor Edmondson spoke about, and I think you can find other examples too.

As to the copepods they seem to have alternative ways of feeding that are just as important as the suspension feeding, so they are much more complicated creatures.

MCLAREN: I think they are a good deal simpler, and I hope to demonstrate this later in the section on nutrition and assimilation.

YONGE: I had a very pretty example recently of the effect of concentration of planktonic food on the nutrition of bivalves. This was during a visit to the Spanish system of mussel culture near Vigo and in the fjord valleys to the north. Mussels are grown on ropes suspended from enormous floats. Each will carry over one hundred ropes reaching to a little distance short of the bottom. On the side facing the open sea, on which the phytoplankton first impinges, growth of the mussels is so much greater that the floats gradually tilt down on that side. This is a very striking demonstration of the utilization of phytoplankton by bivalves.

LASKER: I would like to interject one thing here. Every experiment that is done today, including my own, are all done at concentrations of suspension organisms which are not representative of the sea, and yet every time I present my information to a group of this kind or any other kind, the question is always brought up: Are these comparable to what you find in the sea? I must always answer, "Why, no, they are not, but it is as close as I can get with the instruments I have to measure these things."

The only point I am trying to make here is that you may never get an experiment which will be comparable to the sea, and if anybody sees some hope of this, I wish they would tell me.

CONOVER: If you are talking about concentrations of organisms, in most cases this is true, but if you are talking about particulate matter it is not. We have tried to design our grazing experiments generally to work in the same carbon concentrations that you do find in the sea, perhaps not under periods of dearth but at least under relatively reasonable natural conditions in a relatively rich area. That is where the copepods we are studying come from.

SLOBODKIN: There is a general problem of how to relate laboratory data to field data that should be brought up here. Clearly, a laboratory work in the same carbon concentrations that you do find in the sea, perhaps

experiment is not going to simulate nature precisely, but if you can show a phenomenon running over a range of conditions that exceeds the range of conditions that will be found in nature, you are quite sure that it occurs within the range of conditions found in nature.

A very quick statement of material that you are also familiar with in the *Daphnia* experiments—you can show a linear relation of population size to food supply over a *Daphnia* density range that exceeds the density range that is found in the field. This implies that the linearity in particular holds over the much lower density range that is found in the field. It is a matter of whether the laboratory experiment is an imitation of nature or a technique for understanding nature. They are very different things.

EDMONDSON: There is an additional point, though. If the lowest point of the range you use in the laboratory is still far above the highest in nature, then you may simply be dealing with the top end of a very steeply curved line. Is it not possible practically to get around this? What is wrong with using large volumes but with very low concentrations of food organisms?

CONOVER: It is perfectly possible to do this with a Coulter counter. You can work with concentrations if you are willing to spend time counting.

EDMONDSON: But there is a lot of "noise" there, is there not?

CONOVER: If you are working with very small particle sizes, yes.

LASKER: The Coulter counter has a lower practical limit.

BARKER-JØRGENSEN: If the organisms will not stay alive, it becomes a health problem.

SANCHEZ: I would like to come back to the statement you made in the beginning, in the sense that continuous feeding implies feeding independent of the needs of the organism. This statement made me feel somewhat uneasy because there are some implications in it from the point of view of the evolution of adaptations which are rather critical. It would seem to me, from what we have heard here, that in nature conditions are never such that there is an excess of food with respect to the needs, at least from the point of view of the population. If there is an excess of food with respect to the needs of the number of individuals that are present, the number of individuals of course will increase and it will reach a moment when, for each individual, there would never be an excess of food with respect to its needs. So, it would only be in that sense that continuous feeding is independent of the needs of the organism.

MCLAREN: I do not know about southern temperate zones, but that is not true in the North Atlantic. The food is very frequently in excess of the needs.

BARKER-JØRGENSEN: In areas of strongly varying productivity, there

may be periods of the year where the food is in surplus and other periods when it is in undersupply.

SANCHEZ: But the population would not be larger than was needed for the whole turnover.

BARKER-JØRGENSEN: I was not thinking of the population as a unit, I was thinking of the single animal.

STRICKLAND: I think it is larger for the whole population in the fertile areas of British Columbia during phytoplankton blooms which come up to the order of fifteen million largish cells per liter. I do not think this could possibly be anything else but excess.

YONGE: It depends on the amount of available settling surface. With Quayle of Nanaimo I visited Pendrell Sound near the southern end of the Straits of Georgia in 1959. Here Japanese oysters, *Crassostrea gigas,* have been accidentally introduced into very enclosed waters with almost vertical rocky shores. The oysters form a solid mass for a depth of 10 to 12 feet and for a distance of perhaps 12 miles. There is nothing else but these oysters between tide marks and a little below. And obviously there would have been still more oysters had there been more settling surface.

SANCHEZ: To start with, I do not see, really, any case having been cited of continuous feeding, if feeding, of course, implies at the same time assimilation of the food.

BARKER-JØRGENSEN: No, not assimilation. This is feeding in the sense of uptake of food particles or food material.

SANCHEZ: From the water?

BARKER-JØRGENSENS Yes, and retained in the feeding organs.

SANCHEZ: And it can be excreted untouched?

BARKER-JØRGENSEN: Yes, it can be rejected or accepted, but that is not the point here.

REEVE: In the case of *Artemia,* there seems to be a preferred amount of food which it will consume (FIGURE 9). Conover has already described the type of experiment. As the concentration of cells is increased in separate experiments, the number of cells ingested increases in an automatic fashion and, unlike the experiments Conover was describing, the curve does not reach an optimum point and then fall down. Instead, it levels off indicating that the animal has a maximum or preferred rate of ingestion of food cells(63).

This is the point (*arrow,* FIGURE 9) at a definite food cell concentration when these cells start to get dispersed at the mouth, when the animal is collecting more cells than it requires.

STRICKLAND: Is the gut blocked at that spot?

REEVE: It is the point when the rate at which food is being removed

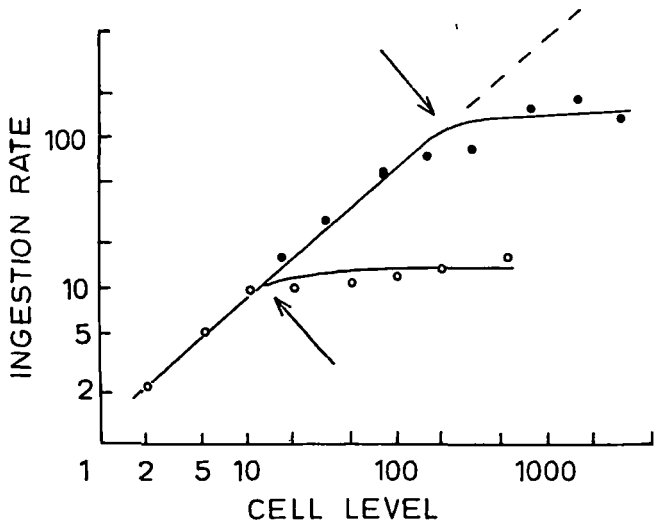

FIGURE 9. The rate of ingestion of cells of Dunaliella (*open circles*) and Chlorella (*closed circles*) by adult Artemia, as a function of the cell concentration of the medium. Ordinate is cells ingested per hr. $\times 10^{-4}$; abscissa is medium concentration in cells per mm.^{3} *Arrows* indicate points on curves where ingestion rates reach a maximum, *broken line* indicates the expected curve if cell ingestion rates were proportional to cell concentration in the medium at all concentrations. Both axes logarithmic.

from the gut either by defecation or by assimilation no longer exceeds the rate at which food can be collected and ingested.

BARKER-JØRGENSEN: Is that the maximum rate at which it can pass food through the digestive tract?

REEVE: Yes. The first part of the curve is the automatic phase where the animal is filtering at its maximum rate and eating all the cells which it collects. For instance, if the food cell is small (e.g., *Chlorella*) the curve will be different to that obtained in an experiment with a larger cell (e.g., *Dunaliella*). The cell concentration in which the animal ceases to consume all the cells it collects is smaller for the larger cell. In other words, it would appear that the maximum preferred number of cells which it consumes is inversely related to the volume of the cell.

PROVASOLI: To the volume of the gut and the time of passing through the gut.

REEVE: Yes, there is a preferred volume of material which can be passed through the gut in a specific amount of time.

PROVASOLI: Is this done with adults or starting with naupli and growing them to adults?

REEVE: The latter experiments with several food cells were done only with adults, though similar curves were obtained with animals of all ages using only one food cell species.

STRICKLAND: I gather from Mullin's work(40), that an animal which is sufficiently replete gets lazy and does not want to digest another meal.

CONOVER: That is a rather loose interpretation of the situation. However, it is a more complex organism.

REEVE: There is another point; this preferred rate for a cell like *Phaeodactylum* at which *Artemia* will take particles in its mouth, does not appear to be a maximum rate; but this animal has a very peculiar behavior. When faced with suspensions of sand particles of approximately the same volume, *Artemia* will ingest far more of these particles in the same amount of time (FIGURE 10).

SLOBODKIN: Is there a difference in the defecation rate between the sand and the *Chlorella?*

REEVE: Yes, it produces far more fecal pellets when fed on sand. Presumably, most of the sand is an inorganic silica and is not digested.

STRICKLAND: Its gut senses when the stuff is not much good and lets it out quicker.

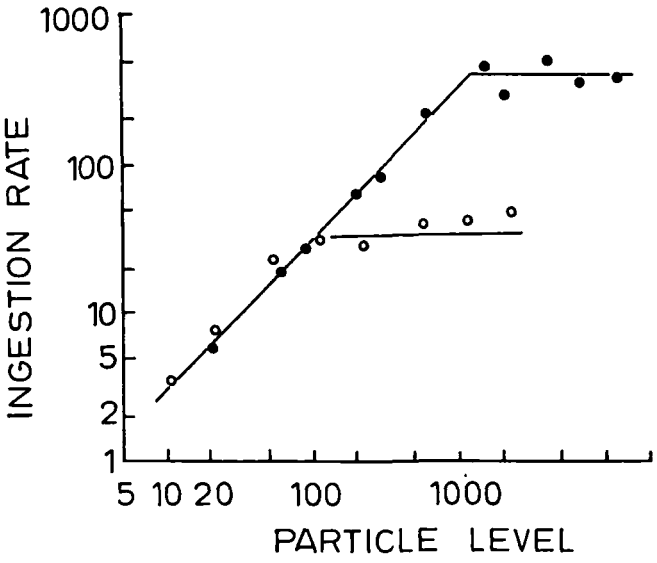

FIGURE 10. Rate of ingestion of cells of Phaeodactylum (*open circles*) and particles of sand (*closed circles*) by adult Artemia, as a function of the particle concentration of the medium. Axes as in previous figure. Note that despite similarity of size the sand and plant cell particles, maximum ingestion rate of sand is about 10 times greater because ingestion rate is proportional to particle concentration in the medium over a concentration range 10 times greater. Both axes logarithmic.

REEVE: Possibly, perhaps by an irritant action on the gut lining.

FAGER: One could almost use this as an index of digestibility. The rate of input multiplied by the size of the cell should be nearly constant for various algal species if in fact they were all equally digestible. If they were not, you might be able to correlate relative digestibility with the relative size of the product.

REEVE: Yes, in the case of two plant cells in FIGURE 9, if one gets an approximate measure of the volume of the individual cells simply by microscopic measurements, then one can calculate the total volume of cells ingested in a given time by finding the preferred rate of consumption of these cells from FIGURE 9. The two resultant volumes are almost identical, so that it seems that the rate of food intake in *Artemia* is limited at the upper end of the scale by the normal gut capacity. When ingesting sand, this capacity is increased several times, presumably because having no digestive value the sand is speeded through the gut.

The rate of fecal pellet production is not a measure of ingestion rate in *Artemia*. This animal produces what is called a peritrophic membrane from the inner lining of the gut. This is a thin chitinous membrane which envelops the fecal matter as it emerges from the anus, and this chitinous membrane appears to be produced at a constant rate. In fact if the animal is put in a medium where there are no particles, these thin ghosts of membranes still emerge; but if it is in various concentrations of food cells, these fecal pellets are opaque and it is not possible to tell by looking at them under a microscope how much food they contain or how much fecal material. In other words, it is very difficult to tell by measuring the number of fecal pellets produced in a certain time how much food is passing through the gut.

STRICKLAND: What is the point of forming a sheet of fecal pellets? What does it do?

SLOBODKIN: Among other things, it takes it away from its competitor.

FAGER: It may also keep the animal from eating it.

REEVE: It has been suggested by Gauld(43) in the case of copepods that it might be to package the feces so that they would drop down below the feeding zone. This is certainly the case here; the feces are heavy relative to the water and they do drop down very fast.

FREMONT-SMITH: Would it have a lubricating effect at all? Would it be helpful in getting food to pass through the gut?

REEVE: This has been the reason suggested as to why certain insects have this membrane, although I think other insects, which are entirely liquid feeders, have it, too.

FAGER: Have you tried something like *Stichococcus?* As I remember, Provasoli's work(44) showed that it is not digested very well by *Artemia.*

REEVE: No, I have not.

BODEN: Are there genera of copepods, mesopelagic genera, that live on the fecal pellets of copepods?

CONOVER: I can conceive of such a thing.

BODEN: I mean these undigested or semidigested pellets.

YONGE: There is a small gastropod, a species of *Hipponyx,* which lives on the shell of a large topshell, *Turbo,* in the tropical Pacific. It just sits at the right place and takes the fecal pellets which are its sole food.

EDMONDSON: In connection with FIGURE 9, may I call attention to some work by Sushchenia(45, 46), working with a variety of Cladoceran genera. The point is, two of them showed the same phenomenon, taking the same daily ration through a wide range above a minimum concentration. The cutoff point still was well above the maximum these animals normally experience in nature. One of the genera he studied did not do this, but through the entire range he studied there was a rising daily ration.

SLOBODKIN: His work is with *Bosmina,* which in a sense is a bottom feeder and will chew up detritus.

EDMONDSON: I would suggest this is exactly what we ought to do in a series of cases like this when there is a difference, not just say, "Oh, well, these things vary all over the place," but try to find the reason.

BARKER-JØRGENSEN: I have read the papers(45, 47) too where he found that there was a correlation between feeding rate and concentration of food particles. Monakov and Sorokin(48) did similar work and obtained similar results. However, the volume of water per animal decreased at the same time as the concentration increased, so you have two factors varying at the same time, and from copepods we know that the volume filtered is dependent on the volume available, below a certain volume.

I looked through the papers rather carefully because they presumably represented an exception to the rule, that the filtration rate is independent of particle concentration, even at low levels of concentration, and both Sushchenia, and Monakov and Sorokin worked within normal ranges of concentration of algae. I recalculated the volume available per animal and it decreased simultaneously with the increase in concentration of algae.

CONOVER: This may be a function of the size of the animal.

BARKER-JØRGENSEN: It may be a function of the technique in making the suspensions, I think.

BAYLOR: May I add a note to what Larry said about *Bosmina. Bosmina longirostris* spends the day on the bottom in the mud, but if you look at

it at night with infrared techniques, you discover that it is up swimming around and looks like almost any other Cladoceran.*

SANCHEZ: I wonder if anybody has anything to say about the properties of mucus. I would like to know, for example, if what we call mucus in ciliary action, or ciliary feeding, is the same in different animals.

BAYLOR: It could not possibly be the same in fresh water and salt water.

SANCHEZ: I know nothing about it but I am thinking that I could make good use of information if there were any.

FREMONT-SMITH: It is possible to accumulate, is it not? I understand that pellets of mucus are excreted and in a starved animal you get a pellet of practically pure mucus. Is that not what I understood from what was said earlier?

YONGE: You get mucus surrounding the fecal pellets in the mollusk. It is a different story in the crustacea but the effect is the same.

FREMONT-SMITH: So it ought to be possible to get enough for some kind of microanalysis. Your question is, has it been done?

SANCHEZ: I do not know whether it is deposited within the organism. It is produced as needed, perhaps.

GONOR: I have tried to find similar information and there is an extensive literature. The chemistry of mucus is very complicated and the substance is difficult to work with. The biochemists have studied the material and have described various kinds of mucus. Most are conjugate substances of polysaccharides and protein. There are mucuses which are neutral in reaction. Some bear charges and are acid; they may have sulfate attached to them, for example.

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* Editor's Note. Although this lengthy discussion of planktonic setae filter feeders touched on many of the major phenomena and unsettled problems, some of the pertinent literature was not discussed, especially that from comparable freshwater animals, particularly Cladocera (Refs. 45, 84, 168, 169). One of the outstanding problems has had to do with the relation of filtering rate to food concentration. It now appears general for Daphnia that the animals filter at a uniform rate in low concentrations of food so that the rate of feeding is directly proportional to the concentration of food in the medium. Above some concentration, the filtering rate slows in proportion so that the rate of feeding is constant, at least within some wide range of food concentration (168, 169). Not all Cladocera behave the same way (45). However, it appears that in the literature, some differences between animals represent, technical artifacts, others are probably genuine quantitative or qualitative differences in behavior. There is still need for a critical comparative review of all published data supplemented by additional experiments to clear up the major discrepancies (42). Edmondson has reviewed some of the literature including that on rotifers, but the adjustment of filtering rate in different concentrations of food was not discussed in detail since the emphasis was on the lower part of the food concentration range (118).

As one who does some taxonomy, I recognize that the classification of mucus is an artificial one. It is a classification of convenience and difficult to use. It depends on the relative amounts of the carbohydrate to the protein, and it is not alwys clear why substances are given specific mucus names. The names usually end up one per kind of substance or source studied, which is a good indication to a taxonomist that the classification is artificial.

That is, roughly, something about the kinds of mucuses. There are a number of workers actively studying mucus in various kinds of organisms. Doctor Sophie Jakowska(49) is studying mucus and has edited a symposium volume in the New York Academy of Sciences series on this subject.

FREMONT-SMITH: This is mucus in humans?

GONOR: The general comparative biology of mucus. There is another volume coming out. At the International Congress of Zoology, there was a section on mucus in invertebrates, and many workers who are interested in the biochemistry of the substance presented their results there.

FREMONT-SMITH: It is very interesting to me that the gastrointestinal tract of some of these very small marine organisms up to birds and humans, produce mucus. Birds, of course, encapsulate their feces in a mucus capsule which goes way, way back to evolutionary ways, back to a very primitive form. I am actually talking about the infant bird shortly after coming out of the egg. The mother knows just what to do with this bit of mucus-covered feces and carries it away.

BARKER-JØRGENSEN: As far as I found out, the chemical characteristics of mucus vary from type to type, but the physical properties are apparently much more alike, so we may draw conclusions concerning the function and properties of mucus in the suspension feeders from studies on mucus obtained from other organisms.

It seems that one of the important properties of mucus in suspension feeding is its tendency to form sheets, which is very pronounced, for instance, in the nasal cavity and in the respiratory tract of higher vertebrates. It has been described many years ago that mucus in the nasal cavity of mammals has a tendency to form very thin and very tenacious sheets of thickness of about 5 microns.

Also in many suspension feeders the feeding mucus may apparently form sheets, which may act as filters. Such mucus sheets have been described beyond doubt in ascidians, *Chaetopterus* and *Urechis* by MacGinitie(50, 51). They have further been found in the gastropod *Crepidula*(52) and they may also be present in bivalves.

YONGE: I think that the undoubted mucus sheets in *Chaetopterus, Urechis* and *Crepidula* are correlated with feeding on extremely minute

particles. I do not see how they could occur on the gill of a bivalve where, in some cases, there may be currents running in opposite directions on the frontal surface. Research students with me have tried to demonstrate mucus sheets by observing the intact gill through windows cut in the shell but without success. I am sure that mucus sheets exist but not in the bivalves.

BARKER-JØRGENSEN: That is quite likely. It is a point of interest whether the mucus sheets as produced for instance by ascidians are of the same type as you see in the respiratory tract of vertebrates. Do the sheets result from the coalescence of mucus droplets produced by mucus cells or is there a secondary structure in the mucus sheets that acts as a filter? As far as I can see, there must be a secondary structure. In the mucus sheets covering, for instance, the respiratory tract, a reticular structure is formed by the mucoproteins and mucopolysaccharides. This reticulum must have pore sizes that would effectively retain even smaller colloidal molecules. But there is no convincing evidence that the mucus sheets produced, for instance, in ascidians are able to retain colloidal particles as small as e.g. proteins. The porosity of the mucus sheet in ascidians is such that particles of about 1 micron are efficiently retained, but not hemoglobin or other proteins.

The only evidence that the mucus sheet produced in a filter-feeding animal should be able to retain colloidal molecules is that given by MacGinitie(53) who found that large molecules as haemocyanin would be completely retained in the mucus nets of *Chaetopterus* and *Urechis*. We also found in *Ciona* that haemocyanin would be rather efficiently retained in the mucus sheet, but we found too that haemocyanin does not make a stable solution in sea water; it aggregates, so you cannot be sure that the particles that are retained in the mucus sheet are of the size indicated by the molecular weight of haemocyanin. It may be the aggregates that are retained. *Crepidula* produces two mucus sheets, one at the entrance of the mantle cavity, and another covering the gill. In the mucus sheet at the entrance to the mantle cavity a secundary structure is very obvious. The sheet is produced by a special organ that forms a rather coarse net from longitudinally and transversally running mucus fibres. Whether a secondary structure is also present in the other mucus sheet is undecided so far. I think it would be extremely interesting to further study the structure of the mucus sheets found in the various suspension feeders that utilize mucus sheets in feeding.

SANCHEZ: I cannot imagine how a mucus sheet works inside the thoracic basket of an ascidian where water must be filtered out. Is it a sheet with holes?

BARKER-JØRGENSEN: It must be a sheet with pores, yes, but the structure of the sheet is unknown.

YONGE: Does it not come out of the endostyle and pass right over the surface?

BARKER-JØRGENSEN: It does, yes.

STRICKLAND: How does it filter anything through that? Is not a hydrostatic pressure necessary to force anything through that?

BARKER-JØRGENSEN: The hydrostatic pressure produced by the ciliary activity in an ascidian is some few mm. of water.

STRICKLAND: And this can push water through something which is four sizes of the order—

BARKER-JØRGENSEN: Of less than one micron, but how much, we do not know.

SANCHEZ: A mucus produced by the surface of the gills in bivalves moves down in what shape? Why is it not a sheet?

YONGE: It is locally produced, to begin with; there is no mechanism for producing a continuous sheet.

SANCHEZ: What happens to the mucus, then?

YONGE: A particle impinges on the gill and mucus is secreted. The whole ciliary mechanism depends on mucus. Knock out the mucus and you knock out the cilia. The final combination of the whole thing is the crystalline style which is a mucoid rod containing adsorbed enzymes with an isoelectric point which permits its existence in the style sac and its solution in the *p*H of the gut. This is one of the prettiest mechanisms in the whole of the animal kingdom. It is the culmination of mucus mechanisms in all bivalve and some gastropod mollusks.

I quite agree that we badly need more knowledge about the nature of mucus.

BARKER-JØRGENSEN: Not so much chemical as structural.

YONGE: Yes, physical knowledge.

BARKER-JØRGENSEN: I think the feeding mechanisms in bivalves may be more complicated. If you look at the literature on the efficiency with which the bivalve gill is able to retain particles, you will have very contradictory results to deal with, because some find that the porosity is very high and variable. We find that it is rather low, that undisturbed oysters and mussels will efficiently retain particles down to one or a few microns.

It may be that there are several mechanisms for feeding in the bivalves; there may be mechanisms that are adapted to various situations. One mechanism of feeding may be adopted under conditions where there is a great deal of particulate matter in the suspension, whereas another way of feeding may be used when there is only little particulate matter present.

YONGE: There are the cilia, there is the mucus, and there is the muscu-

lar contraction or relaxation of parts, or all, of the gill. The whole thing is terrifically complicated, I would agree. There is quite a lot to be done on it yet. You can see in some cases, how the gill will suddenly dilate and particles will be expelled from the surface purely by muscular action.

FAGER: When you say that particles down to a certain size are retained by this mucus net, I am disturbed by the same thing as Strickland is; How does this animal with a 5 mm. head of pressure get water containing these particles through a net with 1-μ holes? Is it not possible that what is happening is that the particles stick on the net as the water goes by and that it does not actually go through?

BARKER-JØRGENSEN: Yes, it is pretty hard to imagine but I think there is no doubt it is done. Of course, there is another theory. Hoyle(54) assumes that feeding in ascidians is connected with the squirting: Water is sucked into the pharynx and squirted out again by body wall constriction; but I cannot see how, by this mechanism, the particles contained in the water taken into the pharynx can get into contact with and be retained in the mucus membrane lining the pharynx. They could squirt a great deal, but it would not be an efficient way of getting the particulate matter in the water in contact with the feeding surfaces. How is the particulate matter in the water that is sucked into the pharynx being circulated so that all particles can be adsorbed on the walls of the pharynx?

SLOBODKIN: I do not know the anatomy well enough, but when the thing contracts, is not some of the water forced through the gill basket in some way—not necessarily the water that is inside the gill basket?

BARKER-JØRGENSEN: No, the water is not forced through the gill basket during squirting. The gill basket is covered by this sheet of mucus. When the animal contracts there is a mechanism that prevents the water from being pressed through the gill because this would probably clog it. Therefore, during squirting the excurrent opening is closed so that squirting will result in a flow of water out of the incurrent opening.

CONOVER: Does this refer primarily to the sessile ascidians?

BARKER-JØRGENSEN: Yes. This is presumably a mechanism that is common to all ascidians with well-developed gill baskets.

CONOVER: Even the pelagic ones? Since the pelagic ones swim by squirting, I am wondering whether they are somewhat different.

YONGE: The point I would make is that the undoubted cases of mucus sheets are those that have been clearly demonstrated in animals inhabiting tubes in mud, i.e., in animals living in completely still water where alone mud settles out. I refer to *Urechis,* a gephyrean worm, and to *Chaetopterus,* an annelid. These mucus sheets do filter out the excessively minute particles which are suspended in this perfectly still water. There are correspondingly delicate mechanisms for drawing water through these mucus

sheets. I am sure you do not get them in bivalves and I have still a measure of doubt about ascidians.

BARKER-JØRGENSEN: Well, this is microscopically proven. You can see the formation of the mucus sheet under a microscope.

YONGE: I know you can, but this question of drawing water through these sheets still worries me a bit.

BARKER-JØRGENSEN: This is easily demonstrated because you can measure the rate at which such an animal clears the surrounding water of particles, and the volume cleared is the volume of water going through the sheets, so it is as simple as that.

The question about the porosity of the feeding organs in the suspension feeders, of course, also has a close bearing on the problem of which fractions of organic matter in the surrounding water are utilizable by the animals. From a study of the efficiency with which most suspension feeders are retaining particulate matter or organic matter from the surroundings, it would seem that particles smaller than, say, 1 micron are very seldom efficiently utilized, so this means that the lower limit of efficient utilization of particulate matter would be close to the lower limit of living organisms, bacteria more especially. It would seem from the results that colloidal material in the sea would be very inefficiently retained, and the consequence would be that their importance, notwithstanding the nutritional value of the matter, would be correspondingly small. This is speaking about their value as a source of energy.

STRICKLAND: Are you suggesting that getting matter from the colloidal state to the gelatinous state would completely alter this picture?

BARKER-JØRGENSEN: Yes.

STRICKLAND: By definition, of course, we would never analyze this in the sea as colloidal material.

I am very confused about bacteria in invertebrates. I have read just about as many papers firmly stating that bacteria are nutritious as those firmly stating this is nonsense. Can anybody give a synopsis of the position of bacteria?

YONGE: I would say, perhaps there are bacteria and bacteria.

STRICKLAND: But as a major source—

YONGE: Yes, I am meaning that. Some are not nutritious and some probably are.

STRICKLAND: You mean a species effect of bacteria?

YONGE: That would reconcile a lot of conflicting arguments and statements, would it not?

CONOVER: I will make a statement about this. There are about 4000 bacteria per fecal pellet in a copepod. This constitutes roughly about 0.01 per cent of the biomass of the fecal pellet. Concentration here,

however, is about 10^{11} bacteria per gram of dry fecal pellets which is pretty high. I just doubt that there are enough bacteria anywhere to make them very important quantitatively.

STRICKLAND: This is on freshly collected fecal material?

CONOVER: Yes.

STRICKLAND: And this is obtained by what method?

CONOVER: This is obtained by plating on enriched sea water agar.

PROVASOLI: Streaking on agar media and not by counting the bacteria present in the fecal pellet directly at the microscope. As you know, in this way perhaps only 5 per cent of the bacterial flora is recovered.

CONOVER: This may be true, but if so, there are an awful lot more bacteria in pellets.

PROVASOLI: That would mean that there are 95 per cent more bacteria present in the fecal pellets, unless the bacteria of the fecal pellets are of a type that will grow well in the media employed. The remark about 5 per cent recovery refers to the marine bacteria found in waters and particles.

CONOVER: The bacteria that grow on fecal pellets may also be rather more inclined to grow on solid material.

PROVASOLI: Quite probably. About the possible role of bacteria in small invertebrate nutrition I may add that some bacteria are a good food for *Artemia*. Sometimes the very rich organic media that we employ for *Artemia* become infected with bacteria, either because of faulty sterilization of some component of the medium, or because we open the test tubes repeatedly to introduce aseptic additions or to manipulate and transfer the animals. The more times we open the tubes, the higher are the chances of infection. We have repeatedly found that most bacterial infections are lethal, under these conditions, to *Artemia,* while some other bacterial infections are very favorable and cause *Artemia* to grow much faster than in the same medium without bacteria. We do not know if the lethal bacteria produce a poison or produce unfavorable conditions for *Artemia*. We have found that the *p*H of the medium is lowered to about *p*H 5 only by the lethal bacteria, the nonpoisonous ones do not lower the *p*H below 7. Since in our media, *Artemia* does not grow below *p*H 6.7, it is difficult to know if the lethal action is simply due to the lowered *p*H or if a poison is also released.

We have also repeated the work of Teramoto and Kinoshita(55) who have grown *Artemia* on a commercial waste of the acetone–butanol fermentation. This product dissolves only partially in seawater. When sterilized by autoclaving or by filtration, it is unable to support *Artemia* growth under aseptic conditions, even after addition of proteins and vitamins. If we repeated the conditions employed by Teramoto and Kin-

oshida (i.e., we added to seawater the fermentation waste, inoculated the nauplii and bubbled air) we obtained adult *Artemia* (50–60 per cent survival). Since the *p*H drops as the bacteria grow, especially in nonaerated cultures, it was essential to maintain the *p*H at 7.8 by repeated additions of alkali to avoid total mortality at the young stages. To assess the nutritional role of these bacteria we filtered out, after addition to seawater of the fermentation waste, the insoluble part. In this medium, the bacteria grew as well but the *Artemia* died at the young larval stages showing that both the insoluble part of the fermentation waste and the bacteria singly are an insufficient diet, but together a good one.

CONOVER: The only point I am making is that you cannot supply energy requirements of organisms by feeding them natural bacterial populations.

PROVASOLI: I know these are artificial conditions and certainly the bacterial populations in the sea never reach even a tenth of the counts in these artificial cultures. But I thought it necessary to mention this experiment. Later on we may speak of bubbling seawater and of the resultant formation of particulate organic matter and of the possible nutritional role of the bacteria growing on them.

Another instance of the nutritional role of bacteria is given by the work done on *Tigriopus*(44). *Tigriopus* can be grown aseptically only for four generations when fed on *Platymonas* No. 5, but it can be grown indefinitely on the same *Platymonas* species if an unidentified bacterial flora is present. This is how it is grown in several laboratories. I think therefore, that we cannot exclude the importance of bacteria as food for invertebrate larvae even in natural conditions.

EDMONDSON: It would seem to me in connection with your first case that it is important to distinguish between those in which the bacteria do something to the medium that is deleterious to the animals like the *p*H change, and other kinds of effects.

PROVASOLI: As I said, it is difficult to differentiate between a possible toxic action and *p*H action. These were not experiments but the results of infections. We can only say that the lethal action of bacteria is always accompanied by a *p*H drop. So much so, that all the experimental media at the end of an experiment now are tested for *p*H after having withdrawn aseptically some fluid for testing sterility in sterility test media. We consider doubtful any tube in which the *p*H drops, even if the sterility tests are negative. Further, we have recently incorporated opportune noninhibitory concentrations of phenol red in media to detect early infections while the experiments are in progress.

EDMONDSON: Can you make a similar *p*H change just by adding acid —does that kill them too?

PROVASOLI: We have tried to grow *Artemia* aseptically in our artificial media at various *p*Hs. They will not grow at all or very, very slowly at a *p*H slightly below 6.8. I do not say that it is impossible to grow *Artemia* at lower *p*Hs. Perhaps it might be possible to do so by adjusting the balance trace metals/chelators, as it has been done for flagellates and ciliates.

RAY: I think I would like to add something else in relation to the possibility of bacteria being used by different organisms. I mention it as a possibility; I think it is interesting enough to mention.

Some years ago we found a number of rather interesting things in raising amebae and in the particular culture I was working with, a rather large but simple soil ameba could grow on solid matter but also in liquid. These are bacteria feeders. The amebae can feed on bacteria, particularly on a semisolid surface, very readily by going around and picking them up, but if growing in a liquid film they will preferentially feed on flagellate material. If you have two species of bacteria, one flagellate and one not, on a semisolid or solid medium, the amebae will eat each one of them equally well, but in a liquid medium where the flagellate bacteria swim around, they are removed from the medium. That is to say, they are removed from the suspension, not by a filtering technique but by a technique that the ameboid cell is able to employ, namely, whenever the flagellate cell hits the surface of the ameba it sticks there. It is an agglutination process which is similar to an antigen antibody reaction and, indeed, can be blocked by specific antiserums.

That this actually is the mechanism involved has been shown in quite a few experiments. But what I want to mention is that this seems to be a property of ameboid cells in general. I am not certain whether something like foraminifera, for example, would utilize it, but given a liquid medium in which there are flagellated bacteria swimming, even though there are only a few of them, the ameba will sooner or later pick them out where it will not get those that are stuck on the surface or are immobile.

So, assuming that an ameboid cell such as a foraminiferum had the same mechanism, it would be able to remove mobile bacteria from a medium even though present in very small numbers.

We know that the amebocytes from a large number of different animals can do this, even with the bacteria present in small numbers, and I suspect, just from casual observations, that this may be one mechanism by which the collar of the choanocytes of sponge cells remove bacteria from suspension because I have seen bacteria on the collars in some dissociated sponges. I think that the feeding mechanism there may be very much the same as it is in a normal ameboid cell.

How many different kinds of higher invertebrates might be able to

employ such a mechanism to remove bacteria, I do not know, but if they are able to do it, I think bacteria could form a substantial part of the food.

SLOBODKIN: This implies a very interesting serological difference between the flagellae of a choanocyte, for example, or one of the flagellated amebae and the bacterium flagellum. I have vague memories of most flagellae having six strand structures.

MCLAREN: Nine.

SLOBODKIN: Does it differ from bacteria to protozoa to sponges?

BAYLOR: Then there is a coat around the outside of that. The antigen antibody reaction, if it is going to occur—does it not seem to you that this is going to be a most remarkable polyvalent type of kind of antigen?

SLOBODKIN: That and the fact that it can ignore the flagellae of the sponge itself.

BARKER-JØRGENSEN: In the sponges you have a filtering mechanism. The collar cells filter; there is a transport of water between the fibrils of the collar, maintained by the activity of the flagellum.

RAY: I am not at all certain how the bacteria may stick to a collared cell. But so far as the amebocyte is concerned, that is where they capture flagellate cells—it is by this mechanism.

SLOBODKIN: And they do not catch flagellated protozoa?

RAY: I am not certain. I myself, have not done any particular work with them except one small observation where I had a very, very small *Micromonas*. There was evidence that it was sticking but the *Micromonas* was perhaps a tenth the size of the ameba and it would break away.

PROVASOLI: This observation of yours may help in solving the mystery of the chrysomonads, like *Coccolithus fragilis,* which form blooms at depths far below the photic zone, and are found even at 2000 meters(56). Since they cannot photosynthesize at that depth they should feed heterotrophically. They have naked protoplasm and many of them phagocytize particles and bacteria. They can also absorb nutrients in solution. One wonders if, at that depth, there are enough organic solutes or nutritious particles to keep them alive. If they possessed the same ability of your soil amebae, they could trap the few motile bacteria and make a living.

We tried to grow some marine chrysomonads in darkness on media rich in organic solutes, but they would not grow. Next we tried media rich in soluble vitamins and containing protein and starch particles. This failed, as also did an attempt to grow them on marine bacteria which were in all probability nonmotile. We did not check that. After what you said we will have to feed them motile bacteria and see if the chrysomonads will then grow in darkness. This would be wonderful.

EDMONDSON: I would like to ask a question about the evaluation of the significance of this. Presumably, it takes some daily rate of income of food to keep an ameba alive, or any other cell feeding on bacteria. If you knew something about the rate of swimming of the bacteria, could you calculate the minimum population density you would have to have to support the ameba? What is the probability of an ameba getting enough bacteria from a given dilution? Then can you relate this to what is there?

RAY: It might well work in that direction. I do not think it does in the other direction, because if you overfeed, you have a great excess, and that is very easy to do in bacteria cultures. The amebae keep making food vacuoles very rapidly and throwing them out sort of half-digested, but only up to a point, and there they level off and you cannot force-feed them any more than a certain amount.

I suspect that they have a certain adaptation too. If you have a very much thinner culture they may feed slowly, the rate may go down and it would be a sliding scale that would be hard to calculate or extrapolate from a single point on the curve.

STRICKLAND: The point is that in a marine environment, irrespective of the method of obtaining the food, we have to have a minimum biomass intake of bacteria of any sort to maintain the organism we are concerned about. Apart from acting as a critical growth supplement, the question is, do bacteria provide a substantial part of the energy intake of organisms? If this is the case, then we have at least to be able to see that we have enough food energy in the form of bacteria to do the job. This is not a difficult situation to visualize in muds and very rich sediments. It is getting rather more doubtful when we get to the open sea, and unless we have some method for estimating total bacterial biomass there will always be uncertainties.

PROVASOLI: Is that true? How good are the data on the quantities of bacteria in the sea? If you are judging only by plating, we are recovering 5 per cent or less.

EDMONDSON: There are direct counts.

SCHMIDT-NIELSEN: What is the present status of small molecular substances, amino acids or sugars, and so on?

STRICKLAND: Quite a lot of them compared to any particulate matter.

SCHMIDT-NIELSEN: But are they not taken up now and again?

STRICKLAND: Stephens(57) reported uptake of dissolved amino acids.

BARKER-JØRGENSEN: I think they have been taken up all the time. The results of Stephens are in very close agreement with the results of Krogh(58).

SCHMIDT-NIELSEN: What do they amount to, quantitatively?

BARKER-JØRGENSEN: They both showed that various organisms are able to utilitze very low concentrations of dissolved organic matter of various kinds. This is, of course, very interesting; it may be a general property of living cells that they possess more or less specific mechanisms for the uptake of organic molecules. However, in the experiment of Stephens, so far as I can remember, he does not show that the animals were able to live on this organic matter. He was able to find that they could cover a certain percentage of their energy metabolism by the uptake of these substances, but what he missed was to show how much they lost at the same time. This was what Krogh did in his experiments. He found that if he kept the experimental animals in a dilute solution of glucose, for instance, some milligrams per liter, he could demonstrate an uptake of the glucose, but if he measured the total turnover of organic matter he found that at the same time the animal had lost more to the medium than it took up.

PROVASOLI: I think that the dissolved organic substances cannot, for the majority of the organisms, be a sufficient source of nutrients. The rate of uptake of the dissolved organic matter seems too low to be sufficient for growth, perhaps it might be useful for maintenance. This, even though the quantity of dissolved organic matter in the sea is far greater than the quantity of particulate matter.

BARKER-JØRGENSEN: But they may be important, of course, as a source of biologically active substances.

PROVASOLI: They may be important, but only as a nutritional supplement in the case of amino acids and carbohydrates, because these nutrients are needed in relatively high quantities for growth. On the contrary, the growth factor requirements may be satisfied by the organic solutes since the vitamins are needed in minimal quantities.

BARKER-JØRGENSEN: But if you consider how close a relationship we generally have between feeding type and feeding structures, it would be rather surprising if all the complicated feeding mechanisms found in the suspension feeders would have remained in the course of evolution if the animals were really living on dissolved organic matter.

PROVASOLI: You are quite right.

YONGE: If the animal has a feeding organ, it is going to use it.

STRICKLAND: This can be a supplement to a small enough protozoa. We are talking about direct utilization.

LASKER: Around San Diego, divers working on the kelp project have noted in areas where the giant kelp has been denuded that the sea urchins continue to grow and reproduce in an area where there are no longer

algae. There is, however, a sewage outflow very close by. If true, this is an exception to the rule.

We have done some experiments just to see if this were true. They can absorb amino acids from sea water but we have not yet determined the rate of uptake or absolute quantities.

PROVASOLI: Did anybody look at the quantities of ciliates, for instance, in this water?

LASKER: I am just offering it as an observation thus far. Whether the urchins can absorb enough material from sea water for growth and reproduction remains to be tested.

YONGE: Surely this is the whole problem, is it not, of animals that are feeding on bottom deposits. What are they actually feeding on, is it organic matter entirely or is it partly bacteria? Are they feeding on the bacteria which are feeding on the organic matter, or are they feeding directly on the organic matter?

PROVASOLI: Or both?

YONGE: Yes, both.

SANCHEZ: I would like to bring up some observations which are not in the nature of experiments because they are very crude, and they have come out of an intent to build a marine aquarium in Santiago, which is an inland town. I have been working with tide organisms, and now and then we bring into town some things, partly because they are beautiful, partly because they provide material for eggs of different sorts. We bring sea water in large glass bottles, and we keep it in a cold room just above freezing, 2 or 3°C. We have been doing this for some four to six weeks, storing it in a dark, cold room, and then using it, just pouring it into the jars where the animals are and aerating with a pump.

It happens, of course, that some organisms in the sea water do not stand this treatment, but it also happens that other organisms have stood it for a tremendous and unpredictable time. When I left there a few days ago, there was no one to take over, so we had to kill one *Actinia* which we have had there for one and a half years. It is a big thing, about a quarter of a liter, very soft—probably 90 per cent or more of the whole tissue is water—but this animal has been living for one and a half years at room temperature, going through the summer without growth, so the size remained the same. The macrocysts and all the rest were there, and the animal was not in a very bad condition; it would react to stimulation although we had not provided it with any food whatsoever during one and a half years. It was getting a change of water once a week. This is sea water in which, of course, in the darkness and at that temperature probably all organisms were dead. We did not check what organisms were alive, but I know if any algae or protozoa were

living in this water in the dark, they would not live for more than a month, and still the *Actinia* kept alive in this water.

We have had many other observations of this type, which, to us, are particularly interesting because they have shown us a sort of selection experiment of the tolerance of certain species to their conditions. What we were after was to have some animals that could live in this artificial situation.

One wonders, of course, what animals can live on for such long periods. There are other observations of this same type: some species of asteroids which I have kept alive for five or six months, and these are actively predaceous in their natural environment. I do not know of many observations of that type.

CONOVER: Do you actually know that the weight or quantity of protein, or what have you, of these organisms, has remained the same?

SANCHEZ: No, of course not.

CONOVER: Their volume may be about the same.

SANCHEZ: Yes.

CONOVER: This is a much bigger organism than a *Calanus* which can survive for six months.

SLOBODKIN: I have some data on the weights that *Hydra* will take after a period of starvation. What we had were *Hydra oligactis,* maintained in darkness and in light, and *Chlorohydra viridis* maintained in dark and in light, and we took weights of the total conglomeration. We put twenty animals in paired dishes initially and then weighed the animals in one dish and left the others alone for 28 days.

The total initial weight of the green *Hydra* was 2383 micrograms, and for the brown it was 2655. These were both taken from stock cultures maintained on a heavy feeding of *Artemia.*

After a period of 28 days, the weights of the green maintained in light was the same as the initial control groups, 2425 micrograms.

PROVASOLI: This would be symbiosis?

SLOBODKIN: In light only. The corresponding value for the *H. oligactis* was 77 micrograms, the point being that in a period of 28 days, no particulate matter was being provided for the green *Hydra.* I do not know what leaks out of *Hydra,* but it is all being caught by the algae with the light on, not being caught with the light off.

PROVASOLI: You have not extended this beyond the 28 days?

SLOBODKIN: Not for weight. We then were curious as to how long the green *Hydra* could make it without any food. We still have green *Hydra* after 91 days of no feeding at all. The brown *Hydra* all died after 42 days.

I think that is the best I can do at the moment. The experiment is

being repeated, however. It is the kind of thing that the space agencies ought to love. Here is this little thing sailing off into the wilderness in a complete little aquarium—a balanced aquarium, all in the skin of the *Hydra.*

SANCHEZ: I was once asked to mail some snails for an aquarium in fresh water, so before doing it I made an experiment to see if these animals would stay alive in a closed bottle. I put some into a penicillin jar with a glass stopper, and I sealed it with paraffin; there was a certain amount of water inside, and a certain volume of air. I left it there and checked one or two weeks later—that being the time the bottle would reach the man, so that was enough. I left it lying there and forgot about it, and after five or six months, putting a room to order, I found the bottle completely sealed and the animal alive inside. It had not more than six or eight cc. of water and two or three cc. of air.

PROVASOLI: We can sent it to Mars and get it back.

BAYLOR: Was it in the sunlight?

SANCHEZ: Not in the sunlight but in room light.

SLOBODKIN: May I add another bit to this? The weight per animal is rather remarkable. The green *Hydra* in the light weighed on the average 23 micrograms and those in the dark weighed 25 micrograms. The total weight of all the *H. oligactis* in the light was 73 and in the dark 77, and the mean body weights in light and darkness were 7 micrograms and 9 micrograms, respectively.

FAGER: What was the initial body weight?

SLOBODKIN: Typically, the stock cultures were 100 to 200 micrograms per animal and they were essentially the same for both green and brown *Hydra.*

FAGER: So in both, individual animals had reduced in size?

SLOBODKIN: Both had reduced in size for the individual animal, and the green *Hydra* simply fractionated itself into a whole series of small animals.

BARKER-JØRGENSEN: * I should like to present some new data on the feeding mechanisms in the appendicularian, *Oikopleura,* which only partially feeds in the same way as the tunicates, generally. *Oikopleura* is shown in FIGURE 11, with a tail that can be used for water transport and swimming. The pharynx constitutes the larger part of the animal; it is perforated by two spiracles furnished with cilia, and it contains

* Editor's Note. This material was actually presented during the last day of the conference, but the record has been inserted here because of better continuity.

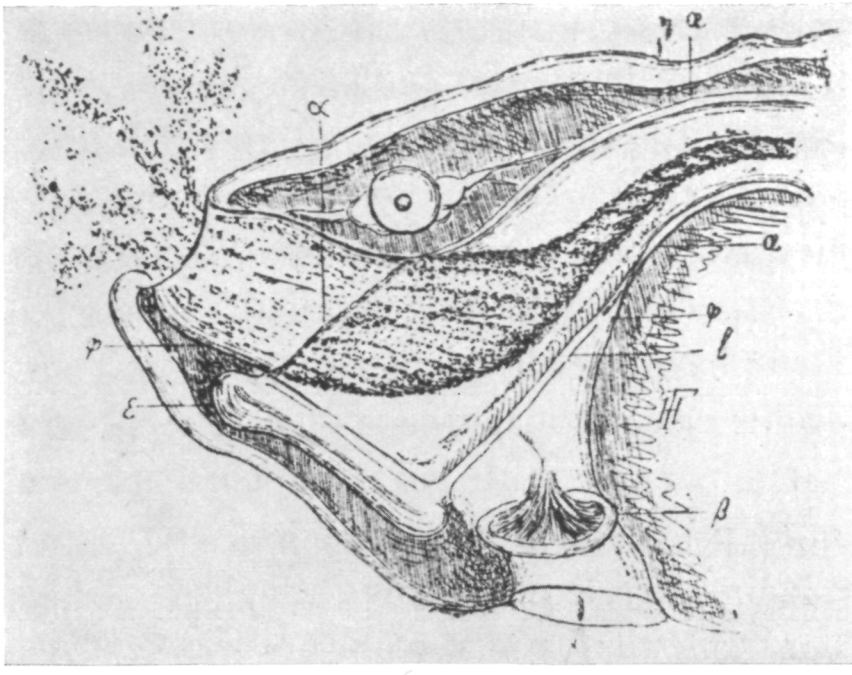

FIGURE 11. *Oikopleura,* lateral view. The figure shows how particulate matter in the feeding current is retained in the mucus net extending from the peripharyngeal grooves (∝) into the esophagus (α).β, spiracle, ε, endostyle. [After Fol(59).]

ventrally an endostyle which is producing mucus. This mucus will be transferred to the peripharyngeal grooves, and formed into a conically shaped net that is twisted at its end into a string by the activity of the cilia of the esophagus, which furthermore draw the mucus string down into the intestinal tract. The cilia of the spiracles maintain a current of water through the mucus net which retain food and other particles in the water.

This was the description of feeding given by Fol(59) in about 1870, but later it was discovered that it was not the whole story. Appendicularians were found to produce epidermal structures that sometimes enclose the whole animal in a house-like structure; this is the case in *Oikopleura.* FIGURE 12 shows the *Oikopleura* sitting in its house. Lohmann(60) described the function of this house in the feeding of the *Oikopleura.* It appeared from Lohmann's investigation that the animal is not taking in the current of water directly from the surroundings, but the water is passed through a special particle-concentrating structure which is shown diagrammatically in FIGURE 13.

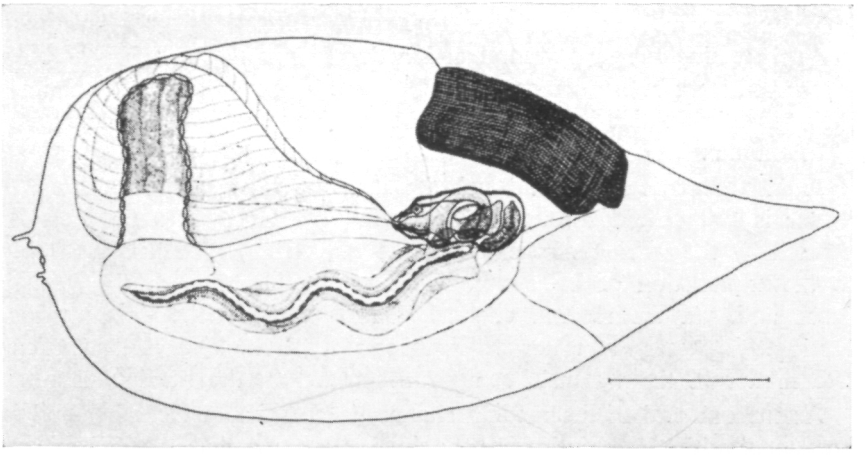

FIGURE 12. *Oikopleura dioica* in its house, semidiagrammatically. Scale 1 mm. [After Körner(61).]

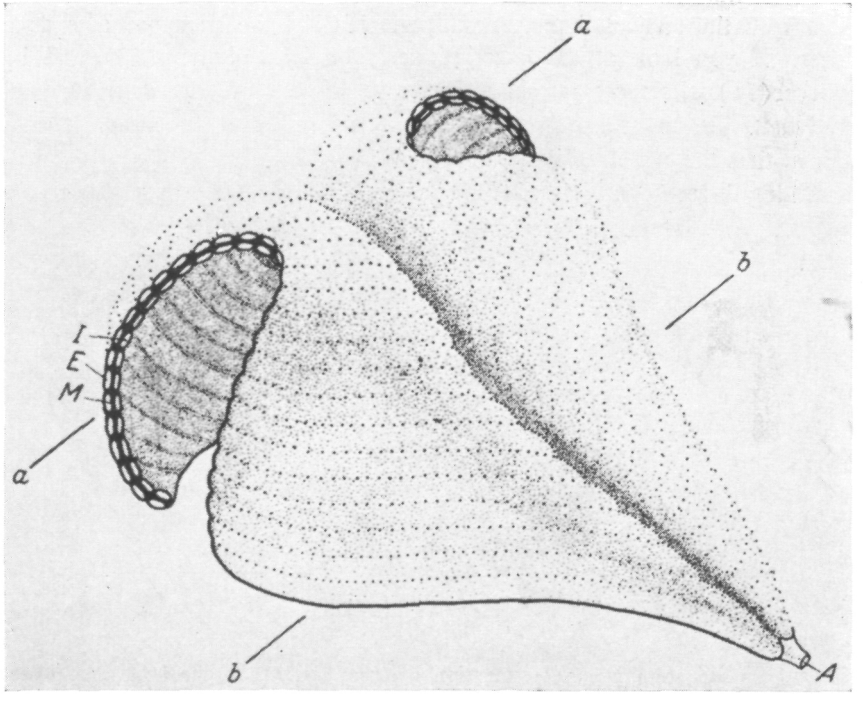

FIGURE 13. Diagrammatic representation of the particle concentrating structure of the house of *Oikopleura,* after Körner(61). I, incurrent tubes; E, excurrent tubes; M, separating membrane; a-a and b-b, levels of the cross sections shown in Figure 14.

The figure indicates that the structure is formed by two layers of parallel-running tubes, a ventral and a dorsal layer. The tubes of both layers and from both sides open medially into a common median channel, the one end of which is closed, and the other connected with the mouth of the animal.

A diagrammatic section through the structure is shown in FIGURE 14. Water is transported through the structure by the hydrostatic pressure exerted by the waving of the tail in the tail chamber. Thus, according to the explanation of Lohmann, water is entering through the ventral tubes and, via the median channel, leaving through the dorsal tubes. During this passage of water which takes place from both sides, particulate matter in the water is being concentrated in the median channel.

As the one end of the median channel is closed and the other end is connected with the mouth of the animal, it means that the *Oikopleura* is inspiring a more concentrated suspension of food than ordinary sea water.

The question is, then: How does the concentration of particles take place in this structure? In text books and other reference works that deal with the subject, it is generally stated that the structure acts as a filter. If you look at the descriptions given by Lohmann(60) and by Körner(61) who recently reinvestigated the function of the structure, you find that they are more reluctant about the mode of function. Körner thinks that the structure is acting partly as a filter, but also that there is a settling down of particles in the median channel, although it is not pos-

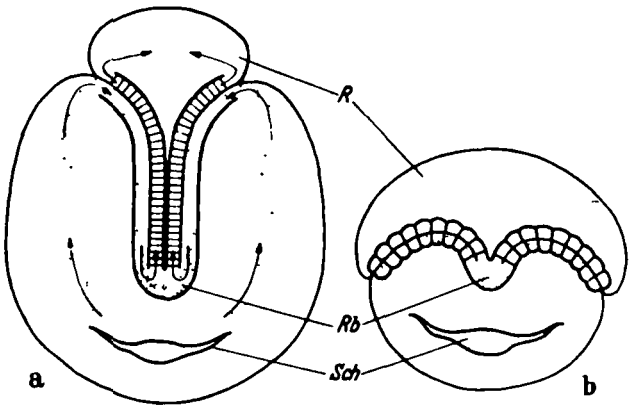

FIGURE 14. Diagrammatic representation of cross sections of the houuse of *Oikopleura* at the levels indicated in FIGURE 13. The arrows indicate the direction of water flow through the house and the particle concentrating structure. R, dorsal chamber; Rb, median channel in which the suspended particulate matter accumulates; Sch, tail in the tail chamber. (After Korner(61).)

sible to see how these two principles can be working; there is no filter to be seen, and apparently no conditions for effective sedimentation of particles in the median channel.

The system might work, however, if the membrane separating the incurrent and excurrent tubes was permeable to water but not to the particulate matter in the water. If the membrane was semipermeable you would have a gradual transfer of water across the membrane and this would result in increasing concentrations of particulate matter as you move towards the median channel. E.J.Fjerdingstad from the Laboratory of General Zoology, University of Copenhagen, and I therefore found it of interest to see what is the fine structure of this membrane.

FIGURE 15 shows a photograph of a transverse section through the structure, cut with a razor blade. This and the following preparations have been made by Fjerdingstad. It may be seen that, in fact, the structure is not built up by ventral and dorsal tubes, running parallel, but consists of a ventral space and dorsal tubes which arise from the folding of the membrane. However, the tubes are not completely separate. The fine structure of the membrane separating the incurrent and excurrent spaces or tubes is shown in FIGURE 16. You see very clearly in the electron micrographs that the membrane is in fact very porous.

BAYLOR: Before you leave that, can you give us the dimensions?

BARKER-JØRGENSEN: You see the dimensions better in FIGURE 17, which represents a partially tangential section. You see very clearly that the membrane is a net with thick longitudinal, and thin transverse fibrils. The distances between the heavy fibrils are about .8 and between the fine fibrils about 0.1μ. This means that particles larger than about 0.1μ in diameter will be retained efficiently and they will concentrate right at the place where the animal is taking in his food current.

STRICKLAND: This is a beautiful dialysis membrane, then.

KANWISHER: Still working on a molecular scale.

CONOVER: Do the membranes actually end at this particular point? Is there some water that is actually making the circuit that you described before, or do you think it is all passing through the membrane?

BARKER-JØRGENSEN: Some water can pass round via the median channel to the excurrent tubes because Lohmann and Körner found that the excurrent tubes get clogged up regularly by particles. After a certain time the animal therefore has to discard the house and build another one. Apparently they can do this several times a day. I think they can make a new house up to six times a day.

STRICKLAND: Another sort of molt. What happens to the old houses?

BARKER-JØRGENSEN: They are just left. They have a special mechanism by which they can escape from the houses, an escape reaction.

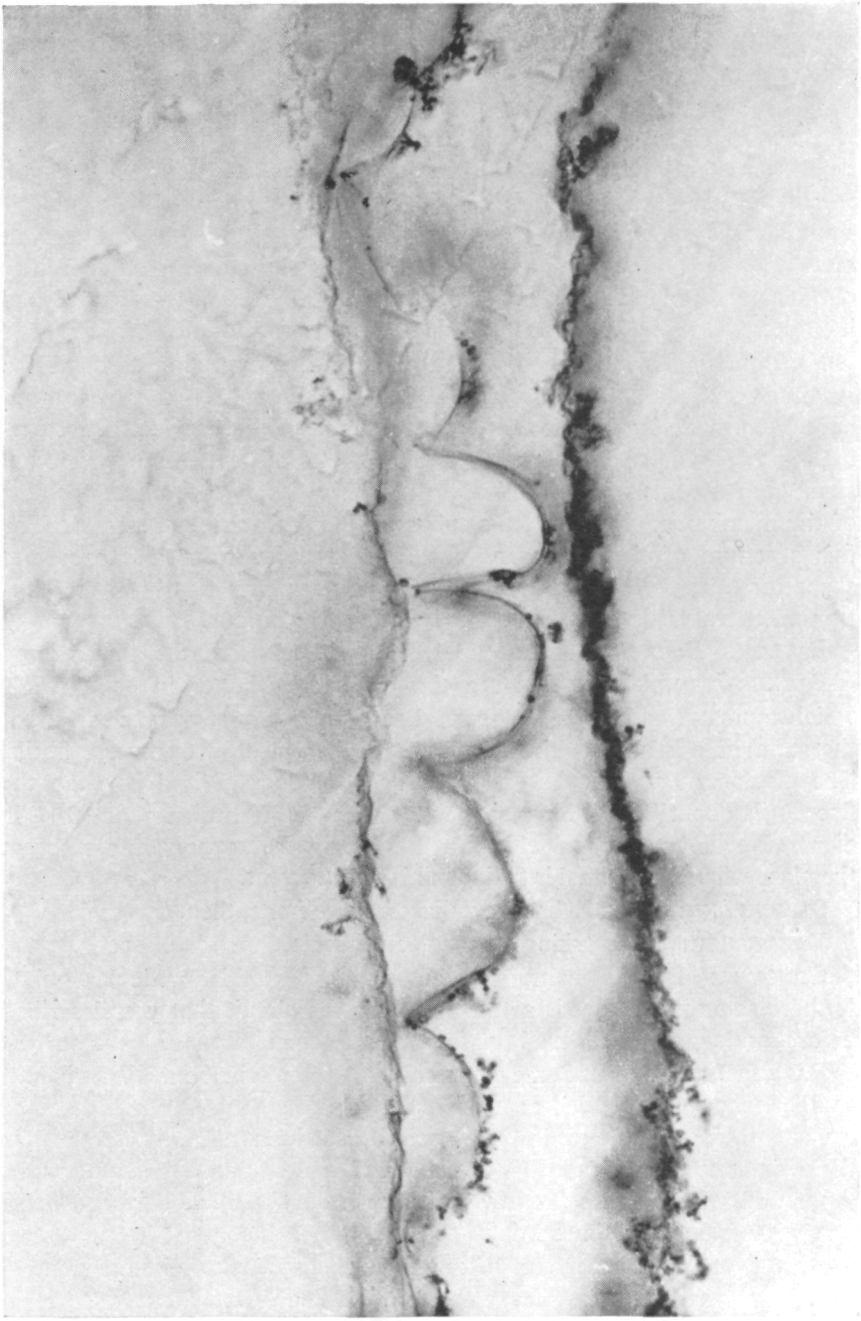

FIGURE 15. *Oikopleura.* Transverse section through the incurrent (*lower*) and the excurrent compartments of the particle concentrating structure. (Original, E. J. Fjerdingstad.)

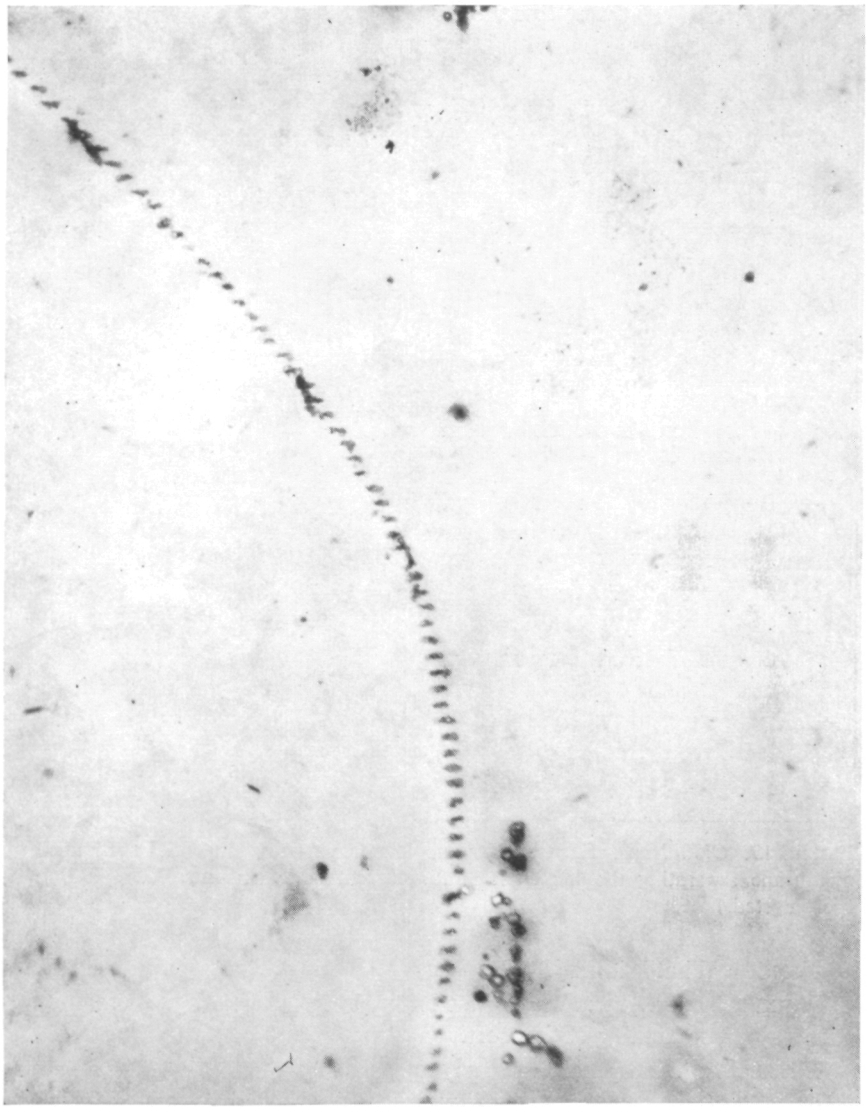

FIGURE 16. *Oikopleura*. Electronmicrograph of a cross section of the folding membrane separating the incurrent and excurrent compartments. (Original, E. J. Fjerdingstad.)

STRICKLAND: Do these things ever form an appreciable biomass, do you think?

BARKER-JØRGENSEN: I do not think so. I believe that they are extremely delicate. I have some figures for the thickness of the walls and they are a small fraction of a micron.

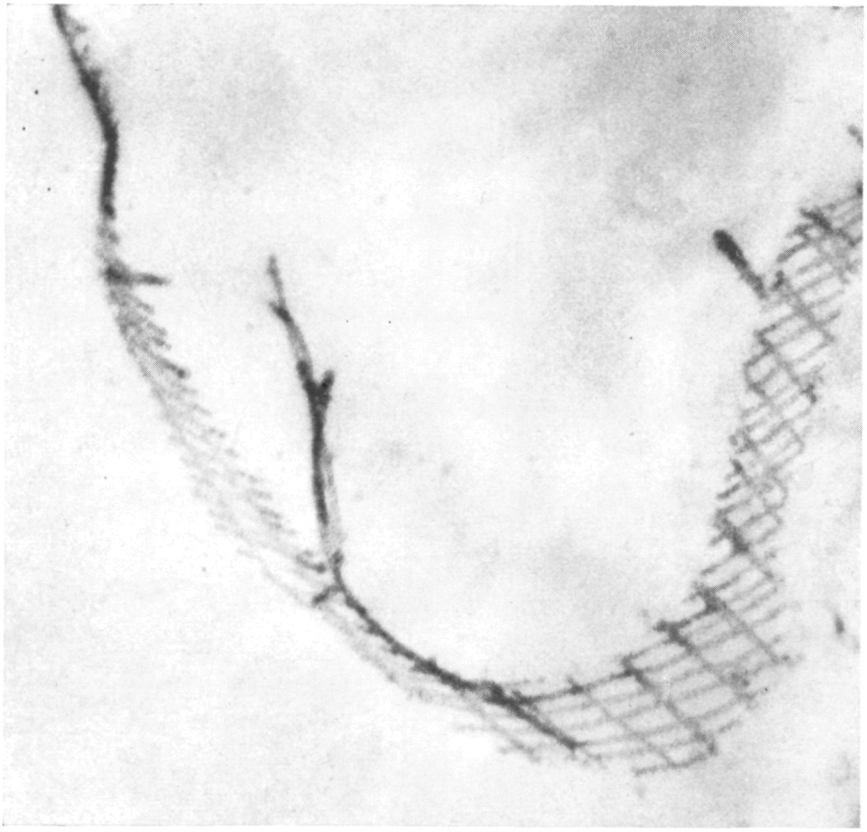

FIGURE 17. *Oikopleura.* Electronmicrograph of a partially tangential section of the membrane separating the incurrent and excurrent compartments. (Original, E. J. Fjerdingstad.)

YONGE: What is it made of?

BARKER-JØRGENSEN: We do not know, but you would guess mucopolysaccharides, something of that sort.

COSTLOW: What part of the body makes it?

BARKER-JØRGENSEN: A special area of the epithelium, where each cell makes its special part of the house.

STRICKLAND: This has been observed, has it?

BARKER-JØRGENSEN: Yes, this has been observed. Histologic studies have shown this.

STRICKLAND: These have not been cultured enough to watch the house-building in the laboratory?

BARKER-JÖRGENSEN: No, but you can follow how the house is secreted

by the epithelium in histological sections. When the house is formed on the surface of the animal it is blown up, exactly how I really do not know. But presumably at some stage the action of the tail produces a hydrostatic pressure inside the house which will blow it up to its normal size, and then it is extremely delicate and very difficult to work with.

The reason why the food-concentrating structures previously were wrongly described is probably because they have not been sectioned so that the detailed structure had to be inferred from observations made on the whole house under the microscope. Fjerdingstad, however, was able to section the food-collecting structures as you see in the Figure.

COSTLOW: Is there a time sequence in the preparation and blowing-up of this thing?

BARKER-JØRGENSEN: Probably, but I do not know.

COSTLOW: I wonder if it were set up before it was properly prepared, whether it would ever be functional. Is it possible that the substance would harden before it was properly prepared—and then it would never be functional?

BARKER-JØRGENSEN: That is possible but I really do not know. What really happens remains to be seen because there are many appendicularians that produce structures that are not investigated at all, so I think this is a very rich field to study the lines of evolution.

BAYLOR: The parrot fish makes itself a house like this every night. Perhaps you might better say it is a tent. Like Penelope, it spins its veil every night, a veil that completely envelops the animal from the mouth backward, and I have no idea what the adaptive value of it is.

FREMONT-SMITH: This is a real fish?

BAYLOR: This is a real fish, the Bermuda parrot fish.

FREMONT-SMITH: Is that tent made of a mucopolysaccharide, too?

BAYLOR: I suppose so. I do not know what the chemical structure is.

FREMONT-SMITH: Does it protect the fish?

BAYLOR: I do not know against what. I have no idea what it is for.

SANCHEZ: Polychaetes make themselves a tube which is rather transparent.

GONOR: By what method do you obtain *Oikopleura* with a house in good condition so that this can be studied? I have only seen a single intact one.

BARKER-JØRGENSEN: It took some years. I got the idea about the function of this food-concentrating device several years ago but it was not until a few months ago that we succeeded in getting the house. But there is a small fjord close to Copenhagen where *Oikopleura* is very common in the autumn. They are so numerous that you can just put a bucket in the water and take them very carefully out. Fjerdingstad had his fix-

atives ready and succeeded in having about 30 houses fixed in a reasonably good state. They were fixed in potassium permanganate.

LASKER: Just an aside, the *Oikopleura* is a favorite food organism for plaice larvae(62); as a matter of fact, they feed almost exclusively on it for a short period in their life cycle.

YONGE: I want to mention a very interesting group of bivalves, the Tellinacea, in which the siphons are separate. Genera such as *Tellina, Macoma* and *Abra* are world-wide in distribution. They live at some depth and with these long inhalant siphons suck in the surface layers of the bottom like a vacuum cleaner. You can see this detritus going down in a solid mass into the mantle cavity.

No system of mucus membranes could operate here. The mantle cavity is absolutely filled with these deposits; after a minute or so the animals expel 90 per cent of it and then take in another lot.

These Tellinacea occur in enormous numbers within any suitable substrate, particularly on muddy bottoms where there is much detritus. The problem is what exactly are they getting out of the bottom. I suppose it is a mixture of organic matter, at various stages of disintegration, plus bacteria. One knows really nothing about what these animals are actually digesting.

PROVASOLI: Very much the situation of the earthworm.

YONGE: Yes, I suppose you are right. Still, they must rely on decaying vegetable matter—a little higher up, perhaps, a little more tangible in the case of the earthworm, or do you not think so?

PROVASOLI: I think there is just as much roughage in the earth as there could be in the mud, or even more so.

FAGER: There is fairly good evidence that a lot of terrestrial organisms that eat decaying vegetable matter are, in fact, eating fungi and that the latter constitute a major part of their food.

PROVASOLI: Or yeast.

SLOBODKIN: MacFadyen* seems to be convinced that many of these soil fauna transport fungi through the soil with the burrowing activities. It is a matter of inoculating buried organic material with fungi.

FAGER: That process certainly occurs in decaying wood.

REEVE: † I want to say one or two words about feeding in *Sagitta* before the meeting ends, because I have made a few observations on it(64, 65). It is a plankton predator. It is often, as many of you know,

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* Amyan MacFadyen, University College of Swansea, Wales, personal communication.

† Editors note: This discussion was actually presented near the end of the conference but the record is inserted here for better continuity.

a very important animal in the plankton community because it is often one of the few animals which predate on things like the copepods. There is little known as far as live animals go because, so far, they have not been easy animals to keep in the laboratory, and the only record, I think, is from one of Doctor Yonge's students who kept them alive for just over 24 hours in Plymouth.

I have been working with *Sagitta hispida* down in Miami and we have been able to keep it alive now for over three weeks in sizable numbers. When kept in very large vessels, in large aquarium tanks, they have been kept for a long time, but the experiments that I wanted to do with them I needed a large number of animals and they are extremely difficult things to get out of a holding tank because they are quite transparent and they are extremely difficult to find. One cannot do too much to them because of the great danger of damaging them.

So far, I have kept them for three weeks in small vessels in which they have been isolated in individual trays, very much the sort that Doctor Costlow probably uses for decapod larvae, in volumes of about 50 ml.

I keep them isolated because they are carnivorous, they are voracious animals, and they will eat each other if they get half a chance, which destroys a lot of experiments.

STRICKLAND: There is always one left, though.

REEVE: In this context, I might say a little about starvation of these animals. Working with adults, I have kept animals alive without food about as long as I have kept them alive with food, but it can be seen that animals which are fed, again on good old *Artemia nauplii,* do grow to a certain extent and also develop their ovaries and they will even release the eggs. A reversal of these trends occurs in starved animals.

We were talking earlier in the week about filter feeding herbivores and how in my case, and also Doctor Conover's case, one could get to a level of concentration of food in the medium so that the herbivores ceased taking in more food, and this is very similar in the case of *Sagitta* feeding on *Artemia nauplii.* For instance, an adult animal 8 mm. long has a maximum ingestion rate of about 50 *Artemia nauplii* per day (FIGURE 18). Even if *Sagitta* is presented with over 200 or 300 *Artemia nauplii,* it prefers to consume about 50.

If you work this out on dry-weight basis, it amounts to a preferred ingestion rate of approximately 64 per cent of its own dry weight of food per day. I do not think there is anything particularly magic about this figure. I am certain it may well be higher if it were feeding on certain copepods, because the *Artemia nauplii* are slightly small for it.

It does have a distinct diurnal pattern in feeding. If the feeding rate

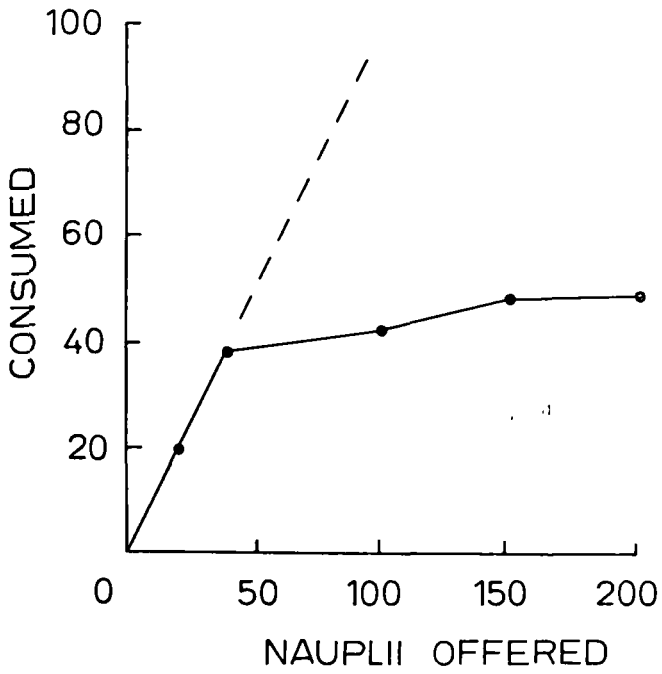

FIGURE 18. Number of *Artemia nauplii* consumed over 24 hr. by *Sagitta hispida*, 8.5 mm. long. The same curve is obtained whether the animals are continuously illuminated or in darkness, in small or large vessels. The broken line indicates the form of the curve which would result if, however much food was offered, it was all consumed.

is measured twice every day approximately at 12-hour intervals, after a certain initial day or two in the laboratory, in which rather peculiar results occur, a very definite feeding pattern can be seen where during the nighttime period of 12 hours it will ingest something like about 30 *Artemia nauplii* perhaps, and about 15 or 20, sometimes less, during the daytime. I have had this cycle maintained quite regularly for over ten or twelve days.

STRICKLAND: In continuous light?

REEVE: No, under the natural conditions of the area. This business about light and dark is of interest in this animal because it does have a pair of very simple eyes but these probably act more as a light meter than anything else. If the animals are kept for the whole 24-hour period in total darkness, or in light for the whole 24-hour period, they consume the same number of *Artemia nauplii* per day.

STRICKLAND: How do they do it?

REEVE: I do not know, of course. All over its body *Sagitta* has thin,

very small bristles which are called tangoreceptors, implying that they are the means by which the animal senses things around it. I presume that these are the sense organs by which the animal detects its food. I have no way of knowing at the moment because I have not had a chance to get to that.

CONOVER: Are these things characteristic of all the species or are they so conspicuous only on this animal?

REEVE: Nothing is conspicuous in *Sagitta,* though these structures are typical of the phylum as a whole. You do not actually see these unless you know what you are looking for.

YONGE: The whole thing is transparent, is it not?

REEVE: Yes, the whole thing is quite transparent. It is a question of observing them in the right lighting conditions.

BAYLOR: There is no lens in front of this eye so that you believe it probably does not form an image?

REEVE: No. It is a simple pigment-cup ocellus of the inverted type.

MCLAREN: On this question of eyes, doesn't Sir Allister Hardy(66) describe *Sagitta* as more or less fixing its prey with its eye, darting through several centimeters of water to catch it?

REEVE: This is exactly how it seems to catch its food, yes.

MCLAREN: And yet you do not feel this is seeing?

REEVE: I do not think so, but I do not know. The evidence, so far, is that the animal will not touch anything which is not moving. This does not mean to say it is not recognizing it by some form of movement, of course.

STRICKLAND: How does it do it in the dark?

REEVE: This is the function of these presumably sensory bristles.

STRICKLAND: You mean, it feels water currents?

REEVE: Yes.

STRICKLAND: Does it wait until one hits it?

REEVE: It gives it a sense of direction. I think there are some possibilities that the tangoreceptors, as they are called, are nervated, but these are some old histological studies.

FREMONT-SMITH: Would they be chemical receptors or touch receptors for water movement?

REEVE: I presume that they would be receptors for water movement or vibration.

FREMONT-SMITH: Rather than for chemical substances?

REEVE: Yes, there is another area of the animal which has been considered to be possibly an area of chemical sensitivity, although, again, few experiments have ever been done on the live animal. It could possibly be chemical but I doubt it.

SANCHEZ: Will it dart at any moving object or only at food substances?

REEVE: I have not, so far, given it a moving object which it could not eat. I have given it objects which it could eat, which were not moving, and which it would ignore completely. For instance, if one can hold these animals for a day or two until they are quite ravenous (even in two hours the food is completely emptied from the gut), and then gives them a mixture of *Artemia* eggs and *Artemia nauplii,* which are roughly the same size, they will go for the *Artemia nauplii* but will not touch the *Artemia* eggs.

STRICKLAND: Have you tried fine minced meat, either meat or clam?

REEVE: No, but with live plankton, especially if *Sagitta* are starved, they eat these very rapidly. I have tried this with plankton which I have killed by warming it up very rapidly to something like 35°C., and cooling it very quickly, so that the whole process does not take more than three or four minutes, and then putting it in with the starved *Sagitta,* but they will not touch this nonmotile plankton.

SANCHEZ: You can collect that on a column. You can have the eggs from dead animals falling through the column and they will—

REEVE: Animals which are simply moving in relation to a particular point, such as the animals which I would be putting in, the dead plankton animals, would not be consumed by *Sagitta.* These would be moving in relation to a fixed point, nevertheless, by virtue of the water eddies set up in the experimental vessel.

BAYLOR: What is the general concept of vibration that they detect in the water; is this in the nature of a bow wave or a shock wave, or is it a sound wave?

REEVE: I do not know. I would presume it is either some sort of shock wave, or perhaps low frequency vibrations set up by the swimming appendages of the prey.

YONGE: You have no idea whether the *Sagitta* has to be oriented in a particular way in relation to the food object?

REEVE: The animal, as was said by someone just now, will only move forward toward a piece of food. I have never seen it turn around and chase after something.

GONOR: That is a very important point if it moves forward and also toward a piece of food. Is this an observation, that always when it dashes forward, it does so at a piece of food?

REEVE: No.

GONOR: It is not necessarily a directed dash forward? It could dash forward and, if it happened to hit something, eat it. That may be the mechanism of feeding, but a mechanism of dashing forward with direction at something is, of course, more precise and different.

REEVE: I might say that in the experiment where the animal eats some 50 *Artemia,* that only amounts to one every half hour. The animal moves more frequently than this, but if the animal is put in 50 ml. of liquid in which there are more than 50 *Artemia,* it will eat about 50. If it is put in 1000 ml. of liquid it will also still eat about 50 *Artemia.*

YONGE: If it were just 50 it would go through the whole lot?

REEVE: Oh, yes; when there are less than 50, it goes through the whole lot, unless they die before they are eaten.

BAYLOR: Does it take much longer in a large volume of water than it does in a small volume of water?

REEVE: I am talking about an experiment where I would put, say, 100 food animals into either 50 or 500 ml. of water, and then count those remaining uneaten after 24 hours.

COSTLOW: What would happen if you put a mirror at one end of the vessel?

MCLAREN: I think Doctor Reeve's evidence is fairly sound, really. We are nit-picking.

STRICKLAND: Have you any views as to why these things are so transparent? It puzzles me that you have animals, so invisible, buzzing around there. Do you think it is to remain unobserved?

MCLAREN: Surely that is not a real question. Why are you not transparent?

FOGG: So as not to interfere with photosynthesis, which they depend on.

PEARCE: Doctor Stephen Wainwright* is conducting an investigation on the transparency of animals in the sea, and it turns out that *some* of these animals actually are not transparent, or as transparent as you might think they are. They are opaque, really, when they are in the water. In other words, they are quite visible. He gave a seminar recently for our group in the Systematic Ecology program and discussed a number of these things.

FREMONT-SMITH: They only look transparent.

PEARCE: They look transparent to us but he has been using a special procedure to measure refractive indices and things of this nature. It turns out that many things which look initially to be transparent are not. Some indeed are, but quite a few are not. In those that are transparent, the standard explanation is that they are dilute and homogeneous. According to Doctor Wainwright, this is not true. Transparency lies in submicroscopic structure.

MCLAREN: Does not McAllister(67) of the National Museum of

* Personal communication.

Canada have a very interesting viewpoint on the lack of gut transparency of some of the bathypelagic fishes, which are otherwise virtually transparent? The gut is lined with these huge melanophores, which make it very black, and he suggests this is to prevent the leaking of light from ingested microorganisms when they sort of go through a violent phosphorescence—which is a fairly good idea.

REEVE: I have also done some other feeding experiments with *Sagitta*. I take them out of the plankton in which they are living and after the *Sagitta* have been starved for a while, simply feed them a mixture of the plankton. The 8 mm. size chaetognaths seem to prefer adult *Acartia* which are about 1.1 to 1.3 mm. long, perhaps a little less. Animals which are smaller than this and animals larger than this they tend not to eat as many of, but if they are given only very small animals on which to prey, juvenile stages of copepods and barnacle nauplii, they will not quibble about eating them.

At the other end of the scale, the largest animal which an 8 mm. *Sagitta* has consumed to my knowledge is a *Lucifer,* which is a crustacean which got up to 15 mm. long. So these animals, if the situation demands it, will eat an extremely wide range of food. If the situation does not demand it, they have a definite preference for size.

STRICKLAND: They will eat these big fellows by worrying at them and picking them a bit?

REEVE: In a way the actual feeding mechanism of *Sagitta* is somewhat analogous to that of a snake because it eats the thing whole, whatever it is. I have often observed two *Sagitta* to attack each other, when they have been starved and in the same vessel. Usually they attack each other head on. *Sagitta* has an armature of hooks on either side of the head, perhaps eight or nine hooks, it depends on the species. Around the mouth they have two rows of teeth. The whole of the head is extremely muscular and can expand a tremendous amount, and if they attack each other head on, they can fight in the dish up to a quarter of an hour. It just depends on who gets his spines outside those of the other one first, and whoever is successful in this has won the game almost inevitably, unless the other one can wriggle free; but almost invariably when the one gets his spines outside the other one, he just works him in and takes him right down into his gut, and you can see the other one in the gut the opposite way round.

Sagitta is often made out to be voracious in the sense of being wasteful in that if it has a tremendous amount of food to eat it will just go on eating. This is not the case. If it has been living under conditions of good food supply, it does not keep eating; it does not keep its gut full. In fact, it eats on an average one *Artemia nauplius* every half hour.

But if it is previously starved, of course, it will fill its gut completely at one session if the food is available. It will go on taking in food until the gut is quite full of *Artemia* nauplii, or whatever it is given.

STRICKLAND: Has anybody made metabolic rate studies?

CONOVER: Jack Beers(68) has done some work at Bermuda. He has also done some work on excretion of nitrogen and I think also phosphorus. I do not know the results of these experiments.

MCLAREN: I attempted to do some respiration measurements on *Sagitta elegans* but I found them extremely touchy, just as you did. They were usually dead at the end of the experiment.

REEVE: The dry weight in a large 8 or 10 mm. animal is approximately 0.2 to 0.3 mg.

CONOVER: That is about the same as for *Calanus finmarchicus.*

REEVE: The advantage with *Calanus* is that it can be confined in a smaller space than the same weight of *Sagitta.*

MCLAREN: The average adult *Sagitta elegans* off Plymouth would have about 100 micrograms of carbon.

REEVE: Those are bigger. *Sagitta hispada* is quite a small species. Anyway, the point I was making was that *Sagitta* takes up a lot of space but it is a very small animal, and this is where respiration experiments get into difficulties, because one can just measure the respiration of a single copepod in two or three ml. of water, whereas to measure the respiration of *Sagitta,* the length of the experimental vessel has to be at least 1 cm., if the animal is simply to lie in the vessel without moving.

If it is to make any sort of movement in any sort of natural way, to be able to make one dart forward, it would have to live in something like 20 ml. of liquid. When you start putting animals together they start eating each other over the course of a respiration experiment, because they are crowded. I have one or two results but I have very little faith in their value. I think Jack Beers has done something here(68).

CONOVER: I do not know how he has done it, if it is this much of a problem.

REEVE: Yes, you can get respiration figures, but—

CONOVER: I cannot see how you can get numbers for nitrogen excretion from one animal.

REEVE: I doubt if he has done it on one animal.

CONOVER: He must have done it with more, in which case if they are eating each other—

REEVE: You can take a chance; you can sometimes get experiments where you have 10 animals and you can finish up with 10 at the end of three or four hours.

STRICKLAND: This is a similar problem to thin, long larvae, is it not?

LASKER: No, it is not. It is a quite different problem. Larvae will butt their heads against the glass, but will not die over the course of a respiratory experiment. As a matter of fact, they stay quite normal so that you can take them out and put them in a beaker, and they will start swimming. It is quite a different problem.

LASKER: With *Clupea,* the herring, you can use an anesthetic to tranquilize the larvae and get a basal rate. I think there are similar things for invertebrates.

COSTLOW: It will give you some sort of range.

BAYLOR: It seems to me it would be an interesting thing to test whether or not the tangoreceptors are actually receiving some sort of sound perturbations in the water by placing a lollipop hydrophone in the water that you play sound into, so that you could measure what level and frequency of sound would serve to prevent their predation of moving particles.

REEVE: Yes, this might also be approached through chaetognaths (*Pterosagitta*) which have two enlarged tufts of these organs. Perhaps these might be put out of action in some way by simply cutting them off or doing something else with them. It is something which will have to be done very shortly.

SANCHEZ: May I introduce a question here, maybe to Doctor Yonge, who made a comment? I have observed frequently that bottom marine animals, carnivores, predators, would eat members of their own species, with the only condition that the one that is eaten is not in a very good, healthy state; I have observed this in *Artemia,* in starfish, and in fresh water *Valdivia* quite often. I do not know whether those that were not eaten were healthier than the ones that were eaten.

REEVE: I think this is extremely difficult to determine. Animals which are not healthy are recognizable and I can always recognize an animal which is about to die, as most people can with the particular animal they are working with at the time; but I cannot say of two animals attacking each other whether one is less healthy than the other.

I would like to say something about the aspects of cannibalism. Of course, if I have had them in a 2 or 3-ml. dish, in order to have a few animals there, they are far more crowded than they are in the sea, since in natural conditions they range something between .1 and 20 or 30 per cubic meter. In other words, they are very spread out, far more spread out than their food organisms, because in numbers they rarely exceed between 1 and 10 per cent of the total numbers of zooplankton animals of the sort that would provide their food, mostly copepods. So it may be that they never needed to have a particular mechanism which prevented them from eating each other.

CONOVER: The distribution of these animals should be hyperdispersed, should it not? That is, it should be more than random in its distribution.

REEVE: Its distribution is certainly patchy.

CONOVER: It is patchy perhaps over the broad section of the ocean but on a smaller scale—

MCLAREN: You mean, they should tend to avoid one another?

CONOVER: If they do not, and they contact one another, there is only one left.

REEVE: If they can get an animal which is more their preferred size for consumption, they would not eat another *Sagitta* of their own size, in any case.

PROVASOLI: How long could you maintain them in your condition?

REEVE: I could maintain them individually in 50 ml. for about three and a half weeks so far.

PROVASOLI: And in a larger container?

REEVE: In larger containers where I have put a lot together, I can also maintain them for about three or four weeks. Their numbers are progressively reduced due to both natural mortality and cannibalism.

PROVASOLI: But that does not happen when one maintains them individually in 50 ml. What do you think are the causes of mortality?

REEVE: The reason for mortality may well be that they are too confined, because they can shoot from one side of the little plastic tray to the other in one movement. In fact, they could shoot much further in one movement if they had an opportunity, and they may simply be bashing their brains out.

PROVASOLI: Have you not tried larger containers for adult *Sagittas?*

REEVE: Oh, yes, they have been kept three or four months where there are extremely few animals in a large aquarium.

MCLAREN: You have done this?

REEVE: I personally have not done it.

MCLAREN: But you have shown an upper limit of food consumption. If you keep food above that level and grow them in an aquarium and examine them, would you not get an enormous amount of valuable data?

REEVE: Yes, possibly, though in small numbers natural mortality tends to loom large, and my experiments have not as yet reached the stage of long-term designs.

SANCHEZ: This willingness to eat each other is quite striking.

REEVE: It is not really a willingness.

SANCHEZ: You cannot keep them without half of them eating the other half.

REEVE: But that was in a respiration experiment where I had 10 or

20 ml. of liquid. In other words, they were bumping into each other all the time.

McLAREN: Mechanisms to prevent cannibalism are not necessary in a well-ordered nature. You can have a perfectly viable system where cannibalism is a necessary part.

SANCHEZ: Surely, but the suggestion has been made that perhaps this large distance between one specimen and the other in nature might be regulated this way.

McLAREN: He simply said the animals are scarce in nature. He has not said anything about their microdistribution.

SANCHEZ: But something must keep them scarce in nature. There might be many things keeping them scarce, but one could be that they eat each other, if there are more than a certain number per volume.

YONGE: They are not scarce, are they? They are very common except they are dispersed.

REEVE: It is a question of the definition of "scarce." They are frequently ten times less numerous than copepods.

STRICKLAND: They seem to be commonly found in plankton on the weather ship "Papa."

CONOVER: Where is this that *Sagitta* is the only thing found?

STRICKLAND: Out on the Canadian Pacific weather ship.

CONOVER: Would it be possible to get some of these *Sagitta?* There have been a couple of people after me to get rather large quantities of *Sagitta* all by themselves, and I never find them.

STRICKLAND: If you wait for the ship to come in after four days' steaming, you might, but it is not very practical. I have only watched other people handle the zooplankton but feel fairly sure that *Sagitta* are in many samples. Its occurrence is, of course, unpredictable. I never realized that anybody thought the animal was particularly rare.

REEVE: I do not think anybody considers it particularly rare.

CONOVER: Not rare.

REEVE: Just less common than the herbivores, most of the time.

COSTLOW: Is the survival of the animal any better in a round dish than in a square dish? Some animals and fish cannot turn corners.

REEVE: Not as far as I know.

COSTLOW: At Den Helder, the Netherlands, they accidentally stumbled onto it. They put curves in the pool and now the fish are quite happy.

KANWISHER: It was the only way they could keep tunafish in Hawaii.

REEVE: I believe that sometimes in the Gulf of Maine chaetognaths can be up to 75 per cent of the total number of zooplankton by number. I seem to have this figure in my head somewhere.

CONOVER: This may be possible. I have never seen it. I know on

Georges Bank this has occurred, but I have rarely seen great concentrations in inshore waters. If someone knows where to get them regularly and in dense concentrations, I think this is worth keeping in mind.

REEVE: Looking through the literature, one gets the impression that the chaetognaths usually represent between 0.1 and 10 per cent by number of the total zooplankton animals.

CONOVER: If somebody wants biochemical quantities, though, he usually wants grams or kilograms of material.

REEVE: Yes; I am just telling you how they are distributed in nature.

GONOR: * The information that I have to contribute is anecdotal rather than analytical. This work has not proceeded to a stage of analysis but only to a stage of observation. No one is working full-time on this. These are observations which have been accumulated by people who are interested in other aspects of the biology of *Sacoglossa.* It is adequate information to pose some general questions about the nutritional biology and its ecological consequences. This is a small group of Opisthobranchs, probably not more than two hundred species worldwide. The species are usually uncommon. This means that one has to go out and search carefully to find one. I do not have figures on abundance.

They are very restricted in habitat to specific algae. Some have shells and are presumably the primitive *Sacoglossa.* These include forms in which the shell has been divided into two valves, so-called bivalve *Sacoglossa.* Most of them, however, have no shell and resemble Nudibranchs in external form and usually are so classified. These are small, at most one or two centimeters long, soft-bodied, untorted snails with various kinds of appendages on the back which are not important for our purpose but make them look like the Nudibranchs.

STRICKLAND: What is untorted?

GONOR: The nervous system has untwisted.

FREMONT-SMITH: How do they come to be untorted?

GONOR: This happened in the past from the phylogenetic sense, and also embryologically.

FREMONT-SMITH: It was twisted and became straightened out?

GONOR: Yes, and in embryology some never develop the twisting of the organs. This group is different from other Opisthobranch groups of equivalent rank in that they are not carnivores. These are herbivores and

* Editor's note: This discussion was presented on the last day but the record is inserted here for better continuity.

show great specialization of food selection, and the morphology of the feeding structures is also specialized. Because of these adaptations, it is a group to which one can address questions, mostly unanswered, about what is the nature of this high degree of dependence on a restricted food source and what are the ecological consequences of such great dependence. For example, questions about what effect can this have on the animal's population dynamics or density. What sort of role does such a specialized organism play in a community? What is the extent of their influence? They seem to be remarkably narrow.

They, in fact, seem to have gotten themselves into a blind alley of specialization. These organisms feed only on the cell sap of green algae, or more rarely red algae, of a very restricted range of species. These usually are the green algae in the Cladophorales and Siphonales. The morphological structures involved in feeding are rather uniform throughout the group in structure and in the method of use.

The feeding apparatus in this group consists of a muscular pharyngeal bulb and a radula composed of a single row of teeth mounted on a basal ribbon (FIGURE 19). Radular production in snails is continuous. The radula originates at the back end of the radular organ and the band of teeth gradually moves forward. The teeth in an anterior position near the mouth are the ones in use and in most snails these wear out and fall off as they move forward. These beasts are called sacoglossans because they retain all of their used teeth in a sac. The teeth are used one at a time and those that have advanced past the point of use cannot be brought

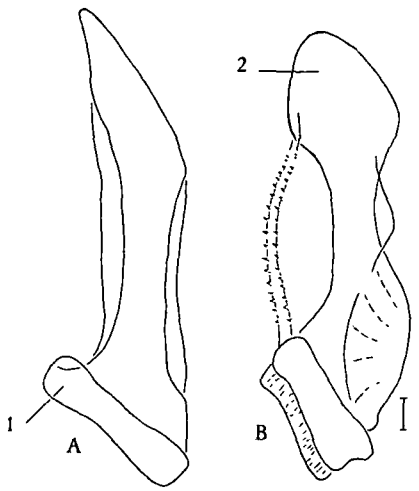

FIGURE 19. *A*. Diagram of generalized pointed sacoglossan tooth. 1. Base of tooth. *B*. Tooth of *Hermaeina smithi*. Bar equals 10 μ. 2. Terminal blade.

back into service. They do not detach from the basal membrane, however, and the entire used radula is coiled up in the sac.

These teeth are rather specialized slitting or cutting structures. From the tooth base attached to the basal ribbon arises an elongate portion ending in a pointed tip or bearing a thin terminal blade. The tooth structure is otherwise similar in all of the species, so that specialization of tooth morphology seems to be for a form of food, but not to species of algae. FIGURE 19A is a generalized diagram of a pointed tooth of the type found in the genera *Elysia* and *Stiliger,* and FIGURE 19B is a drawing of a tooth of *Hermaeina smithi,* which bears a rounded terminal blade. These Figures illustrate the general features and extent of variation found in tooth structure. In feeding, the radula is extended out of the mouth, a tooth pressed against the alga and a slit made in the cell wall. The muscular bulb is then used to pump out the contents of the cell.

CONOVER: How large are the cells that are being fed on here?

GONOR: This does not make any difference. The group feeds on a lot of things and I will go through this.

FREMONT-SMITH: How large relative to the tooth?

GONOR: There is some correlation in size but this cannot make any difference because they also feed on coenocytic algae which have no cell partitions. They can empty a great degree of material from such a tube through a single slit. I expect that if there is some physical limitation here, it is not the size of the alga cell or the form, but the thickness of the wall.

FREMONT-SMITH: Would they feed on very small ones, too?

GONOR: Yes, some feed on *Vaucheria* and *Cladophora* and other algae with separate, small filaments.

FREMONT-SMITH: When the tooth gets dull it is dropped into the sac?

GONOR: It is passed on into the sac and a new sharp one comes into place. The structures can be said to be a slitting and sucking mechanism. It seems to limit them to a type of food, but the difference in radulae between species are rather minor. This cannot be the reason for the restriction to specific algal food.

These organisms feed on only one algal species or on several related species in a genus and do not attempt to feed on others. It is not that they do not succeed. You cannot make them try, so that one wants to know what the basis for the selection of the alga is. It is not algal form, size or shape, because within the group a great variety of algal forms can be used. Some feed on microalgae; others on things we can call macroalgae, bushy things. They feed on filaments, septate filaments, or coenocytic fila-

ments or complex thalli, flat sheets and branched ones; on soft species or on calcareous species of green algae, so that this is not involved.

The selection is apparently based wholly on the behavior of the snail in respect to something chemical, external to the algae. The example that I have worked with is *Hermaeina smithi*(69). This animal is found on the Pacific Coast. It feeds on the septate filaments of a green alga, *Rhizoclonium,* in a mixed algal mat in which it lives.

The snails do not attempt to eat and starve to death in the presence of the rest of the green algae in the algal mat, species of genera which are eaten by related *Sacoglossa* elsewhere.

The diameter of the filaments of *Rhizoclonium* is not important because this *Rhizoclonium* shows a considerable variety in diameter itself. If one starves the animals and puts them in the presence of *Enteromorpha* filaments which have been selected for diameters identical to the *Rhizoclonium,* they will crawl on the *Enteromorpha* and examine it, but they will not attempt to feed on it and continue to starve. They do this for other forms as well as *Enteromorpha.*

They will select the species upon which they feed from a mixture of algae that I have presented them, so that they can detect by chemosensation the proper alga from the outside.

The detection of the proper alga is not something that simply sets off feeding, because you cannot make them feed on any other alga by stimulating them with the right one. They will select among filaments for some time until the right one is found. They will then only feed on the right one and will not go to the one next to it if it is of another species.

STRICKLAND: You think they will not even make an introductory probe?

GONOR: They will touch it, but they will not attempt to slit the cells.

Other species are definitely specialized to a single algal species. *Lobiger serradifalci*(70), a Mediterranean shelled sacoglossan, feeds only on *Caulerpa racemosa,* a large complex coenocytic alga with a thick, latex-containing sap.

Some information is available about the feeding habits of species of about sixteen genera. The species in eight of these genera are confined to one or a few species of a single algal genus. In two of the genera, the species are confined to species of two algal genera. There is another genus with species which feed on three algal genera, two of which are closely related. Then there is one genus, the largest in the group, with species feeding on algal species of four genera in three families. This is the greatest diversity of feeding at the genus level shown within the group. I am using "genera" here because this reduces us down to the least amount of uncertainty. The identifications of both the algae and the snail species are sometimes doubtful in these studies. Twenty-three species are

known to eat not more than two species of the algal genus to which they are restricted. The food specialization in sacoglossans is obviously rather narrow.

I found that despite this specialization there has been one escape which is very interesting. I have found one species, *Olea hansineensis,* which is a carnivore. It eats the eggs of other Opisthobranchs. It eats only the eggs of specific Opisthobranchs, however. It has carried over the habit in the group of being specific and this is really risky. The intertidal algae show seasonal fluctuations but the eggs of other animals show ever more remarkable fluctuations in abundance. This species feeds upon the eggs of two species of Tectibranch Opisthobranchs but will not attempt to feed upon the eggs of any Nudibranch that I had available to present to it. They also will not eat either firm or soft egg masses of prosobranch snails. The sacoglossan feeding mechanism has not limited this species to algae, but it limits it to a food which is much like the algal filament in structure. The egg masses of the prey species are composed of strings of small jelly capsules each containing an egg. *Olea* slits the capsule and sucks the egg out.

Within this group, food specialization is quite high and it is apparently based on behavioral mechanisms which restrict these species to one food source. I am very interested in what comments might be made about the selective advantage of such specialized algal feeding.

LASKER: Are there any specialized chemoreceptors in these?

GONOR: I have sectioned a number of species of sacoglossans and find no more elaborate sensory structures in these than in other Opisthobranchs. There is no other information available on chemosensation.

YONGE: There is the general point you make that in the whole animal kingdom there is no group comparable to the Opisthobranchs in which almost every species is specialized for feeding on one particular plant or animal.

GONOR: I have deliberately restricted these remarks to the herbivores to keep it short. There is actually more information known about the carnivorous animals and a little more information about their selectivity, but it is a longer story. It appears to be mostly behavior within the whole group, both the carnivores and the herbivores.

STRICKLAND: What do you mean, behavior?

GONOR: If two related species are compared, differences in food specializations are not reflected in the structure of the feeding apparatus, but in differences in behavior which result in selection of different food species.

EDMONDSON: Considering one of these specialized food species, can you point to a whole group of other animals that actively avoid it? Within

your group, it is quite obvious that the others are not eating that one because they are specializing on something else.

GONOR: Can I point to one species of *Sacoglossa* which avoids the food that another eats?

EDMONDSON: To put it another way, none of these *Sacoglossa* specialized in a species of food organism. All right, now, who else eats that particular food organism?

GONOR: These are very common intertidal algae. Things like *Enteromorpha* are eaten by other snails indiscriminately. It is very difficult to understand what they might be competing with. I know of no other group of animals which go around selecting the algae so very carefully; certainly no other group of snails. Certain abalones will select a certain kind if they have a choice, but they will eat a lot of other things, too.

I have tried to find some other group which might present a competitor to try to understand what sort of selection pressure had produced this, and I cannot really find an answer or find a competitor for either the herbivores or the carnivores, with this degree of specialization.

EDMONDSON: If there were only Opisthobranchs in the world, this would mean that everybody was competing with everybody else, and I wondered what the pressures—

GONOR: They are not abundant and not many species occur in the same place. Usually in one locality you find only a couple of species of *Sacoglossa*. They obviously are not competing with each other. There are tons of algae in the intertidal area.

STRICKLAND: Could not this selection be a hangover from something else that has now lost all importance.

SANCHEZ: I think that is a very good guess.

GONOR: Yes, it could, although I cannot imagine what it might have been. Other workers have pointed out that the *Sacoglossa* may well be an artificial group (this is counter to your theory, is it not?) And that the morphological specialization is convergence to algal feeding, but why these few algae, and why that way?

YONGE: But it all does fit in, does it not, with the general Opisthobranch pattern, that throughout the whole group individual species are specialized for one particular food organism—for fish eggs, or for a compound Ascidian, or for a simple Ascidian, or for a particular species of Alcyonarian, or what-you-will.

GONOR: If I may give one last example, there is some hope for sophistication in this field growing out of an observation on a Nudibranch in England, *Tritonia holmbergi*(71), which feeds on soft coral—an Alcyonarian which has a white form and an orange form of the same species, otherwise indistinguishable. The Opisthobranch eats white ones. It will,

if starved, eat the orange ones, but the food material passes through the gut relatively undigested and comes out in the feces, so that it is not merely behavioral. There are other physiological reasons for the food selection in this Opisthobranch. It cannot utilize effectively the orange form of this usually white food species.

SCHMIDT-NIELSEN: I just wanted to make one comment; you say you find it only in this group, but in nonmarine environments you find scores of examples of specialization.

GONOR: Aphids; koala bears. These are "marine aphids."

PEARCE: Allan Kohn, of the University of Washington, has investigated members of the genus *Conus* and has found that they seem to be relatively specific on what they feed upon(72). While in Denmark last year, I had an opportunity to observe a little toxoglossan gastropod, *Lora trevelyana,* which is quite a bit smaller than the cones which Kohn worked with. They ranged from 5 to 9 mm. in length. *Lora* has a highly developed poison apparatus and a radular tooth which apparently may be used as a harpoon in much the same way as the teeth of the cones. It is a very specific feeder on only two species of spionid worms.

A recent work by Marcus(73) in Brazil has shown that *Hastula cinerea,* a species related to the toxoglossans, is apparently quite specific in its prey. This species also feeds on worms of the family Spionidae.

Whether the rest of the genus *Lora*—and there are a great number—are specific in their prey is unknown at the present time. It is quite interesting that if quantitative samples are taken, one may collect the snail (*Lora*) and at the same time find the two species of spionids. But at the same time equally small worms of other families will be found. The latter would be of a size suitable for food, yet apparently the *Lora* prefer the spionids.

III. THE QUALITY OF FOOD

Discussion leader:
D. L. RAY
Department of Zoology
University of Washington
Seattle, Wash.

RAY: I am sure that these broad topics are things on which almost everyone here would have something cogent to say, and even the majority of people present probably have some data that will be of interest to us all.

With the general topic of nutrition, nutritional value, the biochemistry of digestion, utilization, assimilation and so on, we certainly cover a broad spectrum of approaches to the understanding of the relationship of organisms to their food. In a way, it falls into two somewhat separable categories. One is the assimilation of food substances by phytoplankton and other types of organisms that do not have, as animals do, a well-defined anatomical structure, a gut, in which the problems are essentially biochemical (although I say that with some hesitancy). The other is the activities of more typical animals where a number of other things come into account: the accumulation of food in the gut and the anatomical as well as biochemical aspects of its treatment.

Perhaps the unifying factor here is the emphasis on the basic digestive processes: which are similar throughout, which are different, what are the comparative aspects, and what, at least so far as animals are concerned, are the aspects of feeding that refer primarily to what is assimilated or utilized as opposed to, or additionally to, what is taken into the gut? It is swallowing versus use.

We have already had quite some indication that there are cases in which animals may swallow food that is not thoroughly utilized. How to determine the nutritional value of food is a question which is not always easy to answer, and there are a number of approaches. One can measure the loss of a food organism in terms of what disappears from what is offered. One can measure the increase in size or in weight or in numbers of individuals in a population; one can measure the reaction products, the production of CO_2; one can measure the amount of waste material that is produced; or one can try to form a balance between what is taken in and what is given out—that is, the difference between the two ends

of an animal, let us say.) All of these things must come into any evaluation of the nutritional value of any group of organisms or food materials, and as Professor Yonge has said earlier, it is extremely difficult to separate mechanisms of feeding, and methods of handling food from their nutritive value and their assimilation.

The topic itself is so broad that I think we ought to feel quite free to range widely and to be able to take it up at almost any point. I think we might ask Doctor Provasoli first of all if he would mind commenting in the beginning, because I know he has data of considerable interest, particularly with respect to the comparative nutritional value of microorganisms.

PROVASOLI: As Doctor Ray has mentioned, several methods can be employed to assess the nutritional value of food organisms. One of them is to establish two-membered aseptic cultures of the prey and predator. This method, by excluding all other microorganisms, permits a complete definition of the nutritional value of single species of algae.

The crustacea employed were *Tigriopus japonicus,* a frequent inhabitant of marine supralittoral rock pools, and *Artemia salina* which grows in brine flats(44). The latter is not truly marine, but both of them are very convenient experimental animals because of their resistance to variations in salt concentrations and temperature.

Several species of marine algae were tried singly. TABLE 3 shows the results with nine species of Chlorophyceae, some of which are common algae of rock pools and others of brine flats. A black half circle indicates that the food organism supports growth from newborn nauplius to adult, for *Artemia,* and two or more generations of *Tigriopus.* The white half circle indicates that the food organism is not a complete food; i.e., it permits growth up to some larval stage but not to adulthood. Our results confirm the results of Gibor(73a) on some species of algae and *Artemia* and extends them to *Tigriopus.*

It is evident that species of the same algal genus may have a different nutritional value. For instance, *Dunaliella parva* is an insufficient food for *Artemia* and *Tigriopus,* while *Dunaliella tertiolecta* is a good food for *Artemia* but not for *Tigriopus; Tetraselmis tetrathela* is good for *Tigriopus* but not for *Artemia* while *T. maculata* is good for both. This shows also that *Artemia* and *Tigriopus* are quite different in their preferences and need for food organisms.

Incidentally, I might add that the results with *Artemia* are based only on one generation, i.e., from newborn to adult, because it is laborious to carry on successive generations aseptically: the durable eggs have to be collected, dried, and kept dry for a month or so before they can be hatched by putting them in sea water. It is easier to obtain successive

TABLE 3

UTILIZATION OF FOOD ORGANISMS BY *Artemia* AND *Tigriopus* (44)

Food Organisms	*Artemia salina*		*Tigriopus japonicus*			
	Stage reached	Days to adult stage	Stage reached (1st generation)	No. generations obtained	*Art.*	*Tigr.*
Chlorophyceae						
Dunaliella sp. (brine)(1)	L*		L			○‡
Dunaliella sp. (marine)(2)	A	18	L			◐
Platymonas sp. (La Jolla)(3)	L		A	3		◑
Platymonas sp. (No. 5)(4)	A	28	A	8→†		●
Nannochloris oculata	L		A	1		○
Stephanoptera sp	A	16	L			◐
Stichococcus fragilis	L		L			○
Brachiomonas pulsifera	A	16	L			◐
Pyramimonas inconstans	L		L			○
Chrysophyceae						
Isochrysis galbana	A	18	A	9		●
Monochrysis lutherii	L		A	8→		◑
Stichochrysis immobilis	A	18	A	2		◐
Syracosphaera elongata	A	18	A	1		◐
Cryptophyceae						
Chroomonas sp	A	18	A	5		●
Hemiselmis virescens	A	18	A	1		◐
Rhodomonas lens	A	16	A	6		●
Euglenineae						
Eutreptia sp	L		A	2		○
Dinophyceae						
Gyrodinium cohnii	L		L			○
Peridinium sp	L		L			○

* Key: L, larval stages; A, adult.

† Arrow represents continuing culture.

‡ See text.

(1) *Dunaliella parva;* (2) *Dunaliella tertiolecta;* (3) *Tetraselmis tetrathele;* (4) *Tetraselmis maculata.*

generations of *Tigriopus* since adults are obtained in 15 days and the female carries in a sac 25–30 fecundated eggs which hatch in a few days.

The results obtained with chrysomonads, cryptomonads and dinoflagellates show again that an alga which is a good food for one predator is not necessarily good for another one. *Isochrysis* and *Monochrysis* are both adequate food for oyster larvae, but only *Isochrysis* supports growth for *Artemia* and *Tigriopus,* and *Monochrysis* only for *Tigriopus.*

The arrow next to the number of generations of *Tigriopus* means that the bi-membered culture (so designated) was still healthy and reproducing

at the date of publication (1959)(44). Where there is no arrow, it means that the particular species of algae permitted a certain number of generations of *Tigriopus* and no more. It is interesting to note that in *Tigriopus* it is possible to detect early signs of a nutritional deficiency. The symptoms are quite clear. At first the developmental period from newborn to adult become longer, from 10–13 days to 15–19 days; copulation and production of eggs are also delayed. In the next generation the mortality of young nauplii and copepodites becomes very high; the few adults obtained are half the size of the normal ones. If the adults succeed in copulating, the females may not produce eggs and, if the egg sac is formed, the eggs may not mature and hatch.

STRICKLAND: And in the case of *Artemia,* what does the half black circle mean?

PROVASOLI: It means that we have obtained adults.

STRICKLAND: But not necessarily happy adults?

PROVASOLI: They were mostly normal but some times they were smaller and only some of the adults laid eggs. The data on *Artemia* are not as reliable as those on *Tigriopus* because we did not try to obtain successive generations on the same food.

STRICKLAND: And this is when things start happening?

PROVASOLI: Yes, with *Tigriopus* the nutritional deficiencies may show up only after five or more generations on the same food organism. The technique is simple: the adults are obtained in 10–13 days, they copulate, then the females develop an egg sac containing 25–30 eggs. The eggs are at first greenish, then become orange red before hatching. To produce a new generation, one female carrying an orange-red case is transferred into a tube in which, a day or so before, the same algal food has been inoculated. When the nauplii appear, the old female is removed from the tube, and the larvae develop undisturbed to adults, copulate, and a new egg-carrying female is transferred to another tube to produce the successive generation and so on.

SANCHEZ: How do you interpret the lack of continuity in generations? Do you imply that through the egg some nutrients are being transmitted that are necessary? Do you imply that through the egg are being transmitted some nutrients that are necessary?

PROVASOLI: Before going into that let me show a table which has been brought up to date (TABLE 4). Only one food organism, *Monochrysis lutherii* can support alone a continuous culture of *Tigriopus* with a median time of 15–20 days per generation. We have obtained 27 generations. The sequence was interupted accidentally—somehow the medium was not good and *Monochrysis* did not grow and the young nauplii died starving. The generation time had been so regular that we were looking at the

TABLE 4

DAYS REQUIRED BY NAUPLII OF *Tigriopus japonicus* TO REACH ADULTHOOD (44)

Food Organism	Generation									
	P	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8	Generations obtained
Chlorophyceae										
Tetraselmis tetrathele	11	12	16–21*							3
T. maculata	11	11	9	9	11	15	18	14–17	19*	9
Chrysophyceae										
Stichochrysis immobilis	13	12*								2
Isochrysis galbana	11	10	10	11	13	14	14	12–20	15–19*	9
Monochrysis lutheri	11	10	13	14	19	17	19	20	17	27**
Cryptophyceae										
Rhodomonas lens	11	10	12	14	13	18*				6
Chroomonas sp	11	9	11	10	12*					5
Mixed food										
T. tetrathele + *Isochrysis*	11	11	10	10	11	14	19*			7
T. tetrathele + *Rhodomonas*	11	9	10	13	14	16	19*			7
Rhodomonas + *Isochrysis*	11	11	11	10	10	10	13	10	9	150

* High mortality at nauplius or copepodite stage, lack of copulation or egg fertility
** See text.

tubes only 15 days after inoculating pregnant female into the new tube. I have no doubt that an indefinite culture can be obtained and that *Monochrysis* is a complete food for *Tigriopus*.

When we found that many food organisms could sustain only a few generations, we tried mixtures of two food organisms. Of these only the combination *Rhodomonas* – *Isochrysis* was successful. We are now (March 1965) at the 150th generation. Since *Rhodomonas* supported only six generations and *Isochrysis* nine, they must supply all the necessary nutrients for *Tigriopus*, but not all the nutrients are produced at the level needed for an indefinite number of generations of *Tigriopus*. The algae which do not support development to adulthood, or permit only one to two generations are an inadequate food either because they produce inhibitory substances or because they supply a grossly unbalanced food.

Partial nutritional deficiencies of single food organisms can be overcome either by a mutually supplementary algal species as in the *Rhodomonas* – *Isochrysis* case, or by a varied bacterial flora. For instance *Tetraselmis maculata* allowed only nine generations of *Tigriopus* under aseptic conditions, but supports bacterized laboratory cultures of *T. japonicus* indefinitely. We have maintained the bacterized strain of *T. japonicus* for the last eight years by transferring egg-carrying females to new media pre-inoculated with *T. maculata;* no other algae are present.

EDMONDSON: It is still a good question: how can *Tigriopus* give as many as nine generations on pure *Isochrysis?*

PROVASOLI: Shiraishi and I were quite interested to find that out(74). We thought that the factor(s) might be micronutrients since many generations are required before the deficiency causes larval mortality and

infertility in the adults. When these signs appeared at the F6 of *Tigriopus* fed on *Isochrysis* and at the F3 of the culture fed on *Chroomonas,* we inoculated the four best females carrying mature egg cases in four tubes, three of them contained only a culture of the food organism and one received, besides the food organism, a nontoxic enrichment (a mixture of trypticase, liver, Oxoid hydrolysed yeast nucleic acid, a vitamin mixture, cholesterol, and glutathione). In the enriched tube, *Tigriopus* recovered normal growth and fertility while in the tubes without enrichment in one or two generations the culture died. Pregnant females taken from the enriched tubes were then cultured in tubes containing various combinations of the components of the enrichment. Only in the tubes containing either the vitamin mix, glutathione, or both, did *Tigriopus* remain normal and fertile.

The stay of one generation in the vitamin-enriched medium was sufficient to allow three or four more normal generations in nonenriched media having as living food either *Isochrysis* or *Chroomonas.* Thus, one generation in vitamins allowed enough vitamin storage for three more generations. Obviously, it is difficult to decide whether: (a) the addition of vitamins modifies the metabolism of the algae rendering them a complete food; (b) the vitamins were concentrated in the algal cells before these were ingested by *Tigriopus;* or (c) the vitamins were absorbed directly from the medium by *Tigriopus.*

SCHMIDT-NIELSEN: Which vitamins did you use?

PROVASOLI: The mixture was rich in biotin, thiamine and pyridoxine, but contained also pantothenic, nicotinic and folic acids, riboflavin and inositol.

STRICKLAND: In the case of *Dunaliella parva* which was an incomplete food for *Artemia* and *Tigriopus,* did it appear to be digested or did it pass through the gut unchanged?

PROVASOLI: Unfortunately, we did not make any observation at the time.

RAY: Do you have any other case in which two insufficient phytoplankton organisms supplement each other?

PROVASOLI: No, we have not tried other combinations lately but we plan to do so. We would also like to extend the work of Ryther(41) who found that some algae are producing substances which are toxic or inhibitory to *Daphnia.* This work has not been followed up. We suspect that some cultures of algae, especially dinoflagellates, may be inhibitory to *Artemia* because when we introduce newborn nauplii into the algal cultures they die in 1–2 days. These nauplii live on yolk reserves for the first three days and survive in general 5–6 days in sea water devoid of particulate food.

RAY: Does the presence of bacteria overcome the insufficiency of all those phytoplankton organisms that are not in themselves definitely toxic?

PROVASOLI: We have not tried, but it is quite probable that a mixed bacterial population would overcome in many cases the nutritional inadequacy of non-toxic algae.

COSTLOW: If you take eggs of the eighth generation of *Tigriopus* grown on *Isochrysis* and put them in a mixed culture will they produce a viable generation?

PROVASOLI: I think so, provided the mixed culture is a complete food as is the combination *Rhodomonas–Isochrysis*.

COSTLOW: Is there a possibility that the egg would be deficient in something which would impair development?

PROVASOLI: It is quite possible since signs of deficiency are already evident in the previous generation. For instance, a lengthening of the generation time, abundance of males, delay in copulation and egg production.

STRICKLAND: I did not understand whether you assumed that the vitamin carryover was in the solution when these transfers were done or in the egg itself.

PROVASOLI: I think that whatever they are, the substance(s) necessary for *Tigriopus* growth are probably stored in the eggs and keep on diminishing in the successive generations.

SLOBODKIN: Eight generations of nine generations seems such a fantastic dilution. Is it possible that the algae were producing a little bit of vitamin but not enough?

PROVASOLI: It might well be. But we do not know if the addition of vitamins is directly responsible for the normal growth of *Tigriopus*.

SLOBODKIN: That is not what I was saying. Let us imagine that there is some nutritive requirement, let us say a vitamin, that the crustacea requires and is not completely deprived of by being put on this alga from the beginning. It is always there, a little bit, so you do not have to dilute through the egg nine times.

PROVASOLI: You are quite right. It has to be a progressive depletion of the necessary substances during successive generations and it involves all stages, larvae, adults, and eggs.

SLOBODKIN: So, you cannot get away with a threefold dilution instead of five or eight.

SCHMIDT-NIELSEN: Do the old dead organisms remain in the culture so that any soluble micronutrient could be redissolved in the water and taken up either by the food organism or by the feeding organism?

PROVASOLI: In the experiments I referred to, we have had very little accumulation of dead organisms. To make a new generation we inoculate

one pregnant female into a new tube freshly inoculated with algae. If there is mortality during the larval stages, their dead bodies remain in the tube, but they do not seem to help (i.e., release nutrients) because high mortality in the young stages is accompanied by other deficiency signs such as adults half the normal size, and inability to copulate or to produce viable eggs.

SCHMIDT-NIELSEN: It is a beautiful system to work with. Are you continuing this?

PROVASOLI: No, not now. We are concentrating on the nutrition of *Artemia* grown on artificial, nonliving diets to find out what are its nutritional requirements. I might speak of this later on.

YONGE: Did I understand you to say that your people have not followed the actual fate of the cells inside the gut of the *Artemia* or the *Tigriopus?*

PROVASOLI: No, we did not.

YONGE: There is rather more knowledge, is there not, about the effects on oyster larvae where it would seem to be the nature of the cell wall or things like that, which make an alga nutritional or not, as the case may be.

PROVASOLI: That might be quite true also for *Artemia.* In our experiments we only went as far as selecting algae which had the right dimensions for being ingested and observing that the gut of the crustacea was coloring. Gibor(73) did a nice experiment after having observed that *Stichococcus* was a poor food and that live *Stichococcus* cells could be recovered from *Artemia* feces, probably because they had a tough pellicle. He fed *Artemia* aseptically on a mixed culture of *Dunaliella viridis* and *Stichococcus* in equal quantities and ended up with many adult *Artemia* swimming in an almost pure culture of *Stichococcus. Dunaliella viridis* is a good food for *Artemia* and is apparently well digested while most *Stichococcus* survive the passage through the gut and continue to reproduce in the medium. Incidentally, this situation is found in many salines where *Artemia* grows.

BARKER-JØRGENSEN: Why does that not happen in nature then, that you end up having cells with tough pellicles only?

PROVASOLI: I do not understand your point.

LASKER: The euphausiid shrimp has a masticating apparatus that grinds up these things and makes a nice puree out of them.

RAY: They also know how tough the pellicles are.

COSTLOW: Maybe their sampling techniques are not any better than ours.

I do not know whether I can add much, but I would comment that, working with decapod larvae, mostly crab larvae, but some work on shrimp larvae, too, a number of unicellular forms have been used as food. To my knowledge, none of the larval stages has developed two metamor-

phoses with the forms that were used. These included *Chlamydomonas* and *Isochrysis*. Crab larvae rarely get to the first molt. If fed on a very good culture of *Chlamydomonas*, for example, they will last for perhaps 10 days and normally they would molt on about the fourth day to the second stage, if they were fed a proper diet. Without the proper diet they will last as the first stage for about 10 days and then die.

The entire time the gut is packed with the green material and form fecal pellets all over the place. If you mix the diet to include animal food, in this case, *Artemia*, you do get development, but it is much slower than with just animal food without the algae.

PROVASOLI: Did you find that the phytoplankton is a good food for the zoeal stage?

COSTLOW: No.

PROVASOLI: In Japan, the Kuruma shrimp is now cultivated by a commercial company (Kuruma Shrimp Culture Co., Ikushima, Takamatzu). The name of the animal is *Penaeus japonicus*. Two prefectural fisheries-stations are also competing for the production of the so called "shrimp hatch" or fry. These are shrimp larvae of about 2 cm. length and 20 mg. weight, which are produced in tanks situated in a long one-floor building. The shrimp hatch is sold to fish farmers who grow it in the open.

The standard procedure is as follows and is described by Hudinaga and Miyamura(75), and by Fujinaga(76). Fully grown females are put to spawn in wooden tanks filled with seawater at 28°C. and aerated. The eggs hatch in 12–14 hours, giving nauplii. The nauplii do not feed, molt six times in 36 hours, and become zoea. The zoea are fed with *Skeletonema costatum* kept in suspension by gentle aeration and molt three times within four days, and metamorphose into 1st-mysis larvae.

The mysis larva requires zooplankton besides phytoplankton. Brine shrimp nauplii, or early stage larvae of bivalves are the best food for this stage. The mysis molts three times within three days, becoming the first post-larva. These larvae are reared in larger and shallow (30 cm.) concrete ponds for about 20 days and are fed, as they grow longer and larger, at first *Artemia* larvae of increasing size and then crushed clam meat (little neck clam, *Paphia philippinarum*). When they reach 2 cm. in length they may be sold and can be cultured in breeding ponds or tanks which have a double bottom. At the bottom there is a layer of seawater, above it a mosquito screen on which is spread a thin layer of sand and above the sand a feet or so of seawater. Aeration is done by an aerating tube contained in a larger tube. These two tubes pass through the screen and down into the seawater layer. The bubbling of air causes the water to siphon and overflow above the sand layer.

YONGE: What is the partition between the sand and the water?

PROVASOLI: A fine net of bamboo fibers or of a polyethylene mosquito screen.

CONOVER: And this is serving as a filter, is that right?

PROVASOLI: Correct. But oxygenation is also necessary. Speed of growth is dependent on oxygen content of the water; the higher the better. The shrimp are in the sand layer and above it, where the food is spread. The Japanese are now planning to utilize the flats, which were employed for making salt, as culture grounds for shrimp. They plan to select localities having a tide of 1–3 meters so that the flats can be flooded and almost emptied once a day to avoid accumulation of organic residues, anaerobiosis, and H_2S production.

RAY: The food essentially consists of three different things?

PROVASOLI: Oh, yes, and for rearing the fry of the black porgy (*Mylio macrocephalus*), even more diverse foods were employed. As the fish larva starts growing, *Oxyrrhis* is fed first, then *Stylonichia,* then nauplii of barnacles, later nauplii of brine shrimps, then young shrimp mysids, and finally chopped fish when the fish larvae are 15mm. long; six different foods in all(77).

SANCHEZ: Has this been obtained empirically or scientifically?

PROVASOLI: In both ways, I presume. The men doing the pioneering work are scientists. For instance, the two partners of the shrimp company were scientists of a fishery laboratory who after retirement set up the company, with external capital.

FOGG: Has this reached the commercial scale?

PROVASOLI: It is reaching it now. Some shrimp hatch is being sold to fish farmers who are subsidized by the Japanese Government as part of a ten-year plan for transforming coastal fishing into coastal cultivation. The two prefectural laboratories also will be able soon to produce shrimp hatch, and the Kuruma shrimp company is growing its own shrimp hatch to commercial size. At the end of one year they are about 15–20 cm. and they weigh about 50–100 g. each.

STRICKLAND: Why do they have the sand?

PROVASOLI: The sand acts as a filter. With outgoing tide most of the water is filtered through. The artificial feeding is continuous and abundant, so heavy pollution has to be avoided. I imagine that a layer of water will cover the sand at all times, even when the gates are open during low tide. Due to a very tight schedule I visited the place at dusk and when we arrived at the breeding tanks it was raining and we were employing flashlights to see! The morning after, I visited a prefectural laboratory in Takomatzu where I saw cultivation of sea bream and yellow tail fishes.

SANCHEZ: I wonder if Professor Yonge or someone else would give some comments on the experience of rearing a bivalve in respect to

whether it is necessary to provide more than one food at a time. Do you carry on with one food and then change?

YONGE: The position at present, both with the work first done in the United States on *Crassostrea virginica* and that done on *Ostrea edulis* in Great Britain, is that you can take them through the planktonic stage to settlement on *Isochrysis* or *Monochrysis*. You still have the problem of feeding them up to the size when they can be planted out in the open sea. So far only pure cultures of *Monochrysis* and *Isochrysis* have been really successful.

PROVASOLI: Under aseptic conditions?

YONGE: No.

PROVASOLI: At Professor Imai's field laboratory at Kesennuma, the food algae are grown aseptically in flasks, then carboys, and finally transferred in clean large plastic garbage pails covered with a protective glass. This last step is not sterile, naturally. Finally, the cultures are fed to oyster larvae. Doctor Imai is now employing algae, because he has had difficulties with the marine *Monas* that he used to employ. At that time(78), the tanks containing seawater were enriched with starch (0.5–1.0 g. per cubic meter). This favored a controlled growth of bacteria on which the *Monas* fed; the *Monas* were in turn the food for the oyster larvae. Recently, he has thought to improve the method and he has been growing in the laboratory *Aerobacter aerogenes* in large flasks on shakers, all the year round. The bacteria are collected by filtration and the paste spread and dried at 40–50 C. in an oven under air flow. The dry powder is kept in cellophane bags in a desiccator. A large quantity can be produced during the year and is employed during the summer for growing *Monas* in tanks; so many spoons per $m.^3$ of seawater. The system is excellent so far as *Monas* is concerned; they grow fast, millions per ml., and they are happy. But these *Monas*, though eaten by the oyster larvae, are no longer a good food for the oyster larvae.

SLOBODKIN: Did he formerly use them dry?

PROVASOLI: No, previously he was fertilizing the seawater and the *Monas* ate whatever live bacteria would grow in the tanks.

SLOBODKIN: I discovered recently, through a silly set of circumstances, that certain tinfoils or aluminum foils are loaded with copper and that particularly when you heat anything on them to dry, copper oxidation products of various sorts form and can be fairly harmful.

FOGG: I am interested to hear that *Monas* eats dead bacteria. Doctor M.N.E. Adams* spent three years in my laboratory trying to grow *Monas*

* M. N. E. Adams, 1959. Studies on a euryhaline species of *Monas*. Unpublished Ph.D. thesis, University of London.

in a defined medium but found that her strain would only grow if provided with living bacteria. Even bacteria killed by the mildest of means were unacceptable.

PROVASOLI: Imai employed *Aerobacter aerogenes,* a fresh water bacterium which, incidentally, is a good food for *Paramecium* and other ciliates. The problem is not at all clear. Imai has not kept stock cultures of the *Monas* that he was employing in the early fifties. A new isolation of *Monas* is done every year from seawater. *Monas* are always present in bays where the eel grass grows. The eel grass after reproduction disintegrates *en masse* favoring bacterial growth; the bacteria in turn support a large population of *Monas*(79). Therefore, either the newly isolated *Monas* are different from the old and are not a good food for oyster larvae or they become an inadequate food for oyster larvae because they were fed on dried *Aerobacter.*

Often bacteria or even flagellates killed by the mildest means are not any more an adequate food. Years ago(80), I fed aseptically *Kahlia aerobates,* a fresh water ciliate, with *Polytoma caudatum,* which was its natural food. As long as you feed live *Polytoma* all goes well, but if *Polytoma* is killed by exposing it for only nine minutes to 44°C., then *Kahlia* will no longer grow and reproduce.

EDMONDSON: These considerations remind me of some work done by Eisen at Woods Hole(81) on two ciliate protozoa, the carnivorous *Didinium* eating *Paramecium.* The *Paramecium* could be kept growing happily on a variety of bacteria but the *Didinium* was particular and one could not maintain it on *Paramecium* that had been fed on monospecific cultures of certain bacteria. The *Didinium* would die rather than encyst. Eisen suggested that this might have affected Gause's interpretation of this system.

PROVASOLI: Doctor Conover, what do you have on selection of foods?

CONOVER: I do not have anything very sophisticated on the matter of nutrition here, by Doctor Provasoli's standards. There is no satisfactory food for copepods because we have not been able to culture these organisms.

I have tried several things. I have attempted experiments in which we set up small populations of copepods, fed them a given alga—in this case we used almost exclusively diatoms.

STRICKLAND: Which copepod?

CONOVER: This is the same *Calanus hyperboreus.* We let things go for about a month and then we compared the weight of the population, the weight of the food that the population has eaten, and we get some

idea of the efficiency with which this copepod is able to convert this diatom into what appeared to be largely this fatty substance which we have mentioned already. It probably is not actually fat at all but an assemblage of hydrocarbons.

FAGER: This is oil.

CONOVER: I have a table (TABLE 5) that shows some of the efficiencies in this process and the efficiencies are, I think, remarkable from Slobodkin's point of view if, in fact, we are talking about the same thing. I am not sure we are.

There are just four diatoms that have been used in this sort of experiment so far and the one that we have used particularly is *Thallassiosira fluviatilis* which is a *Thalassiosira* that does not grow in chains. This seems to be about the most satisfactory food we have. The copepods like it, it grows well, it does not change size appreciably, it grows rapidly. I have already discussed some of the attributes.

I will probably talk a little bit later about assimilation efficiencies

TABLE 5

ASSIMILATION EFFICIENCY, GROSS GROWTH EFFICIENCY, AND NET GROWTH EFFICIENCY OF *Calanus hyperboreus*(82).

	Exptl. temp. °C	Food organism	Food conc. mg. ash free dry wt./l.	Assimilation Efficiency	Based on Weight: Gross growth efficiency	Based on Weight: Net growth efficiency	Based on Calories: Gross growth efficiency	Based on Calories: Net growth efficiency
IV	2	*Thalassiosira fluviatilis*	6.4	44.0	3.7	8.5	5	12
V*	2	*Thalassiosira fluviatilis*	6.4	47.6	17.3	36.4	24	50
IV*	5	*Thalassiosira fluviatilis*	6.7	52 7	13.0	24.1	18	34
V*	5	*Thalassiosira fluviatilis*	6.7	50.9	14.6	28.6	20	40
V*	5	*Thalassiosira nordenskioldii*	2.6	39.6	13.9	32.4	—	—
V	2	*Thalassiosira fluviatilis*	1.7	71.1	28.4	39.4	39	55
V	5	*Thalassiosira fluviatilis*	1.7	64.1	18.6	27.6	26	38
V*	2	*Ditylum Brightwelli*	0.6	53.0	32.3	60 6	46	86
V	2	*Rhizosolenia seticera*	1.7	65.4	29 0	44.2	41	62
V*	5	*Rhizosolenia seticera*	1.4	63.1	30.4	48.4	43	68
V	4	*Thalassiosira fluviatilis*	0.3	57.2	13.3	23.3	18	32
V*	4	*Thalassiosira fluviatilis*	1.8	56.6	36.4	64.0	50	89

that are involved here but for the most part our assimilations are low, ranging from around 40 per cent up to a maximum in this Table of about 70 per cent. The highest efficiencies I ever obtained are of the order of 75 per cent or slightly more than that.

STRICKLAND: What do you mean by efficiencies?

CONOVER: The assimilation efficiency is what I would call simply gross production. It is the proportion of organic matter that has been removed by the copepod in the process of passing this material through its gut, and I measure this as a ratio of ash-free dry weight to dry weight. All I need to know is the organic material and dry weight in the alga that is fed to the animal and the same in the fecal material. The chief advantage of this method is that you do not have to go to this process of quantitatively capturing the feces of these copepods, which I do not think is possible, primarily because I am convinced that they do not put all their feces into fecal pellets. At least, if they do put them into fecal pellets they tear some of them up. I do this by comparing the ratio of the organic matter to the dry weight in the whole culture and in the fecal material, but this does not require that I recover all of the fecal material. I just have to recover a sample of the fecal material.

STRICKLAND: How do you get the food digested? You know how many particles have entered the organism, but how do you estimate the amount digested?

CONOVER: Just by comparing this ratio. You have an organic dry weight ratio of, say, 60 per cent for some alga; you have a fecal pellet organic weight, that is, say 40 per cent of dry weight. Then, you can deduce the amount of material that has been removed, the percentage of material that has been removed as follows:

Assume that

$$U=\frac{I-N}{I}\times 100 \qquad (1)$$

U is the percent assimilated, I is the amount of organic matter ingested and N is the amount egested. This equation can be written

$$U=\left(\frac{(F-A_f)-(E-A_e)}{F-A_f}\right)\times 100 \qquad (2)$$

where $I=F-A_f$, F being the dry weight of food eaten and A_f the weight of ash, and $N=E-A_e$, E being the dry weight egested and A_e its ash. One assumption is necessary and that is that the ash is not digested or altered by passing through the gut. We have evidence that this assumption is correct for silicon ash of diatoms anyway. Hence, $A_f=A_e$ and equation 2 becomes

$$U=\left(\frac{F-E}{F-A_f}\right)\times 100 \qquad (3)$$

Now, it is easy to determine the ratios of dry weight and ash in algae and a small quantity of feces. These ratios may be designated by the superscript prime and written in mathematical terms

$$F' = \left(\frac{F - A_f}{F}\right) \tag{4}$$

$$E' = \left(\frac{E - A_e}{E}\right) \tag{5}$$

Solving for F and E then

$$F = \frac{A_f}{(1 - F')} \tag{6}$$

$$E = \frac{A_e}{(1 - E')} \tag{7}$$

It now may seem that you have two equations and four unknowns; however, $A_f = A_e$ and may be considered a constant, any arbitrary constant C. For convenience of calculation C is usually taken as 10. Thus from the example above

$$F = \frac{10}{(1.0 - 0.6)} = 25 \text{ and } E = \frac{10}{(1.0 - 0.4)} = 16.7$$

$$\text{Hence } U = \frac{25 - 16.7}{15} \times 100 = 55.3\%$$

STRICKLAND: Is that very precise?

CONOVER: The way we do it, I think it is as precise as anything you can do, providing the assumptions are justified.

STRICKLAND: But in this approach, you are relying on 20 per cent difference in your initial parameters. Is that enough?

CONOVER: I can measure the dry weight, and the ash-free weight, with a considerable precision, with a microbalance. I can get these ratios for a series of replicate samples with perhaps 2 or 3 per cent error. Yes, it is not a highly precise number but I do not know any other way of getting it.

STRICKLAND: You put the copepod in this brew for a certain period and then you take a bit of the water with the fecal material and you do a ratio?

CONOVER: No. I take a sample of the algal culture and determine my ratios on it. Then I run a sample of the fecal pellets after they have been feeding on the algal culture for a few hours.

FOGG: The alga cultured is a diatom, is it?

CONOVER: In most cases.

FOGG: So you are fairly safe in assuming that the inorganic material remains unaltered. This might not be true of another alga.

CONOVER: This is probably so. The major portion of the ash is mainly silica. We have tried to do this with the green alga, *Dunaliella,* and it may be the method, or it may be the *Dunaliella,* but we get poor results with *Dunaliella.*

STRICKLAND: Do you get much difference in the fecal compositions from algae such as *Dunaliella*? I do not see why you should.

CONOVER: No, you don't. *Dunaliella* is roughly 96 per cent organic matter and the fecal material is still quite high in organic matter. It is about on the order of perhaps 80 per cent, something of that sort.

I guess you still want to get these efficiencies defined. Assimilation efficiency is the weight or calories assimilated divided by the weight or calories ingested $\times 100$. Gross growth efficiency (which I have called food chain efficiency elsewhere(83) is weight or calories of growth over weight or calories ingested $\times 100$. Net growth efficiency is weight or calories of growth over weight or calories assimilated $\times 100$.

SCHMIDT-NIELSEN: You had a figure, I believe, that exceeded 100 per cent in one of your columns over at the right.

CONOVER: Yes, you get that unfortunate number when you convert to calories. We have a lot of peculiar things that bother us.*

SLOBODKIN: You cannot do that.

CONOVER: I know you cannot, but this is the way it looks. It is a very crude experiment. First of all, it is a relatively small population and relatively large errors are possible, but the point here actually is that your efficiency is much greater if you think in terms of calories instead of just dry weight, because you have a relatively low caloric content in your alga and a relatively high caloric content in your copepod.

SLOBODKIN: Yes, the food chain efficiency, as you use it here, is different from what I have been using.

CONOVER: Yes, it is different from what you use. I do not know whether it is proper to call that food chain efficiency.

SLOBODKIN: I wish you had not. I would have preferred some kind of growth efficiency.

CONOVER: I know that Richman(84) uses gross growth efficiency, which, since he is of your school, perhaps we can follow. Anyhow, this is the number that is around 15 per cent in your interpretation.

SLOBODKIN: No, you just defined it differently so you cannot expect the data to turn out to be the same. The difference in definition is this: When I use the words "food chain" or "ecological efficiency," there is a slight difference between them, but that need not disturb us now.

* This controversial number has been removed from TABLE 4. In the corrected TABLE 4, food chain efficiency has been called "gross growth efficiency."

STRICKLAND: Could you let us have the Slobodkin efficiencies rapidly, please?

SLOBODKIN: I will do it in part. First, the growth efficiency, as I use it, is the calories in an animal's body of some given age divided by the total energy that went into producing that animal and getting it to that age, at that size, that is the cost of the animal in calories. So this is a property of the growth curve of the animal, its nutritional history, and has no meaningful definition for a population. It is something about a particular single animal.

As I use food chain or ecological efficiency, they are defined only for a steady-state population. If this condition is not met, the thing is meaningless to begin with. It is the yield to a predator from that population per unit time in calories divided by the energy eaten by that population per unit time.

So this is defined for a steady-state population only and depends on the activities of the predator. If a predator is not preying on the population it has zero efficiency in this sense.

STRICKLAND: What is the increase of biomass of a given animal divided by the total amount of food entering the mouth of that animal?

SLOBODKIN: This is growth efficiency as Brody(85) has used it, and it is a little bit different in the sense that Brody takes an arbitrary time interval and he can speak of the gross efficiency from age 1 to age 2 or from age X to age Y. This is or can be slightly misleading because if you catch an animal at a very steeply sloping portion of its growth curve, its growth efficiency can be quite enormous over that time interval. It is a growth efficiency. It is not the way I happened to use it, but I do not think it is a major distinction.

STRICKLAND: You mean gross efficiency over a small time interval instead of a large one.

SLOBODKIN: That is right.

STRICKLAND: But you do not give that a different name?

SLOBODKIN: I do not think there is any need to. This, in Brody's standards, would still be a growlth efficiency; that is, it still meets his conditions. The only thing I have done is to take an arbitrarily long time interval.

STRICKLAND: But in experiments with copepods, you do, in fact, generally, take a small time interval.

SLOBODKIN: In Conover's data this is what has happened, yes. Armstrong(86) had data on the growth efficiency over the entire life span for *Daphnia,* or had calculations giving the growth efficiency. There were several conversion constants in all of this.

I will not discuss the so-called population efficiency, which is a some-

what more complicated concept and I do not think need concern us. But while we are here, FIGURE 20 shows the accumulated data I have, to date, on ecological efficiency. On the ordinate is the ecological ef-

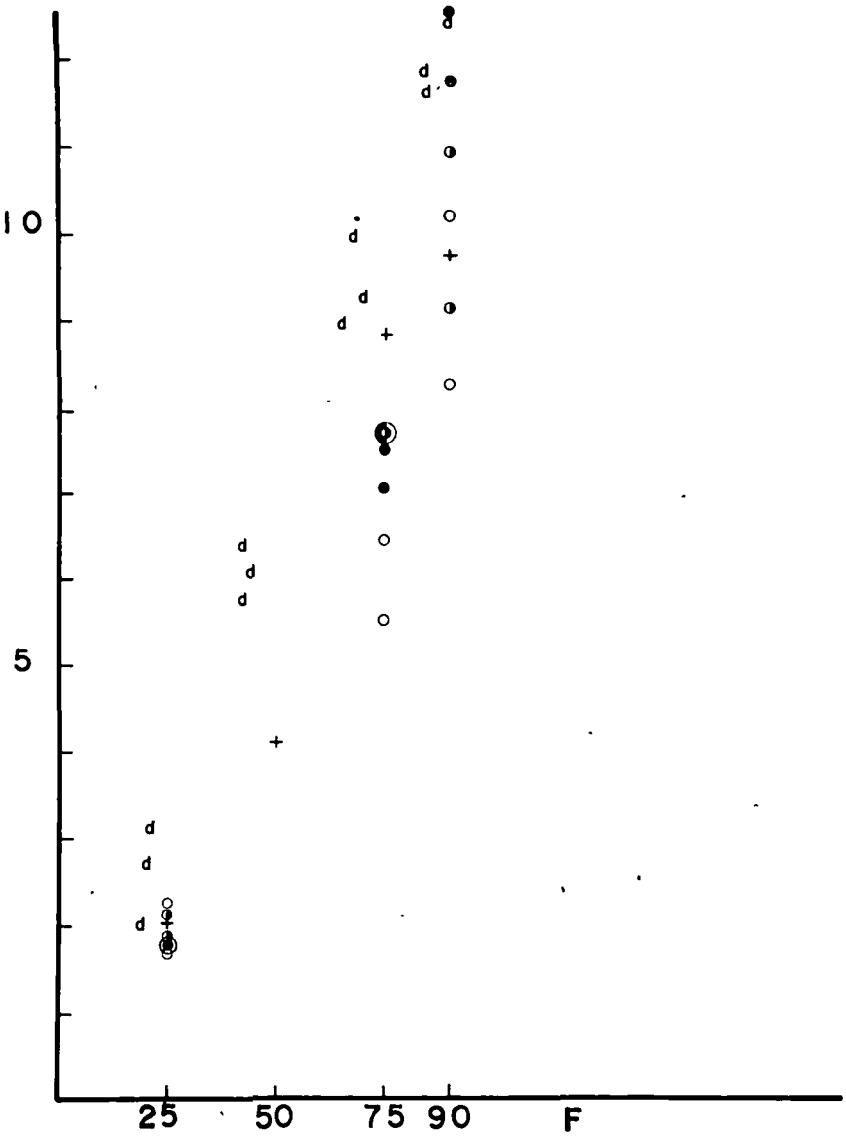

FIGURE 20. Ecological efficiency of steady-state single species laboratory populations of *Daphnia pulex* (*d*) *Hydra littoralis* in light (+), and two species systems of *Hydra littoralis* and *Chlorohydra viridissima* in the dark at various food levels (○, ◑, ●). *F* is the 'fishing' intensity.

ficiency. in percent—and on this axis I have a measure of rate of predation that can go from zero to one hundred. It cannot go any higher without eliminating the population entirely.

I have a diversity of data on this. Each point represents the mean ecological efficiency through a population history varying from three or four months to as much as a year and some months. The d's, represent *Daphnia* populations at multiples of a basic food level at 15°C. I am dividing the yield in calories that I have personally taken out of this population, by the energy I personally gave it.

Others show *Hydra littoralis* in the light. The six points that tend to sit on each other represent two species systems consisting of *Hydra littoralis* and *Chlorohydra viridissima,* the American green *Hydra,* raised at 25°C. in the dark, and these were systems where both species persisted. My point in this (and I have no theory to back this; all I have is observation) is that I can go from an herbivorous *Cladoceran* to a carniverous *Coelenterate,* from 15° to 25°C., one species or two species, and get essentially the same results.

This would imply that there ought to be some theory underneath this. The only thing I cannot do with it is develop it. I do not know what the theoretical basis is. The system will certainly collapse at very high values of *F,* so I am close to the maximum at 90. The food supply doesn't matter for the *Hydra,* either. These data tend to agree with the order of magnitude of field analyses of these same parameters, indicating that the thing in some sense is essentially constant.

Why this should be so, I have no idea. I do not intend to repeat this again, since I am so enamored of the cluster of those points that if I repeated it again I am certain I would cheat somewhere along the line, or if it came out the same I would be certain I had cheated, so I would rather someone here would repeat these experiments, but without telling me.

There are two other points in connection with this. First, Steele* at Aberdeen is convinced that my values are too low. He tried to take the data from the North Sea and see whether he could use it with 10 to 15 per cent efficiency to predict the yield of fish, knowing the various food levels, and so on, with the best estimates he had, and he discovered it does not quite work—that one must have an efficiency somewhere in the food chain of around 20 per cent, he thinks. This is based on the phytoplankton as the sole food source.

I do not know how good these data are, but I am cheered to an extent

* John Steele, Department of Agriculture and Fisheries for Scotland, Aberdeen, Scotland, personal communication.

by the data of Baylor and Sutcliffe(87), and of Riley(88), indicating that there may be auxiliary food sources on the phytoplankton level which would increase the base of this and eliminate the need for the 20 per cent efficiency.

There is also the possibility, which Steele suggested at an FAO meeting, apparently (I do not know how it was received), that this is because the North Sea may not represent a steady-state system within the meaning I have used. How this would theoretically alter the value, I do not know. That is one point. The other point is, when the same experiment is performed using green *Hydra* in the light, there is four times the efficiency. At the highest fishing level, where I get approximately 10 per cent with a two-species system involving green *Hydra* maintained in the dark, green *Hydra* in the light, at the same temperature, goes to 40 per cent efficiency. I infer from that and from the starvation material that I indicated previously that the photosynthetic algae symbiotic in the green *Hydra* are actually being used as a source of nutrition.

BAYLOR: Are you calculating the light calories you put in?

SLOBODKIN: That is the point; I am not. If I consider *Artemia* as my food source, the efficiency of the green *Hydra* comes our 40 per cent and, therefore, to bring it in line with the other data I would like to consider that three-quarters of the energy consumed by the green *Hydra* is derived from light, and I think this relates to some of Doctor Yonge's material(89) where he suggested that, at least in the corals, the zooxanthellae may conceivably be a procedure for eliminating metabolites. The evidence for that was that when you starve the corals they do not digest their zooxanthellae but in some circumstances may expel them. His original statement did not apply to green *Hydra,* in the first place, but had it applied to green *Hydra,* I think this would have constituted a refutation.

CONOVER: Let's go back to the table. It is apparently just a coincidence, then, that these growth efficiencies often do appear to be rather similar to food chain efficiencies. I do not think they always do. I think Doctor Reeve would more or less agree with me on this point. The point here, really, is that in simply converting the available food in the environment into a form which is available to the next trophic level, the copepod *Calanus hyperboreus* does this with a fair efficiency. The asterisks indicate that in some cases the experimental growth was actually statistically significant.

In these cases, you get a range of values from roughly 12–13 per cent to around 36 per cent, using dry weight as a basis for calculation. When you use the caloric values for the algae and copepods instead of weight to calculate your efficiencies, they are substantially increased. In some

cases the values particularly for net efficiency, may exceed 100 per cent, which is embarassing.

The whole point of this thing, though, is that this animal, which lives most of its life in the high Arctic, eats for only a relatively small part of its life cycle and it has evolved a rather efficient mechanism for converting the food in its immediate environment into this high-energy storage product on which it is dependent to complete its life cycle, including the process of reproduction. The whole cycle is essentially completed on the results of one meal lasting, in the Arctic, say, a couple of months at the most.

I have a few more casual observations on assimilation that I might mention. We have relatively low assimilation of a soft green alga, *Dunaliella,* and we have relatively low assimilation on *Peridinium.* We also have low assimilation of *Artemia nauplii.* In each case, the values are lower than are obtained with most diatoms.

PROVASOLI: Did you try chrysomonads?

CONOVER: No, I have not tried any of these yet. I started doing this rather recently.

PROVASOLI: Besides efficiency data, do you have any data on growth or molts?

CONOVER: What we are trying to do at the moment is to use the efficiency of assimilation as an index of whether the material is used in any degree by the organism.

PROVASOLI: That means that you rarely obtain a molt?

CONOVER: We try to get them at a stage when they are not likely to molt.

LASKER: Do these adults molt?

CONOVER: No, the adults do not molt. Most of these experiments were run with stage V, copepodites. I have some early experiments that were done with stage IV and in the case of stage IV you can usually get a molt, but at stage V molting seems to be much more a function of season than of food availability. It complicates life to have molting in the middle of these experiments. The animals frequently stop feeding before the molt and you often get a fairly high mortality during the molting process. You will produce some males which do not feed after they have molted, and a few things like that.

PROVASOLI: Can you tell us something about the size of *Calanus hyperboreus?*

CONOVER: As far as its anatomy is concerned, it is a *Calanus finmarchicus* blown up to about three times life size. It is a very nice organism from this point of view. Physiologically, it is similar, and its food habits are virtually the same.

There is one generation a year, apparently, wherever this thing occurs. The time of breeding seems to be shifted with latitude. The time of the year that the animal appears in the surface water or in the upper water is dependent on the season of the spring bloom, and the rest of the time the organism spends in the deeper water, apparently in a state of relatively depressed metabolism.

GONOR: The inevitable comment about oil in Arctic animals ought to be made at this point. This is of general applicability to Arctic animals and particularly the Arctic crustacea. Both shrimp and amphipods in the Arctic undergo a process of rapid accumulation of oil until the bodies are filled with large oil droplets by late summer and then there is a subsequent production of eggs sometime during the winter.

SANCHEZ: In what tissue is the oil deposited; in the muscle?

GONOR: I do not think that is known. If you pick one up and look at it, it looks full of droplets of oil, and big ones. There is a shrimp at Point Barrow which is literally greasy if you squash it. It is full of large, apparently fluid droplets of oil. It is not dispersed throughout tissue or in cells as one might expect in an adipose tissue. It appears to be free oil.

BAYLOR: What keeps all those oil droplets from coalescing with each other?

GONOR: Some of them look like they have coalesced, because those that I saw were different sizes. I can conceive of this happening in the haemocoele without really causing too much difficulty.

MCLAREN: It is very much localized in the copepod.

CONOVER: It is in *Calanus*. In *Calanus* it occurs in a discrete sac which is a diverticulum off the gut, but there are other copepods, particularly carniverous ones, in which the fat or oil appears as discrete droplets scattered about through the tissue. It occasionally happens that *Calanus* also develops droplets outside the oil sac.

MCLAREN: Usually outside the normal storage season as well. Also, this is not only an Arctic phenomenon.

STRICKLAND: You can produce oil by biosynthesis in the animal using a protein or carbohydrate diet without having to assimilate the lipid directly from a plant.

CONOVER: Unless there is differential assimilation, I think you have to assume that somewhere along the line they are reducing other materials.*

* Editor's Note: This section of the conference concluded with some more discussion of the variety of concepts of efficiency in describing utilization and transformation of food.

RAY†: I would like to mention once again that this problem of nutritional value, what is assimilated as opposed to what is swallowed, is a problem that has been around for a very long time. Just to emphasize that point, I would like to quote from a very fine figure in the history of zoology who wrote in 1797 in connection with the nutritional value of the food of one particular organism which has happened to be a favorite of mine. This is *Limnoria,* which you probably will not be able to avoid hearing more about later on when we talk about poor diets. In 1797 Rathke reported on the question of what *Limnoria* eats in these words:

> "Investigating the food which fills the intestinal tract of Limnoria, sometimes over its entire length, we always found that wood fibres, minute chips of wood, and so on, formed the main components. We always succeeded in finding at least some elements among these fibres which by the presence of bordered pits betrayed their origin in an unmistakable manner. Whether wood fibres are the only food which the Limnoria ingests, we dare not say. The main reason why they burrow in wood is probably that they feed on the wood fibres. Even if we admit that it is not necessary to assume that they live exclusively on these fibres, the latter in all probability do form at least the main course of their menu."

And finally, later, in summary, he wrote:

> "This Isopod understands the art of concentrating from the wood that which she needs for her nutrition. Whether or not this is her only food is very hard to decide."

So, I think it is indicative that the problem has been one which has puzzled people in marine biology, as well as in other fields, for a very long time. We are constantly searching for ways of clarifying the problem of finding other ways to understand what is going on and looking constantly toward new approaches and more effective ways of studying the problem.

The creatures are not large and they live almost exclusively within the burrows that they construct, mainly in wood. They are usually found

† Editor's Note: Much of the following discussion consisted of a detailed description of the anatomy of the wood boring isopod *Limnoria lignorum* illustrated with lantern slides. Much attention was given to the structure and function of the gut diverticula, the localization of enzyme production, digestion, absorption, etc. The discussion has been greatly abbreviated and rearranged by the editor for this publication. Much of the omitted material and the references can be found in the symposium edited by D. L. Ray. 1959. Marine Fouling and Boring Organisms. University of Washington Press. Seattle, Wash.

down head-in into the burrow; they are quite sensitive to light and as soon as you split open a bit of wood they will start backing out away from where they are. These burrows tend to go down into the wood in parallel lines. The tunnels will be in somewhat of a straight line in a good fresh piece of wood, upwards of 1 or 2 inches in depth when the invasion first begins.

BAYLOR: How are those oriented relative to gravity?

RAY: I do not have any special measurements on this at all, but, rather than being oriented to gravity I believe they are oriented away from the surface. They tend to invade a floating piece of wood from the bottom side, so that their burrows go upwards and they are at the inner part of the burrow; in which case they are upright with respect to gravity. If, on the other hand, they are invading from an upright position, from a pile, they tend to go down at about a 45° angle, generally, but this is not universal. Once a piece of wood is well infested, they go every which way and the tunnels begin to intersect, and so on.

In the laboratory, I tend to keep them on rather thin slices of wood because in that way you can pick them out again; they go right through it very simply. They have a tendency to go along the grain. This differs quite a lot between different species of wood. If you take a soft wood like pine where the grain is very prominent there is quite a difference in density or hardness between the long strands of vascular tissue, I guess it would be, and the intermediate parts, they tend to parallel the grain very, very nicely, but if you are using a hard, dense wood like mahogany, or teak, there is much less orientation.

STRICKLAND: They will go through teak?

RAY: Yes, if you give them a little time. The largest specimens in our part of the world are about 3 mm. in length, and perhaps ½ mm. in diameter.

I read you a little bit earlier about the early opinions that the animals, since they always have wood in their gut when taken from nature, must be living on wood. This opinion was held for a very long period of time until the early decades of this century when, probably as a result of the magnificent work on termites and wood-inhabiting beetles, it became clear that the creatures involved were not themselves digesting wood, but, rather, were depending on the activity of the microbial symbions to take care of the woody digestion itself.

Because of the widespread occurrence of bacteria, of fungi, of protozoa, and so on, in the gut of practically all wood-eating animals, the opinion became widespread in the case of *Limnoria* either that the animal was subsisting on some other kind of food material taken in along with the wood chips, or must be dependent on a microbial symbiont in order to

handle the wood itself. The examination of the gut, on the other hand, shows that this is not the case.

Coming back to the symbiont question, in the cases in which an animal depends on microorganisms in the gut to be able to take care of some portion of the digestive process, it is a two-way partnership arrangement, and the host has to provide, somehow, for the microorganisms a place to live. We find that normally this involves an anatomical adaptation of one sort or another and that the animals who have microbial symbionts, have some kind of diverticulum or special chamber in which the symbionts live.

Secondly, whenever there is a microbial symbiont involved in digestion, those organisms have to be present in reasonable numbers, and by "reasonable numbers" we mean really quite a few. You cannot break open a termite gut without being aware of the fact that there are protozoa there. You cannot break open the gut of a wood-boring beetle that has cellulolytic bacteria in it without finding both the anatomical chamber where these creatures live and the evidence of their existence.

In a gut like that of *Limnoria* which is nothing more than a simple foregut and hindgut and two diverticula on each side of the midgut area, the only conceivable place where microorganisms could live would be in the midgut diverticula, and it is very easy to examine these. It is only a single cell layer thick, and they can be seen, dissected out very readily, and examined in a variety of ways, and as a result of many, many examinations of fresh material, of stained material, of sectioned material and so on, under very good microscopic conditions, we can say with complete confidence that, at least so far as every *Limnoria* I have ever laid my hands on, which is a good many thousands of them, is concerned, there are no microbial symbionts in the gut.

If the creature is living in a place where the substratum is itself highly infected either with fungal bits of hyphae or with other kinds of microorganisms, one can sometimes detect bits of the substratum that will be chewed off and swallowed, and find it somewhere along in the main part of the gut, but there is no particulate material of any kind in the midgut diverticulum, there are no bacteria there, and for all practical purposes we can say with a good deal of confidence, that this is one of the few and rare examples in the animal kingdom of an animal that has an aseptic gut.

This does mean that for certain kinds of investigations it is a beautiful experimental animal, its small size notwithstanding. It occurs in large numbers and when one does want to go into an analysis of the digestive enzymes present, one does not have to worry about the question whether

the enzyme that you find has been produced by the animal or by some bacterium that lives with it.

This is a problem, of course, which has interfered with the studies of cellulose digestion in the case of *Teredo* which, being perfectly good bivalves, do have a good deal of bacteria in the gut, so that you cannot separate very easily what the animal is doing in the way of producing enzymes, the kind of enzymes it is producing, and what the bacterium is doing.

STRICKLAND: Where does it get its vitamins from?

RAY: I wish I knew that.

STRICKLAND: You are quite sure there are no bacteria?

RAY: Yes.

YONGE: Yes, but the burrow is far from sterile.

RAY: The burrow is far from sterile, that is quite true, but, on the other hand, it is also not heavily contaminated. If you have a piece of wood that is itself rather heavily contaminated with all kind of things, it is usually not very well infected with *Limnoria,* or they are about ready to leave it. You can take perfectly clean, unaffected wood, that is to say, wood in which you cannot detect the presence of bacteria or fungi or anything else, and offer this to *Limnoria* and they go into it with great vigor.

I would like to separate the question of fungi from the question of bacteria for just a minute because there has been some difference of opinion among those of us working with these animals as to whether or not fungi play any particular role in the digestive process. Some years ago a group of workers under Doctor Dechert at Berlin Dahlheim and also Charles Lane at Miami and a few others claimed, and cited evidence as a basis for the claim, that, actually, although the *Limnoria* could not have any microorganisms in the gut, nevertheless they are dependent on microorganisms, and particularly fungi, present in the surrounding wood for their nutrition. In some cases, they believe *Limnoria* need these entirely for the energy supply part of the food but also for other vitamins and the nitrogen source, because, of course, wood itself is notoriously poor in nitrogen.

It was our belief that this was not the case, so there ensued quite a nice dialogue for some time.

STRICKLAND: You mean poor in protein nitrogen?

RAY: That is right. The question of whether or not lignin can be attacked is one that is completely unresolved and not an easy one to study, because there is no way of doing a definitive experiment. To extract lignin from the wood involves degradation and it is very difficult to test

for lignin. In fact, you determine the lignin content of wood usually by difference.

STRICKLAND: You cannot feed these things on cellulose—force-feed them in a defined medium with just cellulose?

RAY: Yes, you can, but you cannot do this over a long enough period of time to prevent some growth of microorganisms in the culture, because you cannot sterilize the outside of the *Limnoria.* His gut appears to be quite aseptic. His body surface is not. It is covered with all kinds of tiny little hairs and so far we have been completely unable to wash it clean or even to take eggs or young from the brood chamber and wash those clean, because even there they will have bacteria stuck on the surface. Growing them in the presence of antibiotics and fungicides, and so on, they do not survive very long.

BARKER-JØRGENSEN: Is there lignin in the feces?

RAY: Yes, 40 per cent. As far as all the specimens I have studied are concerned, both in Friday Harbor and in Naples, both sexes burrow. We have sexed them and separated them and the males are just as active in burrowing as are the females.

YONGE: And you find two in the same burrow, so that at some place there must be a changeover?

RAY: No, there are very seldom only two in a burrow and very often the burrows have only one animal in them. Whenever there are two, it is a matter of chance—at least in the count we have made—whether it is a male or female at the burrowing end. By using these rather thin slices of wood that are just about as thick as the body dimensions of the creatures, we have been able to keep them over months of time and watch them burrowing and copulating and laying eggs—I should not say laying eggs, but the young hatch.

YONGE: That is quite a change in the classic story.

RAY: Yes, that is right. One can, as is so often the case when it is a matter of counting the numbers, go along and open up the wood, and the first dozen or fifteen burrows might have a male in front or female in front, and then you find maybe the next fifty of them are the other way around, so you have to look at rather large numbers.

YONGE: Unlike *Teredo,* these animals are not irrevocably fixed. You can get them out and they will infect new wood. They have opportunities of getting other sources of food, have they not?

RAY: That is right.

YONGE: As much, anyway, as is needed for purposes of acquiring vitamins, and so forth.

RAY: Yes. The tendency, I believe, is that if they are in a sound piece

of wood which is better infected than a piece of wood that is somewhat punky, they do not tend to leave it unless they become overcrowded.

We have examined the walls of tunnels and made sections and tried to examine them, freshly opened, and we do not find much of a bacteria growth coming down the wall of the tunnel to where the animal usually is, head-buried at the bottom. It may back up and grab a few bacteria and go down. It does, after all, have to get nitrogen from some place.

YONGE: It is creating a respiratory current all the time, is it not, with water entering through "manholes" overhead?

PROVASOLI: What happens to the feces?

RAY: This collects in the burrow. Every once in a while the animals create a current and kick it out. They do not eat their feces, as termites do.

LASKER: We tried to grow sardines under aseptic conditions. Sardine eggs were dipped into a solution of merthiolate. The sardine larvae which hatched out were normal in all respects once they had been washed free of the merthiolate and put into sterile sea water. It seems to me that this is really the key experiment; to obtain bacteria-free animals for experimentation.

YONGE: Could you get the eggs out of a brood pouch?

RAY: Yes. I have never succeeded, however, in washing them or soaking them in a variety of things, and then having them completely sterile thereafter. On examination, I have never found a bunch of eggs that did not have a few stock bacteria sticking to them. You actually have to remove the membrane, I think, or leave them for a long period of time.

EDMONDSON: The nitrogen content of water is small. What is the amount of nitrogen in a cylinder of wood the size of a burrow? How does this relate to the amount in the animal?

RAY: I cannot answer that. The amount of nitrogen in wood is small, something on the order of 0.4 per cent, I guess, on a dry-weight basis. That is a very rough figure and differs by an order of magnitude not only from tree to tree of the same species, but also in different species in the same tree. It depends on whether the tree was cut in the spring or in the fall, whether the wood is seasoned or green, and all kinds of things like that, so that to say how much nitrogen is present, even any kind of figure is somewhat misleading.

EDMONDSON: An interesting figure would be the minimum related to what is in a *Limnoria,* would it not, unless your minimum is zero?

RAY: It may be.

STRICKLAND: How much nitrogen is there in one of these beasts? Are they largely carbohydrate?

RAY: You mean the total nitrogen content of a single *Limnoria?* I am sorry, I do not know.

EDMONDSON: Doctor Provasoli, are any animals that you know of, able to use nitrate?

RAY: This also is a question I would like to know the answer to.

PROVASOLI: Not that I know of.

RAY: Do we know it is impossible? Do we know whether it is impossible for an animal like *Limnoria* to extract nitrogen from sea water? Unlikely as it seems, I do not think it should be completely eliminated as a possibility.

Coming back to the wood business, there are always, and over and over again, reports that some particular kind of wood is resistant. Every wood that we have been able to get our hands on to test, the *Limnoria* are perfectly capable of going into. If they have a hunk of teak and all kinds of Douglas fir, you may find them in the fir and not the teak, but if you take them in the laboratory and give them teak and no fir, they will go into it alright and they can live on it perfectly well; so while there may be some kind of advantage to using a very dense wood for construction, or something like that, it does not mean necessarily that the animals cannot or will not attack that particular wood and live on it.

BAYLOR: How do they make out on palmetto?

The reason I ask is that there are palmetto pilings in Florida, approaching one hundred years of age, that are apparently still sound.

RAY: Yes, I can tell you that there are pieces of pine piling in some places approaching the same age and still perfectly fine, and Douglas fir and oak. They will eat oak like everything, and it is a very puzzling question why these differences occur. These kinds of things keep cropping up and it makes one very angry because it does not seem to make any sense.

FAGER: Perhaps this is related to the same thing: The termite people told me that a new house is tremendously subject to termite attack, but that in an old house, say fifty years old, you can forget about termites, at least in Southern California. This is true even though they are built of the same kind of wood.

RAY: Yes, it is the same wood. I am sure it is the same kind of problem, so the question is, What really is the nature of the problem? I have an hypothesis. I cannot call it anything more than that, perhaps a speculation.

Fifty years ago (that is a pretty good number, I would guess) the wood that was being cut and used, either for piles, dock construction or heavy construction, or made into lumber for a house, was pretty much wood that we could call virgin timber, not in the sense that it was the only wood

that ever grew on that spot but the lumber industry was mainly exploiting new areas and cutting over lands that had not been cut over previously.

Think about the conditions under which such trees were growing; it was a standing forest, trees grow up and trees, like other plants, like all of us, accumulate a lot of gunk along with everything else. Whatever odd-ball kinds of things might be found in a soil, particularly an ore-bearing soil—all of these things can be deposited in the wood fibers by the growth of the tree, not chemically combined but physically combined so that they do not leach out very easily.

For example, we know that trees grown on the tailings of lead mines have a lot of lead in the woody tissues. Trees grown on some of the soils in the Carribean area, these aluminum soils and others, have a lot of metallic content to the wood that has been physically adsorbed during the growth of the tree. That, incidentally, is a very good place for termite attack, whereas the timbers that were originally cut in some of the Caribbean Islands were marvelous for shipbuilding because they were resistant, apparently, to *Teredo, Limnoria* and so on. In some of the old, old houses out in the country, old blocks of wood are sitting on the ground and are not infected at all, but the newer ones made out of new lumber, are.

STRICKLAND: It should be easy to check this.

RAY: Not so easy.

COSTLOW: As an advocate of old houses, I cannot let that record stand. In Beaufort they had up until about eighty years ago access to what they called lighter heartwood of trees and, basically, it is nothing but turpentine held together with a little cellulose. This is what they used on the old houses and those that are standing today, that have not burned down (of course they make a beautiful fire) are impervious to termites.

The modern lumber is green while they are putting the nails in it and it is the sort of thing that they would have burned eighty years ago. They would not have had the nerve to use it in buildings, so this is a much simpler explanation, I think.

RAY: I think it is not the only explanation, however, because it may hold for houses and it may be a perfectly good explanation, but it does not hold for a dock. These timbers in old docks were often untreated. This does not mean that all old docks are any good. At least some of them are.

COSTLOW: It will not hold for docks or houses if the lumber gets wet and stays wet.

RAY: It is a matter of leaching, which is why I was starting to indicate that there are conditions under which certain things can be deposited in wood, deposited by the wood, by the tree itself as it grows rather than

forced into it by pressure treatment or soaking. Because of this natural growing these things do not leach out easily or leach out only slowly over a long period of time. The silicates, for example, that are deposited in certain types of tropical forests. Timbers in the Argentine have a very high silicate concentration, so much so that you can see crystals in between the wood fibers. They cannot saw the wood because it breaks up the saw. This wood is very resistant, so the trees were transported to Hawaii to be grown there, and used for future dock construction.

They did this and the trees grew quite nicely, the project was coming along beautifully. The first place they used them was in a trestle across an estuary to start a development on a little island offshore, or peninsula, or something like that, and the first train load of goods that went over the trestle fell into the estuary because the whole thing collapsed in a hurry. The timbers were found to be completely riddled with *Teredo* within a few months of the time the trestle was built, and on examination they found that no silicates had been deposited in the trees at all.

So it is a combination of climate, factors in the soil, and so on, that may give you differences in various extraneous material deposited by the tree in the wood. One careful study has examined white pine grown on the two sides of the Cascade Mountains, and also correlated the time at which the trees were cut with the resistance to infection by many of the wood-destroying fungi. There is a very big difference between the two sides of the Cascades—quite a different climate, of course, the same species, and whether the trees are cut in the spring or fall.

FOGG: Is the starch content important here?

RAY: Yes, I think it would be, but also the amount of protoplasm left, the sap. If a tree is cut in the spring there is as much sap in the wood as there is going to be. Although there is a drying process, it leaves a lot more constituents of living material than you have if you cut the tree in the dead of winter when the sap is out of the trunk of the tree. Those two trees may be grown on the same soil under the same conditions, and one, in the end, would have a far different content so far as the organic material is concerned, particularly, I think, the nitrogen content.

In what we call second growth, the timber is grown on grounds where the crop has been harvested, and all the microconstituents have not gone back into the soil again to be taken up into the next growth. When this next crop is harvested, the lumber from these woods is less resistant to all kinds of things, whether fungus in a fence post or termites in a house or *Teredo* in a dock.

This is a broad, broad generalization but I think there may be something to it.

STRICKLAND: If I may comment, I was associated with work that planned to use trees to try to find copper deposits etc. in British Columbia. There are a host of quick methods for copper, lead, and other trace metals available and if you suspect the presence of one of these elements to be critical, I should think one could bore into pilings that have not been infected and analyse for copper or lead, or what-have-you.

The same remarks apply to nitrogen. Perhaps the question of whether you have sapwood with freshly deposited material fairly high in nitrogen, and whether this is subsequently removed is relevant. I would have thought the amount of copper even in sapwood is so small that it would have little effect on *Teredo,* etc., but one cannot be sure. Probably they do not like the taste of some organic component in some trees.

RAY: There is this difference. The things that are used to protect wood are essentially copper paint and impregnations put on from the outside, and this can and does leach out in sea water, whereas if the tree has grown on an ore-producing soil this does not leach out. All the *Teredo* or *Limnoria* has to do is to wait until the thing has been in sea water long enough to get the chemicals out.

STRICKLAND: But I believe *Teredo* are fairly resistant to copper; they do not mind it.

RAY: I think *Limnoria* are less so. They can detect—well, I should not say that, I do not know, but if one of them goes in and dies, the others do not, you see. If they do not establish a population for a while, the few that are lodged there make fairly little inroad on the total population in the sea, and after a while the copper is leached out from the surface and away it goes. Even with the best copper paint you can put on the bottom of a wooden boat, if you do not do it every year you will get an infection.

There is one thing that the *Limnoria* can do, and does very effectively: when it goes into a piece of wood it can spit out everything until it gets down about a millimeter. That gets it beyond the area of high enough concentration so that the copper paint on the outside does not make any difference.

YONGE: You say that a *Limnoria* will know there is wood below the paint?

RAY: I do not know, but we have seen it happen and we have to say that he keeps going. I do not think it is a matter of knowing there is wood there because they will start gnawing into all kinds of things. They will not stay there if they do not come to wood after a while, but they will go through coatings of a sort and they will do this without swallowing very much of it, whereas if you have even a low concentration of something like copper or lead deposited in the wood fiber itself, it simply does

not know any better and swallows it and begins to digest that wood. In the process, I think the metallic content would be released.

SCHMIDT-NIELSEN: Is this not a rather meaningless discussion unless you can say with certainty that virgin wood contains more copper than the second growth, and the virgin is also second growth, is it not?

RAY: Using that term in the relative way that I meant it to be used, that is, cutting within a reasonable period of time, the tree will have grown on ground where previous crops have also been present and decomposed, and so what they have accumulated is still there. It is the harvesting that makes the difference, I think. It is only speculation.

SCHMIDT-NIELSEN: This whole argument reminds me very much of a laboratory assistant my father once had who insisted that glass got stronger and stronger, the older it was. One day he took me into the stockroom and said, "Look at those beakers up there, they are 28 and 30 years old and they are still good, but this is what we got in this year, and the students have already broken 40 per cent of it. Those up there are so good I do not give them to the students any more."

RAY: A very good point, and I did not mean the argument to sound that way. I said it is only speculation, but I think one can say there are differences in the extraneous constituents that may be there between virgin timber and timber which is grown very quickly as a second growth.

SCHMIDT-NIELSEN: And the lousy timber that was put in houses and docks one hundred years ago is gone long ago while the good timber remains and makes us think that all timber was good in the old days.

RAY: There are cases where docks are known to be still standing, of untreated wood of the same species as now gets infected very, very readily. Also I should point this out, that in a dock, for example, not all of the timbers are attacked. You will always get a few of them that are not. Pilings of the very same wood, which are all put in at the same time, have some that remain sound and others do not. The explanation for this, I do not know. It certainly is an example of patchiness, and that may be the explanation. It may also be very slight differences in the nitrogen content or these extraneous materials from tree to tree.

KANWISHER: Can you take a sample of wood from an old pole that has not been treated and put it in a dish with hungry *Limnoria* and will they chew on it?

RAY: Yes.

SANCHEZ: Do these organisms burrow exclusively in wood?

RAY: There are those that live in the kelp holdfast.

SANCHEZ: The same species?

RAY: They are described as different species. I think they are not very

different. The ones I have seen, tend to be somewhat slighter in build and softer of tissue, and their mandibles are not so heavily chitinized.

YONGE: It would be a distinct species, though, would it not?

RAY: I suspect so.

SANCHEZ: It is an interesting problem to try to think, How did these things get established in wood? I presume there was not that much wood in the sea prior to, say, the crustacean, when docks and ships and things—

RAY: I think there has always been plenty of wood.

MCLAREN: Drifting has been used to colonize distant islands in various parts of the world.

SANCHEZ: I know there is drift, but there are no big rivers on the Pacific side, so I am not familiar with much driftwood.

SCHMIDT-NIELSEN: All the driftwood on the coast of Greenland is of Siberian origin—a lot of it, big timber.

STRICKLAND: We have talked about mollusca and isopods. Are there any other different types of marine organisms going into wood?

RAY: There is a gammarid, *Cheilura,* which at least in Australian and New Zealand waters is quite commonly found in wood, and probably living off it.

YONGE: It is equally common in Europe, too.

STRICKLAND: So, we have three specializations in very different types of organisms.

RAY: The amphipod is fairly closely related to the isopod, and there are two crustacea and one mollusk.

PROVASOLI: From a purely nutritional point of view, would you say that they definitely live on wood and nothing else?

RAY: With the difficulties inherent in the possible ingestion of microorganisms growing on the surface of wood fibers, I would say yes. We do not know what contribution that is. So far as their main energy-producing activities are concerned, yes, the wood constitutes their food. This has also been investigated by getting the dry weight of the wood offered and collecting all of the pellets and dry weighing those, so that we can calculate the total weight of the wood passed through the gut, which gives about 40 per cent in total dry weight that is lost. Comparing also a general analysis of the wood constituents in terms of cellulose, hemicellulose, the polysaccharides that are not cellulose, and the lignin fibers with the pellets, it was found that they are capable of removing practically all of the noncellulose polysaccharides which are lumped in this way. In the Douglas fir that I have used mainly, this amounts to around 8 or 9 per cent dry weight in the wood offered and less than 0.2 per cent of dry weight in the pellets, and similar amounts of the hemicelluloses

amount to about 12 per cent dry weight in the wood and about 2 per cent in the pellets, and about half of the true cellulose.

STRICKLAND: This is very different with a *Teredo.* As I understand it, a *Teredo,* once it gets its nose in, stays in and never comes out.

RAY: That is right.

STRICKLAND: So, it could not come out for a cheap dose of vitamins and fat.

YONGE: When it is feeding in a normal way, it is drawing in water currents all the time.

STRICKLAND: That is what I mean. But it had bacteria in the gut, you said?

RAY: That is right, and it has the mechanism to sift out of the water passing through any particulate material that it wants to remove.

And that is what the *Limnoria* must have. The respiratory currents need not pass the head at all, and it does not have any filtering mechanism to remove from a water current anything that may be coming in. It might do it, but it is by chance.

STRICKLAND: This makes it look like the *Teredo,* in other words, it more or less had to have this great diversity to supplement its diet, seeing that it is stuck in the wood.

YONGE: *Teredo* has the normal bivalve feeding mechanism but has developed this habit of boring into wood, possibly having originally bored in clay or rock. But it certainly digests some of the constituents of cellulose although also feeding normally on plankton. I would like to make a confession at this stage and just say that I arrested the wheels of progress some 30 or more years ago when I did experiments on *Limnoria.* I was working on *Teredo* at the time, and I got very large numbers which I ground up with a mortar and pestle and I tried the effect of this extract on wood, on wood fragments, and on filter paper, etc., and I could get no trace of cellulase. I published this and I now retract what I then published.

RAY: We did your experiments over again and we could not get any trace of cellulase at all. I think that this is a very good lesson for homogenate-type experiments, this type of biochemistry, if we can call it that. Certainly that is true, and the only way one can get a preparation which does have cellulase activity is to remove the digestive glands themselves and make your homogenate. Why the homogenate of the whole animal does not work, I cannot say, but then, on the other hand, if you put it into a different order of magnitude, if you ground up a whole elephant and then tried to check for amylase, or something, you might not detect it, and that is essentially what is all too often done.

SANCHEZ: These animals are active? They move in the tube and then you take them out of the tube and they move around actively?

RAY: Yes, they can swim.

SANCHEZ: The eyes, for example, are normal isopod eyes? They are not the ectropic eyes of burrowing animals?

RAY: There is no question but what they can come out of the burrows, they do come out of the burrows, they swim around, they walk around the surface. I only question how much they do this and whether they do it to do any supplementary feeding.

SANCHEZ: Could they not eat some larvae that are fixed on the wood?

RAY: Yes, they could do it. In all the tests we have run to try to make them do this, they have been quite recalcitrant. For example, you take filter paper and grind it up and make a pellet out of it. You can do this by compressing and drying it; you can do it with ground filter paper and nothing else, and it will stick together if it is well compressed and well dried. Now, taking such a filter-paper pellet, you can also grind it together with cultures of bacteria, with yeast, and so on. We have dried this by taking and isolating microorganisms from the wood on which they are found, making cultures of it and then harvesting the microorganisms, mixing it up with the filter paper pellets and presenting these to the animals. Whenever we do this, they usually prefer or select to go into the filter paper that does not have the microorganisms on it or involved in it at all, and will avoid or reject those that do.

SANCHEZ: Have you grown them in filtered water?

RAY: Yes, but I have to say that this water remains microorganism-free for only a short period of time, a very few days at the most, even at low temperatures. Yes, we can start them aseptically but they do not stay that way for long.*

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* Editor's Note: A return was made to the problem of quality and selection in a later discussion of feeding by sea urchins. See page 196.

IV. SEASONAL ASPECTS OF FOOD RELATIONSHIPS AND BREEDING

Discussion leader:
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MCLAREN: I think what I have to say probably comes under the general heading of metabolism, assimilation and growth, and introduces perhaps some shortcuts to these questions.

I take it that most of you are interested in questions of feeding, assimilation, nutrition, etc., as parameters of production, perhaps. These things have intrinsic interest, of course, individually, but production is the final expression which many of us would seem to be getting at.

I do not know whether the approach I am about to offer is completely new, but I will let you be the judges. There are three kinds of organisms, two of which have been spoken of here with rather more frequency than the third. There are organisms at one end of the spectrum which degrow. There are other organisms, which have a rather indeterminate growth, such as *Daphnia*. You can give them a given amount of food and expect them to grow at a given rate and reach a given size, within limits. I think the length of *Daphnia* can vary essentially by 25 per cent, or something of that sort, which would be about twofold in weight.

There is another class of organism which is a good deal more prevalent than has been suspected, I think, (and that is those organisms which grow in strict relation to temperature rather than to food;) that is to say food can slow down the growth rate, but the development rate and final size, if food is sufficiently abundant, are (strict functions of temperature,) (and if food is not sufficiently abundant these animals do not grow to a smaller ultimate size but simply stop growing.) There is a kind of step function, or a very rapid approach to an asymptote, at any rate, which makes these perhaps a bit different from the ones which are used more commonly in the laboratory.

The (first example shows *Sagitta elegans* from various parts of the North Atlantic (FIGURE 21).) What I have done is simply to take a

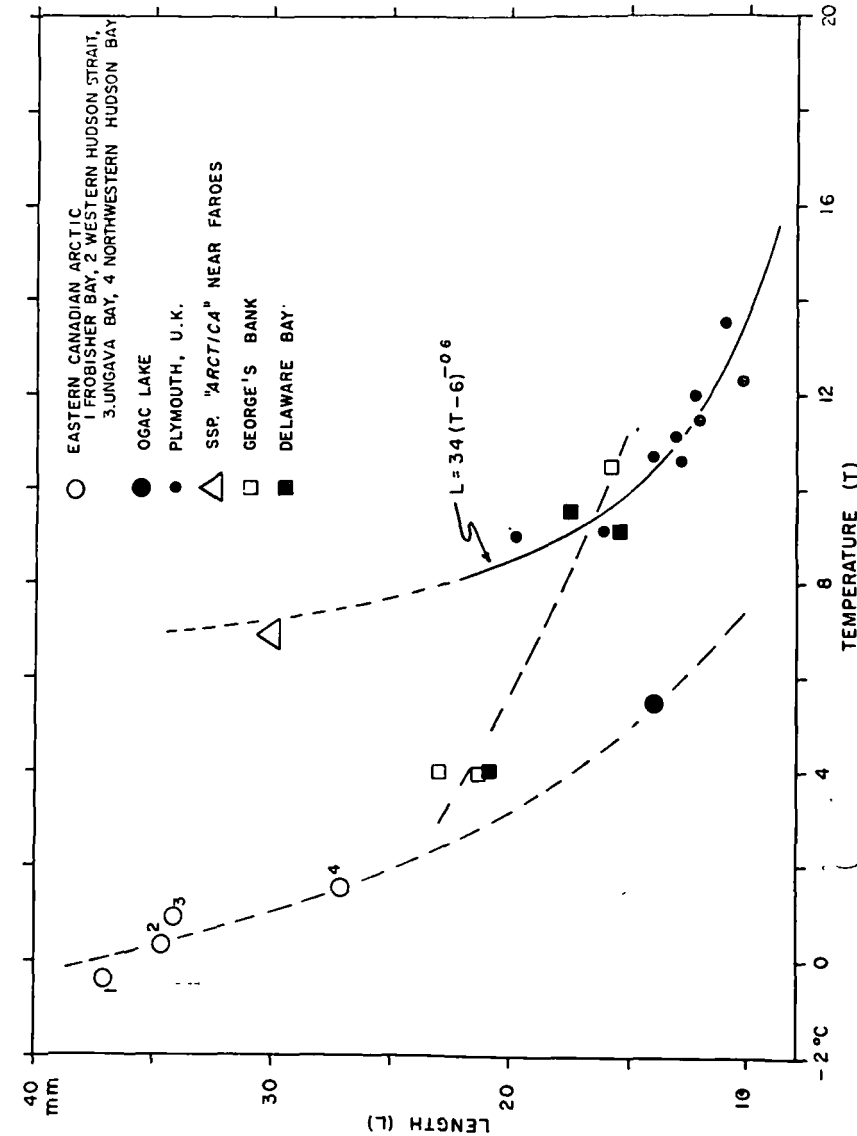

FIGURE 21. Adult size of *Sagitta elegans* from different localities plotted against estimates of mean temperature during their development (90).

very crude measurement of mean temperature during development in nature, and express adult size as a function of this. I have taken what I imagine to be the entire growing season for each of these populations in these localities. This can be fixed very easily in the case of the curve from Plymouth, where Russell gave information on the length of the developmental period as well as final size, and I was able to get mean temperature during that development season and fit this curve. This I did for a paper I published recently (90). The other material is new.

The dashed-line extrapolation of the analytical curve fitted through the Plymouth animals passes close to the approximate position of so-called subspecies *arctica* from the Faroe Islands region, which I think probably belongs to the same eastern population of *elegans*.

The other points for the eastern Canadian Arctic and the east coast of the United States are all from published information, so that I have not introduced any personal bias here, except at point 3 in the Canadian Arctic, which is one of my own from a small landlocked fjord I am studying.

You see that the temperature responses are quite different between these, the Canadian Arctic, the eastern Canadian Arctic, western Atlantic, and eastern Atlantic. I can also show that the amount of food, at least in this case, does not distort this pattern at all. The same is true of another organism, *Pseudocalanus minutus*.

SLOBODKIN: Is the difference in temperature between these three curves in the Figure supposedly due to some specific differences or genetic differences?

MCLAREN: Yes, in fact, genetic differences, which I think make it quite impossible for these things to interbreed because they are different species in some physiological sense.

FIGURE 22 shows exactly the same thing, really for another organism from the same localities, *Pseudocalanus minutus* (all from published data except the point for Ogac Lake). Again you see exactly the same general response in these areas, a shifting of the temperature curve downward in the Canadian Arctic relative to the Eastern Atlantic, and a flattening of the curve in the Western Atlantic, and this is correlated with the fact that the temperature range is exceedingly narrow in the Canadian Arctic and the Eastern Atlantic and exceedingly wide in the Western Atlantic.

I have also gathered evidence that if food is above a certain threshold level, development is a distinctive function of temperature, a function of the same general form as represented in these size-temperature relations (FIGURES 21 and 22). In conditions of sufficient food, these animals

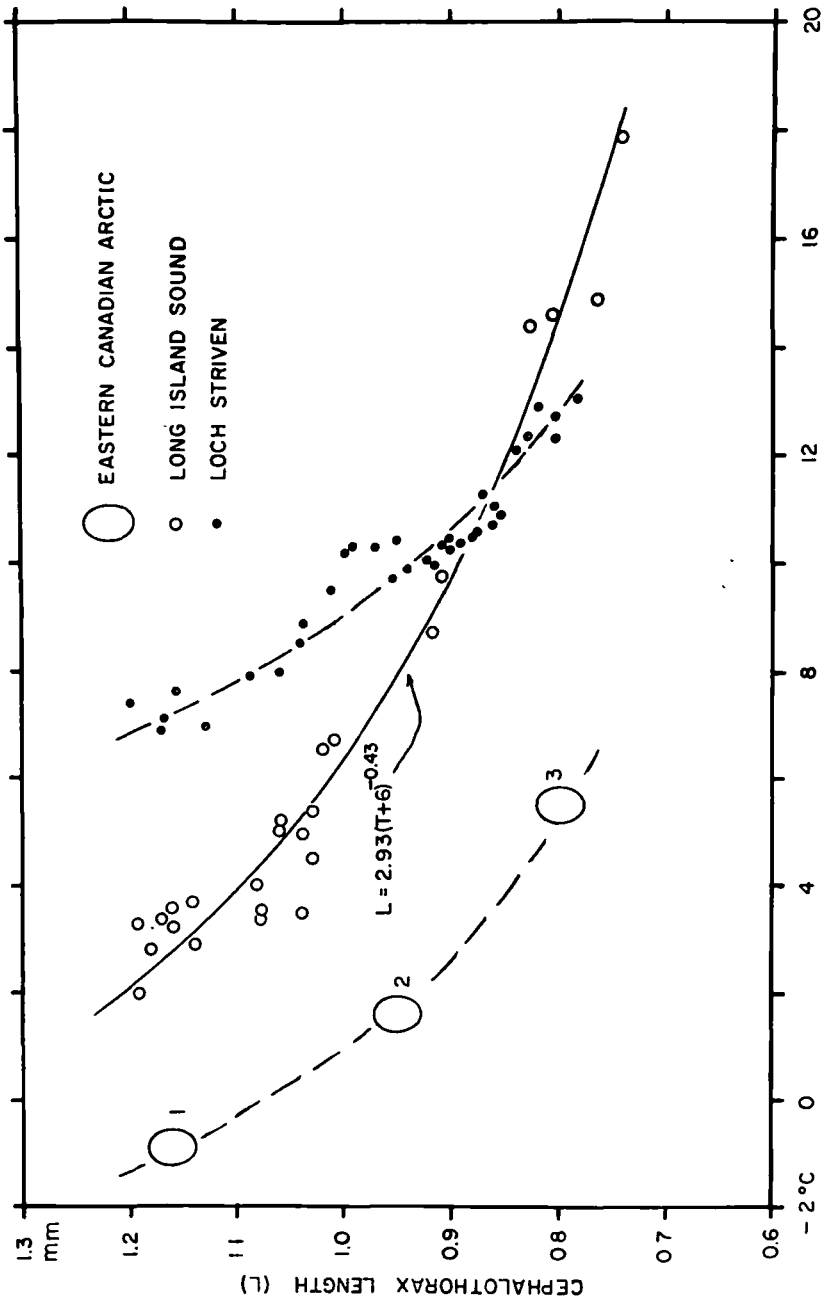

FIGURE 22. Adult size of *Pseudocalanus minutus* females from different localities plotted against estimates of mean temperature during their development(90).

will grow in a rather strict relation with temperature, and you can deduce all sorts of things from this.

STRICKLAND: What is the time scale? This does not say how long they have taken to get to a given maximum length.

MCLAREN: That is a separate question. The rate of development, I can show you, will also be a strict function of temperature, if food is above a certain threshold limit and this threshold is reached at a level which is probably much lower than the natural level of food in the sea during certain times of the year, particularly during the spring bloom, for example, for these organisms. These organisms are, in fact, important bloom animals, both *Sagitta* and *Pseudocalanus,* the former being secondarily dependent.

FAGER: Is there not a possibility that the quality or quantity of food is correlated with temperature and that this is a secondary correlation?

MCLAREN: No, for *Pseudocalanus minutus* from Long Island Sound and *Sagitta* from Plymouth, I have evidence which shows that the degree of scatter which exists around the size-temperature curves is not accounted for by food at all.

MCLAREN: *Pseuodcalanus elongatus* is in there somewhere too. It may simply be a temperature-morph of one sort or another.

FIGURE 23 shows the same kind of curve, a three-constant curve fitted very gaily to three points. This, of course, would be a very fast thing except that this particular function was chosen on other grounds.

The constants are fitted, of course, but in a paper I wrote on vertical migration(90), the exponential constant shown here (FIGURE 23) was used as a guess, and now turns out to be almost exactly as predicted.

This simply shows the development rate of eggs of *Pseudocalanus.* Ideally, one should get the laboratory development rate for the whole length of life, but I know, or, at least, I think from other organisms, that it will follow the same sort of curve.

CONOVER: This is actually the time the eggs are carried? The time from the laying of the eggs to the hatching of the nauplius stage?

MCLAREN: This is the development rate to hatching, the reciprocal of development time to hatching.

SLOBODKIN: Is that not what one would ordinarily expect of any egg; that if you raise the temperature you speed it up?

MCLAREN: Yes, of course, if you can put together development rate and ultimate size (and size, of course, at any stage), solve for size at any stage, using the same temperature function, then you can express production, growth or what-have-you in terms of temperature, when food is adequate.

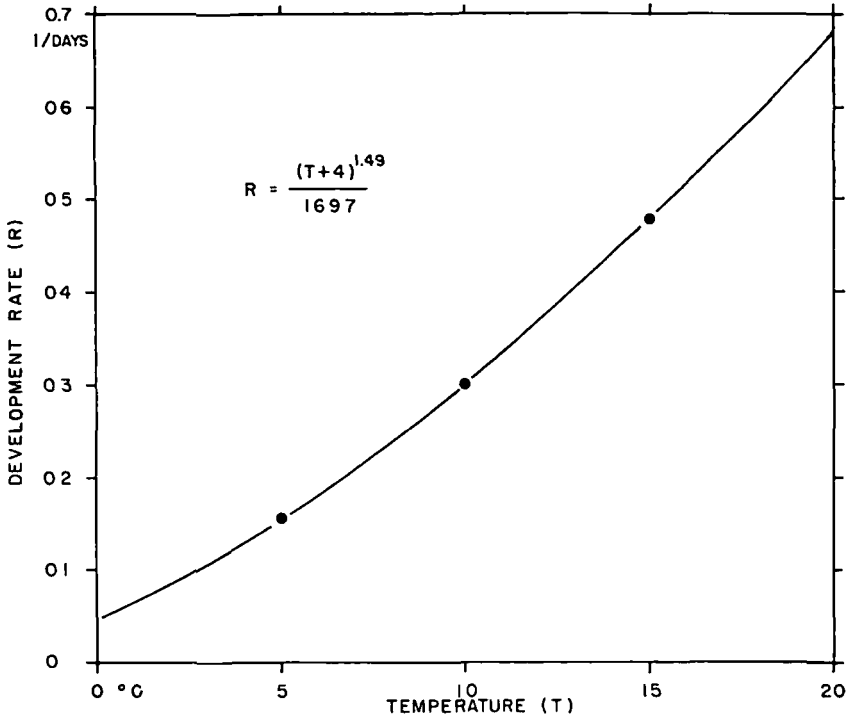

FIGURE 23. Development rate of eggs of *Pseudocalanus minutus* from Loch Striven. [Data kindly supplied by S. M. Marshall(91).]

FAGER: In each of your expressions I have noticed a $T+a$ constant value. How do you determine that constant value?

MCLAREN: This is fitted by least squares. It is simply a scale correction. You will notice, for example, for the Eastern Atlantic where the temperatures are higher, the scale correction is above zero, fitted at around 6° for *Sagitta* (FIGURE 21), which is very rarely, if ever, experienced in the Eastern part of the Atlantic. In the Western Atlantic and the Canadian Arctic, the scale correction is below zero. It is a "biological zero," a rather commonplace notion in physiological ecology.

KANWISHER: Let me see if I interpret these properly. Your second curve here shows that at 10° over 0° you had a six times rate of development, and yet in the previous one at 0°, one got twice as large as at 10°. It takes twelve times as long to get to be an adult as it would at 10°, if you put these together. I do not know whether you are talking linear dimensions or weight here.

MCLAREN: You mean if you put development rate and final size together?

KANWISHER: Yes.

MCLAREN: Final size is adult size, regardless of the temperature involved.

KANWISHER: And yet in cold water there is certainly a shorter season, is there not? Intuitively, this is not something you would expect.

MCLAREN: These are field data. I will defend them shortly.

The other parameter which is easily measured from that is egg number, which is very easily done in case of an animal like *Pseudocalanus* or like *Sagitta,* because they carry their eggs in very neat bundles and this represents a full clutch size.

For the Western Atlantic, Loch Striven, I fitted the relationships between cephalothorax length(90) [this is from Marshall's work in Lock Striven (91)] and egg number (FIGURE 24) the exponential form of the curve being chosen on general principles, of course; the exact fit is probably closer to cubic in the truth. At any rate, you can express egg number as a function of adult size, and, therefore, egg number is a function of tempera-

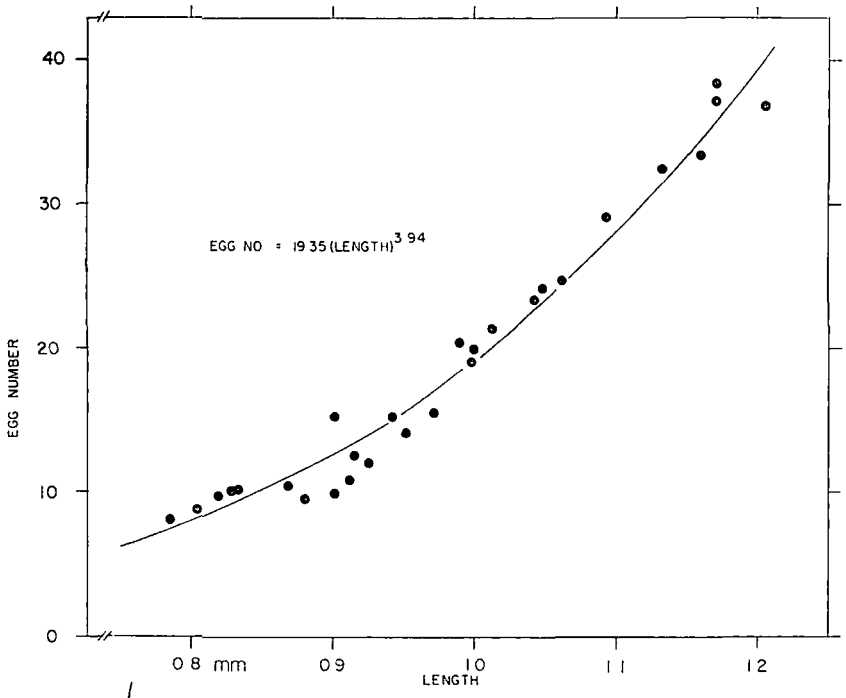

FIGURE 24. Relationship between number of eggs in clutch and female size of *Pseudocalanus minutus* in Loch Striven. After McLaren(90).

ture. Therefore it is possible, given an adequate food supply for these two organisms (and I think this is true of the generality of plankton in the North Atlantic, possibly in other latitudes, too) to express development rate, size, egg numbers, all of these as functions of temperature when food is adequate. This means that you can express practically everything you want to know about production of plankton in terms of temperature because these things can be integrated within the same expression and give you an absolute intrinsic rate of increase, potential rate of production—well, realized rate of production in certain circumstances.

This is very convenient, but does not hold universally. FIGURE 25 shows the same curve extrapolated on a graph, and material from various localities in the Canadian Arctic, is superimposed. You can see they do not fit on this curve, so we cannot argue from the Eastern Atlantic to the Canadian Arctic on this question of egg number directly. Does this mean, then, that we have to examine every locality separately and find out exactly what the relationship between size and egg number is in that locality? Apparently not. There is a clue in that egg size in different localities differs, as well as egg number. In the Canadian Arctic mean egg size for each length group differs between regions. I have got some raw data from S. M. Marshall recently* which enables me to give a tentative estimate of egg size in Loch Striven. In Loch Striven the eggs are very much larger than in most Canadian Arctic localities.

At the top of FIGURE 26 is a group of eggs which I am going to discuss, and which I think are of great importance, very large eggs. At any rate, you see that in the Canadian Arctic, the open circles and squares, the eggs are smaller than in Loch Striven.

If you then take this relationship and attempt to correct the curve in FIGURE 25 relating egg number to size everything gets back on the right curve again. Total volume of eggs produced by a female is a strict function of size, regardless of where she is found, but the number will vary because the eggs vary in size.

CONOVER: Is there a relation between time of development and egg size?

MCLAREN: Yes, there is, which I am going to get on later—another clue, another approach, another way of transforming data very easily.

This is what one is able to do: examine a population of *Pseudocalanus* at several times during a season, say, when the animals are developing in a plentiful food supply but at different temperatures, work up the relationship between size, female size, and temperature, try to get some-

* S. M. Marshall, Scottish Marine Biological Association, Millport, Scotland: Personal communication.

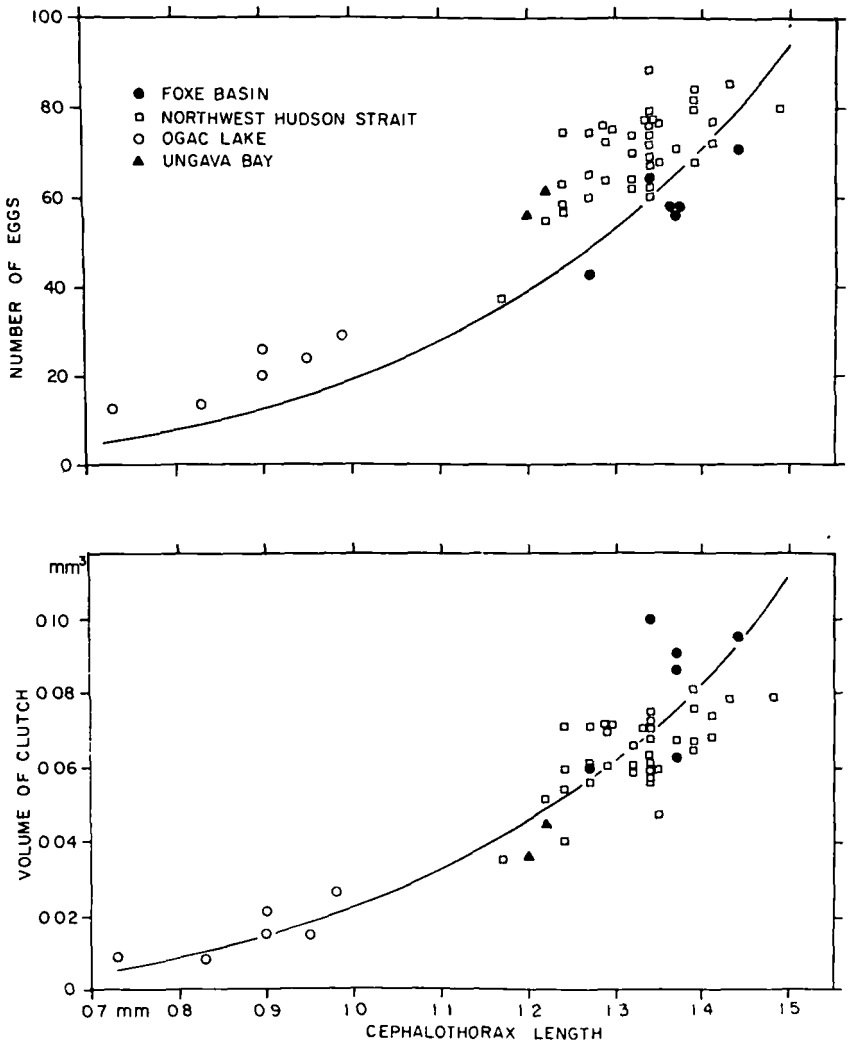

FIGURE 25. *A* (*top*). Egg number of *P. minutus* from the Canadian Arctic compared with the extrapolated relationship of egg number and size in Loch Striven. *B* (*bottom*). Total clutch volume of *P. minutus* from the Canadian Arctic compared with the extrapolated relationship of clutch volume and female length in Loch Striven(90, 91).

thing on development rate of the eggs, measure the number of eggs or measure the size of the eggs, and then you can automatically get the number of eggs for a female of any given size. Then plug all these things together if you want some measure of intrinsic rate of increase or potential

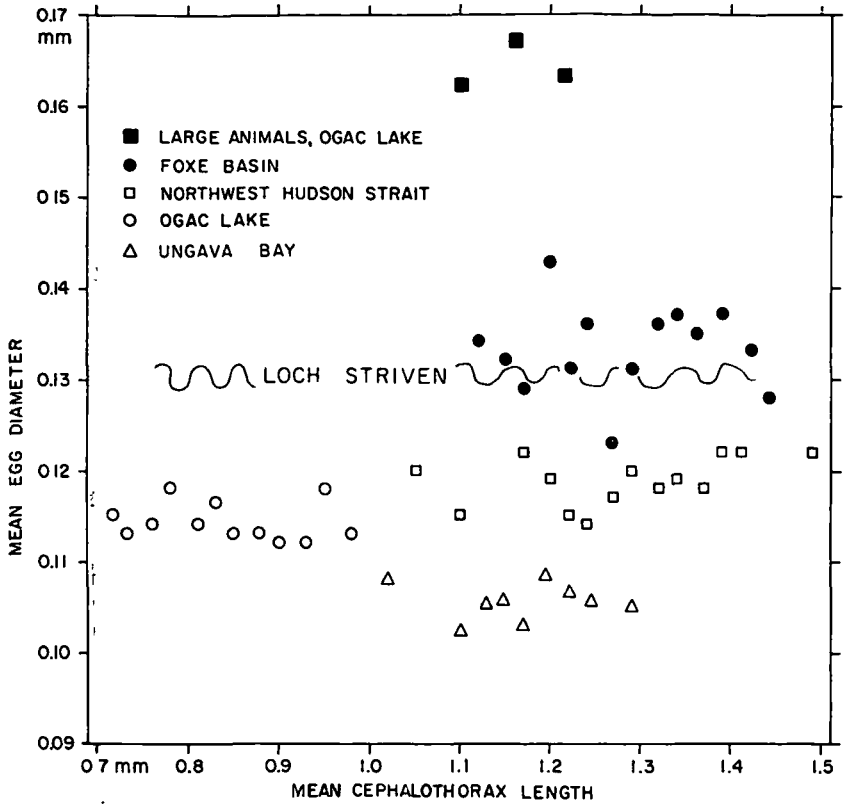

FIGURE 26. Egg diameter plotted against female cephalothorax length from various Canadian Arctic localities. The tentative size for Loch Striven eggs is based on measurements kindly supplied by S. M. Marshall, based on six eggs taken in May 1963. The points from the Canadian Arctic are each averages of three or more egg diameters(91).

production, which you can convert into carbon or energy, or what-have-you, depending on your choice of expression.

It is, I think, a very neat way of getting at some of these questions in the field, but the transformation is difficult for different localities. I have shown you one example, one type of transformation where you can determine egg number from egg size. Egg size is a much simpler thing to measure than egg number, but there are further kinds of transformation which are beginning to peek out. I am not sure where it is going to lead. For example, egg size is a very important clue. I have in this little lake I am working on two kinds of *Pseudocalanus*. One is an ordinary temperature dwarf compared to the one living outside, but it has eggs exactly the

same size as the animal living outside the lake. The other is an animal which is much larger, and which I had suspected in the past was simply an animal introduced from the sea and which had not had its size, as it were, reduced through a series of molts by the higher temperatures in the lake. But I discovered in the spring of 1961 that these large animals in the lake, which are very rare, something of the order of 1 to 2 per cent of the total population, were carrying much larger eggs (FIGURE 26). They are, in fact, about three times the volume of the eggs in the smaller race in the lake, and the adult females are about three times the volume as well. It looks as though here is one possible transformation.

(If you measure egg diameter, you can get the linear constant of adult size as a function of temperature.) Whatever the curvilinear function is (I have chosen one kind of function) the linear constant determining the difference in slope (not difference of curvilinearity, however complex that may be) can be expressed, I think, as a function of the diameter of the egg; so if you know the diameter of the egg it is of immense help in transforming these simple equations.

SLOBODKIN: Are these rare large copepods members of the same species as the rest of the population?

MCLAREN: That is a matter of definition. I think they are hexaploids. There are clues in the literature that this sort of thing might occur among copepods.

SLOBODKIN: Actual hexaploids?

MCLAREN: I am assuming that from the volume ratios. This is a standard thing, I gather, for tadpole or DNA people, cell physiologists, etc., to come across, namely, that the volume of a cell of a given kind is roughly a proportionate function of the amount of DNA or the number of chromosomes, or what have you.

SLOBODKIN: But this is volume of the animal.

MCLAREN: Well, yes, each cell is three times as big, the whole animal is three times as big, the egg is three times as big.

RAY: How many chromosomes do these creatures have?

MCLAREN: I think *Pseudocalanus* as a haploid has eleven, but I am not sure. I do not think it has been properly examined for many years. *Calanus* has been examined recently. Anyway, I hope to get the right material next spring to check this out. This is incidental to the possible usefulness of this approach, but it is an interesting question.

The other thing is that the linear constant of development rate seems also to be a proportionate function of egg diameter. This is something which is 'way out at the moment, but I think it might actually prove generally true.

In Ogac Lake, my landlocked fjord on Baffin Island, where these two

copepods exist, in 1961 I set up a fertilized column like Goldman's(92) and in that fertilized column the big animals grew; and thrived quite happily. It was easy to follow the developing broods through the season, and compare maximum development rate of the large and small form. It turns out that the ratio of development rate of the small to the large form is aboût inversely proportional to their length, and in this case to their egg diameter. There is a possible dynamical explanation of this that I will not go into at all. Again, it may be useful to transform material.

The sorts of development curves I get in Ogac Lake are extremely easy to follow (FIGURE 27). For example, you can follow the upper brood quite handily through a sequence of dates. If you can then convert this sort of thing from such a simplified setting as Ogac Lake into realized production, you might be able to transform the results for any other part of the world where this animal exists by the quasimathematical devices I have suggested.

KANWISHER: What does the figure show?

MCLAREN: These are absolute samples where all stages are fully represented taken with No. 20 nets which I might say are very rarely used on the east coast of the United States. No. 2 seems to be the popular net choice in the eastern part of the United States, and this excludes everything from stage V copepodite down (FIGURE 27).

This is just a representative sample. This is not one I would use in any serious way but in such samples you can get direct measurements of production, realized production, simply by integrating survivorship with growth. This is being done very handily by the Russians(93) these days, but not so much by ourselves.

You can take the direct measurements which can be expressed as production per individual, of course, or per unit biomass, whatever you wish, convert these back into the other parameters which I dealt with earlier in the female, adult size as a function of temperature, development, and so on, and then apply these same parameters of production universally throughout the range of the organism.

The question of distinguishing between net and gross production, or assimilation and growth, and so on, may be considered in a backward kind of way in this whole approach, and I am not sure I should take up more of your time.

FAGER: Before you go on, may I ask a question about FIGURE 27? Are you not somewhat disturbed by the fact that the most obvious initial brood there, the one that was by far the most abundant, is precisely the one which you cannot follow in a logical sequence, or at least it does not appear to increase in size, whereas one which is a slight hump in the upper stages does follow, I agree, logically in time.

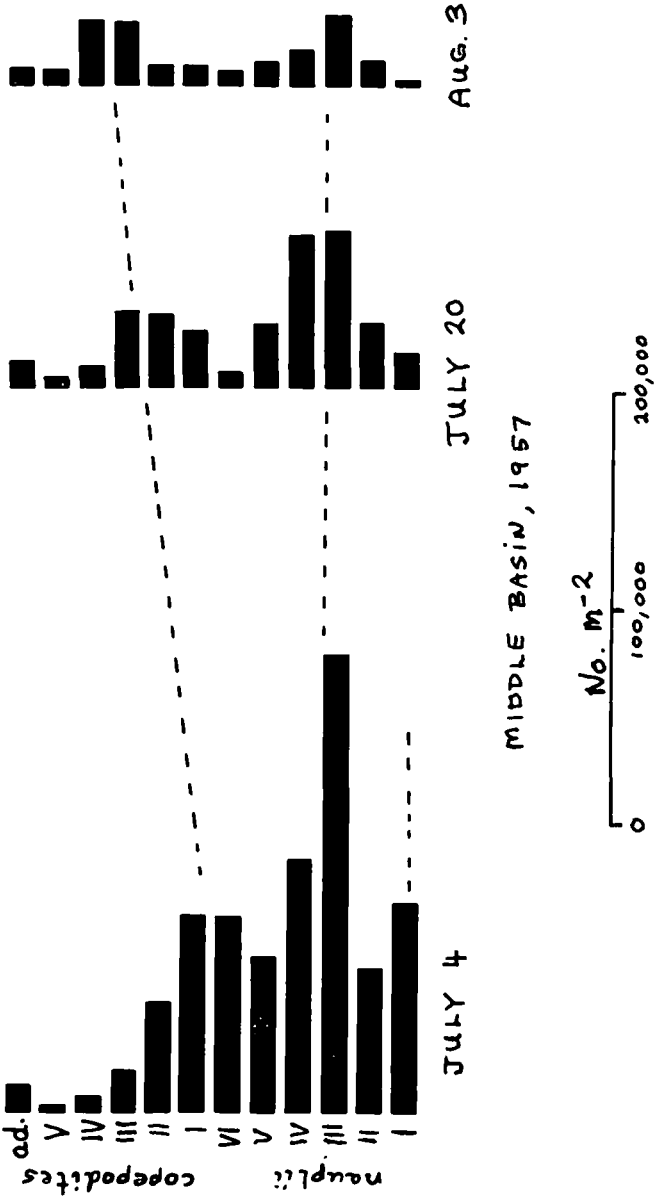

FIGURE 27 Development of the copepod *Pseudocalanus minutus* in Ogac Lake, a landlocked fjord on Baffin Island. Unpublished material.

McLAREN: You made the error of assuming that that lower brood was the initial brood. It was the second brood which was doomed to be born in a very poor food supply.

FAGER: It never grew up; is that it?

McLAREN: It never grew up. The first brood got off because it timed pretty well with the phytoplankton bloom here.

EDMONDSON: Earlier in your presentation you said several times, "as long as there is enough food," or something like that.

McLAREN: As long as there is sufficient food. I know you people are following an entirely different tack, but if you can show that female size is a strict function of average temperature during development, the way it seems to be on those graphs, and you cannot show that food has anything to do with change in size, you can deduce from that that the female will only mature, in fact, when there is sufficient food—will only develop when there is sufficient food. It will stop growing when there is insufficient food. Therefore, there must be occasions in the world ocean when food is always sufficient for it to grow at this temperature and rate. It may stop.

YONGE: What certainty is there that this question of the size of the egg is anything but phenotypic? What certainty is there that it is genetic?

McLAREN: It may perfectly well be phenotypic. I am not prepared to argue it fully except for one point, and that is, at least the relationship between female size and egg size is a relatively constant one.* You might suppose that since the seasonal environment imposes marked differences in female size, there might be seasonal differences in egg size. Yet, in different localities there are differences in egg size, although when you transform this into total egg volume, they all fit on the same curve, which is the thing I am interested in, and that suggests, although it does not constitute proof, of course, that it is not phenotypic but genotypic because something is constant in the system in the egg volume.

SLOBODKIN: There is something in Doctor Yonge's statement and Doctor McLaren's acceptance of it which I find very disturbing, and I will come back to it at greater length later but I would like to mention it now. The phenotype is an intensely underrated thing.

I read through Mayr's(94) new book, and in the last couple of chapters it dawned on me that the only thing that is being held constant is the phenotype; that you catch your miscellaneous fruit flies, or what-have-you, and you find their genes are switched all over the place, they are loaded

* I have since found that egg size may in fact vary seasonally within a locality, although much less proportionately than female size. However, this does not affect the conclusions offered here.

with recessive lethals, their biochemistry is swinging in every direction, but the number of bristles stays fixed. In some peculiar way the phenotype is the thing that faces the world and the end product of the whole evolutionary process and the key to the evolutionary process lies precisely in features of form and size of the sort that have been indicated.

If an animal has a genetically fixed size, it is because there is some evolutionary significance in having a genetically fixed size. If an animal has a phenotype varying with an environmental parameter, there must be a way of asking the question which we have been walking around ever since someone invented biochemistry: Why? What good does it do the animal to have that particular form or phenotype? This is a respectable kind of question. We will get to the respectability of it another time.

McLAREN: I thought I might finish this up, to show how general this sort of thing might become. This is a very simple open-system equation which expresses a lot of things that were said yesterday:

$$\frac{dW}{dt} = af(W) - kg(W)$$

It says simply that the rate of change of weight in time is equal to some constant times some function of weight, minus some constant times some function of weight, $af(W)$ representing uptake, assimilation, whatever you want to call it, and $kg(W)$ representing everything else which conspires to reduce the biomass. It could include predation, if you wanted to become ecological, but in this case it is best confined to questions of growth of the individual.

I have recently shown in a paper about vertical migration that if $\frac{dW}{dt}$ is a function of temperature, and indeed you have seen that the growth, however expressed, is a function of temperature, you can get at these functions on the right hand side as functions of temperature.

I have used a special kind of solution of this equation(90), but there are other possible kinds of solutions. This means that you can get at things like gross production and net production as functions of temperature. This has been done by myself and a number of people. I have seen three papers published simultaneously with mine in which this kind of approach is being used. Erik Ursin(95) in Denmark has done the same kind of thing for a variety of populations, using an entirely different temperature function from mine, but one that is nevertheless satisfied over the narrow temperature ranges involved.

So I just put this to you, that instead of analyzing each of these functions separately, which is what you do when you feed animals in the laboratory or measure the feces, why not try growing them with food in plentiful supply and getting this information out?

There are also more very powerful ways of using temperature to get at these questions. Why not feed them at one temperature, get them into diurnal rhythm which might simulate vertical migration, and let them spend the rest of the day at another higher or lower temperature? This I am sure would distort the temperature function of dW over dt in such a way that you could get at the constants very easily.

The equation gives a growth rate, but this, itself is a function of temperature. If you can express this as a function of temperature, you very quickly get at input and output as functions of temperature, if you perhaps feed them at one temperature and grow them on the average at another temperature—this kind of thing. I just suggest that this kind of approach—simply growing organisms with a plentiful supply of food in varying temperatures—may help us get at questions of assimilation, uptake, growth, production, and so forth, with a few shortcuts.

SLOBODKIN: Do you mean that if you have the dW/dt function at some particular temperature, then you take the dW/dt function as a function of temperature?

MCLAREN: Yes, "a" can be taken as a function of temperature; it is the metabolic activity of a unit of the organism. And $f(W)$ is a separable function of the mass of the organism.

SLOBODKIN: What you are saying is that this equation is subject to some sort of a uniform transformation with temperature?

MCLAREN: Yes, that is right.

SLOBODKIN: And that the thing we are talking about is not this equation itself but the transformation system?

MCLAREN: The possibility of transforming the whole thing as a function of temperature. If you want to get at the coefficient of anabolism, or gross production, or whatever, and the coefficient of catabolism, temperature may be of assistance. Very simple experiments involving temperature variations may be used. I am not able to perform this, but I throw it out as a possibility.

I might say that these kinds of relationships with temperature have a certain universality. You can show them for fish, for copepods (two or three species of copepods), for bivalves, and for chaetognaths, and I am sure this sort of thing is going to prove more universal in the sea than we might conclude from *Daphnia* and *Hydra* experiments.

STRICKLAND: What is the basic thing underlying all species which have the same temperature function, some critical enzyme system?

MCLAREN: Not the same temperature function. The parameters are different, of course—the same form. I think that this function which I am using is simply an approximation to something which may or may not be analytical, and may vary in fact between organisms. But the simple

function which I was using, where rate or size is equal to some constant times a temperature corrected by a scale correction, alpha to some power, will describe almost any monotonic curvilinear function over a fairly narrow temperature range, and there are other functions which will work equally well.

STRICKLAND: Then k depends on the species?

MCLAREN: Yes; so does a.

STRICKLAND: You were just assuming the form of the equation?

MCLAREN: Yes. But, nevertheless, with these species in different localities, these constants all vary. I have suggested ways in which the constants may be transformed within species with a minimum of work, by going out, picking up a few animals, looking at their eggs, and this sort of thing.

CONOVER: In some species, size and number of eggs is going to be more important; the number of eggs is going to be a function of the size of the adult.

MCLAREN: I think at least in the organisms which I have here, *Sagitta,* this is true, as well as in *Pseudocalanus.* The two are linked very strongly; size and number of eggs are in constant relationship.

YONGE: Is not the size of the eggs dependent on the limited period in which food is available?

MCLAREN: It may be for some organisms. I claim no universality, but it is not true of *Pseudocalanus.* You can see that egg size is constant seasonally or against any other variable, within a locality.

YONGE: And that is going how far, 'way up into the Arctic?

MCLAREN: Yes, Eastern USA, and I have material from Long Island Sound, the Arctic and from Plymouth and Loch Striven now which all conform. The same seems to be true of *Sagitta.*

RAY: I am still confused about how you determine the temperature for any particular species. Is it the ambient water temperature at the surface or at some depth, or daytime or summer or winter?

MCLAREN: You see the points are lined up in a kind of reasonable way. That suggests there is some meaning here, but I have been very approximate and very bold, perhaps, in choosing the proper expression of temperature. In some cases there was sufficient information in the paper from which I was analyzing the data, enough information so that I could get mean temperatures during the development period, which was worked out pretty well by Marshall(91), for example, for *Pseudocalanus.* She says that animals born in early February mature in March.

STRICKLAND: At what temperatures?

MCLAREN: Mean temperatures.

STRICKLAND: Of what, the whole depth?

McLAREN: In the best examples which I have, the whole depth was fairly unstratified. This is true off Plymouth and not so true in Loch Striven.

In the Canadian Arctic, I simply took the mean temperature during what I imagined to be the growing season, the middle of June through the middle of September, in the upper fifty meters in the case of *Sagitta,* and in the upper twenty meters for *Pseudocalanus.* That is where the animals came from. This is very crude, but the results make it seem as though it is not unreasonable. I do not think I am introducing anything artificial into the system by doing that. I am introducing anything artificial into the system by doing that. I am just making the data less reliable. You notice I put dotted lines into the Canadian Arctic because those points were from different localities, and I have some evidence that each locality, which I depicted on the Figures, has different properties, so it is just an approximate curve, but, at any rate, you can see the whole downward shift of temperature.

RAY: It would be hard to figure that out for intertidal forms where you have a wide variation over a mean growing season on an exposed beach, which is afterwards covered with water, and so on.

SLOBODKIN: Do you think that the shift with temperature is a function of a physiological property—that is, for example, an enzyme system of something of that sort that was accelerated or decelerated by temperature, or do you think it is an adaptive overall phenotypic syndrome related to the role of that animal?

STRICKLAND: Let us have a phenotypic syndrome identified for the record.

SLOBODKIN: I would rather wait, because it fits into another context.

FREMONT-SMITH: Could we have it both places, or is it going to take a long time?

SLOBODKIN: Why do you not answer Doctor McLaren, and then let me do it?

McLAREN: I think this is an overall, adaptive thing. I think temperature is irrelevant in some sense. I think that the animal adjusts its physiological rate not according to temperature as such, but according to the necessity for growing at certain rates in that environment. I have definite evidence of this from *Sagitta elegans,* I think. This animal you saw (FIGURE 21) had its temperature response shifted downwards in the Canadian Arctic relative to the English Channel. Yet in the Arctic, the animals are very much larger than they are in the English Channel, and they are biennial. In the English Channel they breed, of course, five or six times a year.

Why does not the animal shift the temperature-response curve down

even further and breed annually at a smaller size, as they do in fact in my "lake"? This is a question which can only be answered if you have enough information: egg number, development rate, from which you can extract a realized, not an intrinsic, but a realized rate of increase. You also have to have information on mortality rate. I have attempted to do that by taking information from Professor Max Dunbar's work(96). If you take these realized rates of mortality based on the difference in size of two modes from year to year, and plug into an equation with egg number and development rate (either annual potentially or biennially, as it is), you will find that it is very marginal, indeed. The advantage of having a large number of eggs does not quite overcome, on my analysis, the disadvantage of a biennial as opposed to an annual development rate, but my data are probably very badly biased because I do not have material from early enough in the season when most of the *Sagitta* do, in fact, breed. I am quite satisfied that it is advantageous to mature, not in one year, but in two, in terms of the realized rate of increase—which is zero, I suppose.

EDMONDSON: Did I understand that right, that you are suggesting that it is better to breed once every two years than once every year?

MCLAREN: In this instance, yes. You cannot breed but annually or some simple multiple thereof. You have to breed in the spring when the young nauplii are present for your young, so you can breed once a year. I think that the second year, when you take all factors into consideration, is the most advantageous.

EDMONDSON: Ordinarily, one gets the picture that shortening up the period of immaturity will have a greater effect than simply adding on the same amount of time to the length of life.

MCLAREN: Well, the only way to analyze this question is to do just that: measure the number of young which are produced and the eggs which are produced, the development rate and plug that into a suitable equation and come up with figures. I have concluded that it is slightly more advantageous to be annual; but the data are biased.

EDMONDSON: These numbers will be enormously different to make up for that difference of a factor of 2.

MCLAREN: I have a curve somewhere showing the relationship of egg number of *Sagitta* and length. It rises rather steeply logarithmically.

YONGE: But surely the whole thing comes down finally to the amount of food the animal can get, does it not?

MCLAREN: That is right, the food is the primary thing; temperature is irrelevant.

EDMONDSON: Finally it comes down to what happened. This animal

has evolved its whole response system and the result is that these species exist today rather than having been liquidated.

McLAREN: It is commonly said today by the environmental physiologist that an animal is ill-adapted because it has not quite the metabolic rate it should have in these cold waters, but maybe this is irrelevant. Maybe what the animal is metabolizing for is to improve the chances of its offspring.

SLOBODKIN: Now may I try to answer Doctor Strickland, because I think we have examples of the kinds of problems that arise about this concept. That is what I was waiting for. There are two ways of analyzing a biological situation. One on which we, and most people, spend most of our time, might be considered a mechanistic analysis; that is, you have an organism and then you analyze it into a certain number of parts and you can handle those, in principle, at least, by extensions of physics and chemistry. There is another kind of argument which just happened now, and I figured it would, and that is why I did not want to say anything before it had, where you say, "Well, what good is this for the animal and how is the animal winning by doing this or that kind of thing?"

The possibility which has been advocated by various primitive biochemists (and I use the adjective deliberately, I think you will see what I mean in a second) is that to argue in the second pattern is simply illegitimate, or, at best, archaic. What I want to suggest is that the second type of argument is absolutely vital and legitimate, and if I may have around four minutes I can present you with an analogy which will demonstrate why it is vital and will also indicate why, under certain circumstances, arguments about what an organism is trying to do sound empty.

Let us imagine a group of investigators coming into a room where people are playing a game, say chess, and the chess players are as silent as chess players usually are, and the investigators have never seen a chess board before. By constant and careful intellectual activity, they discover that regardless of the size, color, shape or texture of the chess board, chess men and chess players, the games being played all over the room are identical—that is, the same game in a sense is being played, and this is defined by pointing out that the same initial number of pieces are present, some of them are haploid, some of them are diploid, some of them are as much as octoploid. They have polarity in their movements on the board, and the horse seems to move in an alpha helix.

You can see how this would build up. At that point they feel they understand the game of chess. In fact, they have completed their analysis of chess and then one small person in the group says, "Yes, but half the players lose." Well, that is a matter of chance. How can you tell it is a matter of chance? You can tell it is a matter of chance because we

are all playing by the same rules, and some players will lose some times and win other times, and there does not seem to be any universal pattern of moves that results in winning, and this implies that you cannot build a theory for how to win at chess.

But as a point of fact, you can. A book on how to win at chess differs from a rule book of chess in several critical ways. First, it is much longer. It is more ambiguous in the sense that this move is usually a good move if thus and so happens; but if thus and so has not happened, it is a bad move. "It is usually a good move," means that if the opponent does the kind of thing that you expect opponents reasonably to do, this move will lead to your benefit, but if the opponent is either wise enough or foolish enough, an ordinarily good move can become a bad move.

It has been suggested by Lewontin(97) that the evolutionary process can be considered as a game played by organisms and that they adopt an evolutionary strategy, and this, incidentally, is why the phenotype is such a fixed thing. The thing that faces the world is the phenotype.

There are two problems that arise. First of all, can you really use game theory as an analog of evolution? I will point out that you cannot —not quite comfortably, in any case. In a game (and this is absolutely critical and why the argument was starting just a moment ago) the players typically play on a gaming table, a chess board, a tennis court, a dice table or something, and Huizinga(98) has pointed out in his *Homo Ludens,* which is not in the biological literature but in a sense ought to be, that if you play a game you play for certain stakes and you either win or lose. What you mean by "winning" is that you take your stakes and you leave the gaming board and you cash in your stakes somehow. It may just be money, in which case it is simple, or it may be master points in chess or in bridge, or it may be a laurel wreath which carries social advantages or sexual advantages in another society, and one can visualize that the winner has something he can take away from the gaming board and use.

But in the evolutionary process, there is no place else to go. The organism, if it is playing a game, is playing the kind of game that Kafka might have thought of where you play, say, poker with the stipulation that anyone who leaves the poker table because he has lost all his money is killed or is dead, or just does not exist anymore. In fact, the only existence is at the gaming table. You would play very differently in that kind of situation than in a situation where you have stakes that you could put in your pocket and walk away with.

There has been talk, and we have heard it this morning, we have heard it over and over again at biological meetings, that an organism is increasing its growth rate, or increasing its mass, or increasing its production

or productivity or something in the evolutionary process, as if this were a good thing to increase and as if in some sense it was winning by getting this increase.

Now, this implies that somewhere there is another world in which you can cash in on your productivity or your abundance, or something similar —but there is not any other world. In our poker analogy, one would have to consider that the way you would play a game of this sort is not to try to win too much yourself, because winning does not do any good—you just want to make sure you do not lose too much—and in the process of trying to make sure you do not lose too much you will also, if at all possible, not force anyone else to lose too much either because if you have been playing successfully for five, ten, twenty milennia, which is the scale of our game, with a certain number of players around the table, then all the coalitions, all the dangers that might have happened have by and large happened, and you have weathered them. If you force anyone out, other shifts are going to occur, everyone else is going to have to shift their strategy a little bit, and the next one who might leave might be you, and it is certainly not to your advantage to drive anyone else out since you have no place to cash in your money anyway. So if organisms are evolving toward anything—and I think they are—it is toward homeostasis in the most general sense possible.

This has been said before and as I say it now it is almost empty, but despite its being almost an empty statement, it tends to destroy a whole series of other statements which are not only almost empty but to the degree they have content they are false: that is, statements of the form, "Organisms evolve toward higher efficiency"; "Organisms evolve toward maximum numbers!" These are false statements, I think, by this analogy.

The only thing that any organism can possibly in any sense win by, just from the fact that we have just one world to live in, is homeostasis. And, therefore, an argument as to why does this animal adjust its egg number to its size in such-and-such a way—well, it really ought to do it another way, someone says—but that is not the point. The animal has done it. It has been a successful player at the evolutionary game so far.

Our business, perhaps, is to legitimately ask, To what degree does this contribute to the homeostatic structure of that organism or of its population; not to suggest that the animals should reproduce more or less, or get bigger or smaller. That is why I delayed my answer.*

SANCHEZ: I do not know if this is pertinent at all to the theme of the

* Editor's Note: Doctor Slobodkin has published extended comments on these matters; see L. B. Slobodkin, 1964. The strategy of evolution. *Am. Sci.* **52**: 342–357.

meeting. I would subscribe to most of what Doctor Slobodkin has said except that the connotation of the word "homeostasis" is somewhat dangerous, because, for one thing, it would lead one to assume that if the program of evolution were to continue, if the game were to continue along this line, probably a time would come when no more evolution would occur.

FREMONT-SMITH: Excepting that the environment is changing.

SANCHEZ: That is it, so that part of the game is changing environment which does not allow a reaching of a real homeostasis. I would think that probably the gain in the game is to remain in the game.

SLOBODKIN: That is right.

SANCHEZ: And if to remain in the game it is advantageous to increase or decrease size, number of individuals, life span, or whatever it is, then those things would be achieved.

STRICKLAND: Change in environment is change of the chess moves.

SLOBODKIN: Yes, and the evolutionary process seems to occur in spurts; that is, there seems to be from the geological record and common observations the general idea that things do not tend to change very much until they start changing, and then they change quite rapidly for a while, and then stop again. I suspect climatological changes or geologic changes spill new beasts in or eliminate something.

McLAREN: I might say that this whole question of evolution as a game has been examined in extenso by F. E. Warburton, now teaching at Barnard, who wrote one of the most stirring theses I ever read.* I think he has written something which will link up ecology, population genetics, and heaven knows what else in an extremely fruitful manner.

FREMONT-SMITH: Has any abstract of this been published?

McLAREN: So far as I know, no. He should publish it fairly soon.

FREMONT-SMITH: Can you put in a little more of the meaning of this?

McLAREN: He started out with things like chess and "Button, button, who's got the button?"—this is a very powerful and potent analogy—and finally abstracted to the point where he was dealing with various esoteric probability expressions, and he set up a system which can be translated upwards into population ecology, downward to the DNA molecule, outward to Mars and, in fact, he has attempted to deduce the whole of population genetics and things like some of the more mathematical aspects of ecology, the structure of genetic material—he has attempted to deduce all these things from the basic assumption that natural selection has occurred.

* Warburton, F. E. 1963. A model of natural selection based on a mathematical theory of guessing. McGill University Thesis.

SLOBODKIN: May I suggest that I would like to introduce for myself, and purely personally, a note of pessimism about a thesis that I have not read. Given any theory that does that much, I am always surprised that it does anything. I may be wrong.

EDMONDSON: I think you are right that the nature of homeostasis needs to be examined because so often when you use this, what you are talking about is staying the same in the face of a changing environment, not changing yourself because the environment has changed, and if you are truly talking about homeostasis, it is staying the same.

SLOBODKIN: Not quite. There are two things. First, the general evolutionary theorem that fitness of a genotype is measured in one sense (and I will define the sense in a second) with reference to the reproductive rate of that genotype; this has the boundary condition on it that this is a relative, productive rate within the population of that species. It does not carry in any sense the necessary implication that this is an increased relative reproductive rate with reference to other species, and that takes care of part of it.

The other point is that homeostasis, the process of homeostasis, involves changing yourself in some way as the environment changes in order to keep yourself constant in some other way. That is, if you have a thermostat in a house, its job is to keep temperature constant. The environment changes; it goes from summer to winter. The state of the house changes, the furnace turns on, but the internal temperature stays the same, so that something is being maintained constant in the biological system, the probability of extinction is being kept constant and low.

FREMONT-SMITH: Is this not in accord with Claude Bernard, that some aspect of the constancy of the internal environment remains constant to provide a freedom of life?

SLOBODKIN: Push it to the next level. The probability of becoming extinct within the next short time interval must be minimized. Everything else, all the phenotype characteristics, all the physiologic characteristics, genetics, etc., etc., etc., are all keyed to this, and in this sense we become (a) universal and (b) almost empty.

PROVASOLI: But in essence are you not saying that the primary business of an organism or a species is to remain alive?

SLOBODKIN: Not quite. The business of a species is to remain alive.

PROVASOLI: Exactly.

YONGE: And one move ahead—potentially one move ahead?

SANCHEZ: One move ahead in time, not in form.

SLOBODKIN: I am really not sure how far one can push this idea. Perhaps the primary value it might have is that the kind of purely biological speculation which has been considered unrespectable for at least

forty years—for example, why one valve of a bivalve grows twelve times the size of another valve of a bivalve—is reasonable. Put it another way: We ought to be in a position, as marine biologists (I am not really a marine biologist, but some kind of biologist), if an organism came to us and said, "Look, I have been thinking of switching my phenotype, getting my nose fixed, or something; what will this do to my evolutionary role?" to be able to provide some sort of an answer and we ought to be unashamed about our desire to provide this kind of answer.

To tell the poor beast, "This means you are going to have to change your acetylcholine concentration," is no help. In an interesting way it is not a help.

YONGE: I have worked on living animals all my life and this is the basic assumption on which one goes all the time, and it is so gratifying to realize that one can get to it on first principles as well as empirically.

FAGER: It seems to me that your whole argument hangs on the assumption of homeostasis and some long period of time in which these players have been playing together, so that everything that is going to happen has happened. Under these conditions it would be advantageous to keep the same group of players. On the other hand, in your answer to Sanchez you admitted that homeostasis was an illusion in the sense—

SLOBODKIN: I hope not.

FAGER: —that things did change; that you did not have the same rules all of the time or the same group of players. If the latter is true (which is what I understood you to admit to Sanchez), then I think it could be shown that the greatest advantage would be in having this group of players as small as possible because then you reduce the possible number of combinations of things that could happen. The ultimate of this is, of course, to have yourself as the only player.

FREMONT-SMITH: Or have it as large as possible so that you have enough players so that, no matter what happens, some will go on.

FAGER: Oh, but as a species you are worrying about yourself becoming extinct; you do not care whether some go on, but you do care whether you go on.

MCLAREN: Group selection heresy in new forms keeps cropping up. By the way, on the question of homeostasis and environmental change that Doctor Sanchez has brought up, there have been a number of papers recently in which the question of the asymptote of faunal saturation has been considered. In fact, there are areas of the world where some sort of faunal saturation seems to occur.

SLOBODKIN: Nikolsky(99) has placed great emphasis on this in connection with the fresh water fish faunas of Russia.

MCLAREN: We have MacArthur's and Wilson's work(100) on birds.

YONGE: You would not say that of the Caspian Sea, would you? There is a high form of insufficiency there.

SANCHEZ: Probably because of historical reasons.

YONGE: I suppose so, yes. The converse may be true.

MCLAREN: Small numbers of organisms do not necessarily imply faunal insufficiency. Margalef(101) considered this recently. There is a situation where the environment is itself seasonal or otherwise unstable and this will impose what Margalef, I think misusing the term, calls a constant state of immaturity; but in fact this is perhaps the highest level of diversity that nature can permit.

SLOBODKIN: Can we return to Doctor Fager's point, which I think was a very good one? If the environment were to stay constant, the process of sexual reproduction ought to be abandoned—and I think that can be shown. That is, let us say an animal could regenerate all of its parts, as we can regenerate some of our parts. In that case, there is no point in replacing a reproductively successful adult with a brand new baby who might not be reproductively successful. Why jump from a fairly successful animal to a more doubtful one? We can imagine making this jump if certain parts of the anatomy, by a series of evolutionary accidents or evolutionary steps, if you will, are nonmaintainable, like the wings of a butterfly, and they wear out and you have to replace them. This is one point. But if the one which you were to replace it with is going to have precisely the same role in the world as the parent did, why replace it? Why go through sexuality? What you would like is to make a precise miniature of the adult, since that is your best bet on what position it is going to have in the future. But because environments tend to change, it becomes worthwhile trading an adult animal for a series of approximations to itself. That is, there are certain circumstances, in fact, when it is best to replace yourself with an identical image; others when it is better to replace yourself with a series of approximations.

MCLAREN: Even in a stable environment, though, somebody else might by chance break the rule.

SLOBODKIN: That is true.

MCLAREN: And this, of course, would upset your argument somewhat.

SLOBODKIN: It does not upset the argument. What it does is keep the process of evolution going.

STRICKLAND: Where does a mutant come into this? A mutant is something that breaks the rules, I assume.

BAYLOR: Most mutants are lethal.

STRICKLAND: But the ones that break the rule do it successfully.

SLOBODKIN: Very, very rarely. Evolution does not wait on the occur-

rence of a positive mutation. This is sort of a dictum. The mutation is already present in a deleterious, buried form. All that changes is the selection.

SANCHEZ: The advantages of these deleterious mutations are usually much greater than the deleterious effect itself. It is a balanced system, really.

BAYLOR: But you are conferring immunity to malaria by adding sickle cell anemia.

SANCHEZ: I would like to comment on Doctor Fager's comment. Though on a sort of geometrical situation one would assume that the more perfect game would be the game played by just one player, the historical fact really is that this thing has come to a point where the most efficient game is that played by the larger number of players in a balanced system that keeps balanced because of the presence of all the others. You strike one of the players and the whole group, as Doctor Slobodkin has stated, has to readjust; so given that condition, the more advantageous thing is to preserve the existing structure.

As things are, you need at least two players, one from the plant kingdom and one from the animal kingdom, at the very least. You cannot reduce it to one. You could reduce it to the plant kingdom, of course.

FAGER: It seems to me that what we are saying is that there are a number of kinds of advantages, and what you are saying is that evolution as we see it is a balance of these advantages. No one of them is so overwhelming that it has gone completely in that direction.

RAY: I think we still have quite a bit of interesting information to bring out about selective feeding, about the nutritive value of food, assimilation and so on.

LASKER: This past year Dr. Boolootian of UCLA and I have been examining the digestion of brown algae by the purple sea urchin, *Strongylocentrotus purpuratus* (102). The approach was quite simple. We just weighed a fraction of the algae being eaten to get the wet-dry weight ratio and similarly weighed the feces as they were produced. We fed four species of brown algae: *Macrocystis,* which is our common kelp; *Egregia,* which is the alga with the strap down the middle (we fed them only the fronds though); *Halidrys* and *Petalonia,* which are two small encrusting brown algae.

SANCHEZ: How did you do this?

LASKER: We put them in a small plastic container with holes in it to allow water circulation. The bottom part of the container has a shelf. The food and the animals are put in together. The material is put in

loose. The bottom part has no holes. The sea urchin is inside and feeds on a piece of kelp or other alga. Any feces produced fall to the bottom. There is gauze around this so that nothing gets around the holes.

PROVASOLI: The bottom is open?

LASKER: No, the bottom is closed.

PROVASOLI: Where is the gauze?

LASKER: Around the whole thing.

RAY: Is this whole thing submerged, then?

LASKER: It is all submerged, yes. It is floating at the end of a holder.

Much to our surprise, and somewhat to our gratification the digestibility coefficient—and I define this as being the dry weight of food minus dry weight of feces divided by the dry weight of food eaten times 100—came out to be about 80 per cent on *Macrocystis.*) The values ranged from 79.3 to 93 per cent for seventeen animals, a somewhat narrow range. We used different animals for these experiments. We had to kill the animals at the end to recover the material in the gut; therefore, feces includes gut content as well for the calculation of digestibility coefficients.

(It is interesting to note that it does not matter whether you feed them continually or feed them one meal—initially these are starved animals—you get the same coefficients.) That surprised us because we had always noticed that as you feed the sea urchins continually, they defecate considerably more than they do when fed a single limited meal. The curve in FIGURE 28 shows the amount of food eaten, and fecal production which follows the feeding curve exactly except that the scale is quite different. The amount eaten is approximately 10 times the amount of feces produced.

You can see it is quite regular, but as long as you are feeding they will produce these feces. As soon as you stop feeding, they stop producing feces, but the digestibility coefficient remained the same.

FAGER: If you can weigh the animal before and after, can you account for this?

LASKER: Yes, you can, but these are rather short experiments lasting about 14 or 15 days. The growth is not tremendous during that time. We do have some growth information.

FAGER: What weight of food are you giving them?

LASKER: The dry weight ranges anywhere from a half a gram to three grams of *Macrocystis.*

FAGER: Over the whole experiment?

LASKER: That is right. For example, in 15 days of continual feeding, they will take a total of two and one half grams of *Macrocystis* dry weight.

CONOVER: This is the amount assimilated, or does it matter?

LASKER: No, this is just eaten. They assimilate 80 per cent of that. For

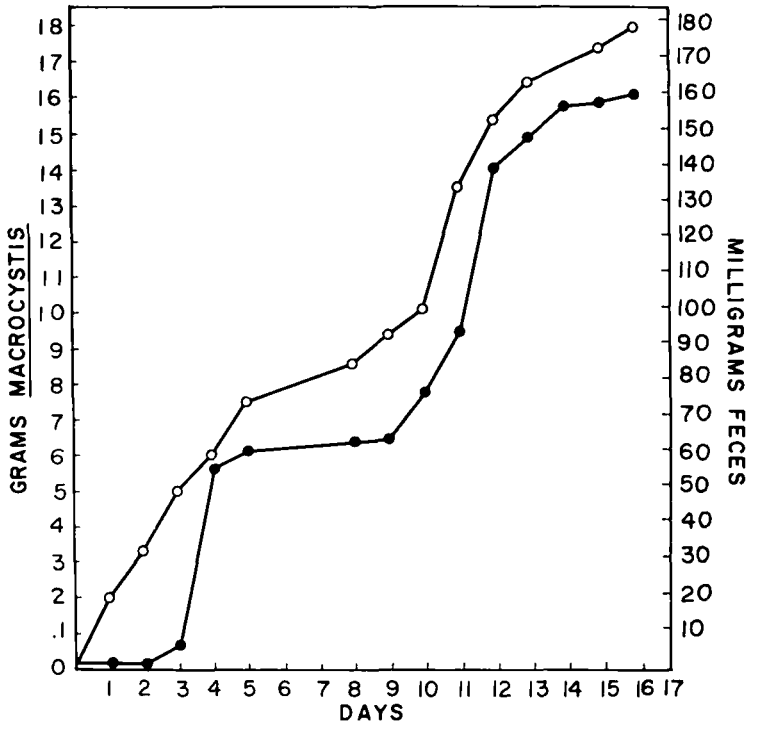

FIGURE 28. *Macrocystis* consumption and fecal production of the sea urchin, *Strongylocentrotus purpuratus* Note different ordinate scales. Open circles: *Macrocystis;* closed circles: feces. [After Boolootian & Lasker (102).]

Egregia the figures are considerably lower, with an average of 62 per cent. For *Halidrys* the average is lower still, 46 per cent; and for *Petalonia* it is 52 per cent.

These figures surprised us because we thought the animal would do as well on any brown alga. The chemistry of *Macrocystis* has been worked out rather carefully by W. Vaughan(103) who wrote his doctoral dissertation on it. It has not been published to my knowledge, but the thesis is available at the University of California at Berkeley, Calif. Two pieces of information are interesting as regards *Macrocystis*. Thirty per cent of the dry weight of *Macrocystis* is mannitol (a sugar alcohol) and forty per cent is alginic acid. The rest is comprised of solubles, laminarin, cellulose, and proteins.

Doctor Eppley and I(104) looked into alginic acid decomposition and the sea urchin was found to be a very effective depolymerizer of alginic acid. Presumably the acid can also be broken down to its monosaccharides.

We have a graduate student at the Scripps Institution, David L. Leighton(105), who has been doing some studies on the preference of the sea urchin for various types of brown algae. He has found that invariably it has a greater preference for *Macrocystis* than for any other alga presented to it.

SANCHEZ: How do they establish preference?

LASKER: I am sorry I mentioned that now. Why not let Doctor Fager tell you, because I am not familiar with the details.

FAGER: What Leighton has done is to put approximately equal weighed amounts of seven species of algae in a container, mix them all up and then put 10 animals in and let them feed for a while. After the animals were taken out the algae were separated and weighed. The difference between initial and final weights measures what was consumed. The experiments were repeated many times. An analysis of concordance showed that *Macrocystis* was consistenlty favored over the other six species. The pieces of algae were small enough and the activity of the animals was large enough so that they came in contact with all kinds.

YONGE: I should like to ask what season of the year this took place. Certainly, in the brown algae constituents like mannitol vary enormously in amount through the season.

LASKER: These experiments were all done during the summer, and that is all I can tell you.

YONGE: You would not know whether the various weeds were in the same chemical state?

LASKER: All of these experiments were started at the same time, on the kelp population.

YONGE: How are you measuring growth, by diameter or by displacement?

LASKER: You mean the growth of the sea urchin? It is by diameter.

YONGE: In a sense, you are measuring calcium metabolism, are you not?

LASKER: That is right. We also do this by wet weight. We also looked quite extensively at the uptake of radiocarbon from *Macrocystis* which has been labelled with radioactive carbon, and have found that the products of digestion show up very rapidly in the coelomic fluid. We got a confusing picture after a short period of time because the gonads are very large and it seemed inconceivable to us that we were getting soluble nutrients into the center of the gonads simply by diffusion. Furthermore, there were some experiments by Nakano and Monroy(106) which showed that if sea urchin eggs simply sit in a radioactive nutrient in sea water, there is little or no uptake into the eggs, but if the nutrient is injected into the coelomic fluid the eggs take it up very rapidly. Campbell and Boolootian(107) found that there are many connections of the hemal

system of the sea urchin which were heretofore unknown. These penetrate into the deep tissue of the gonad. We have suggested in this paper and from other evidence that the hemal system may be a true circulatory system in the sea urchin. Now a controversy has arisen between two groups, one favoring the coelomic fluid as the method of nutrient transport and the other favoring the hemal system. It should be interesting to see which the evidence will support in the next few years.

RAY: Do you know whether, in effect, the urchins are metabolizing the mannitol in the *Macrocystis?*

LASKER: No, but I would like to show you what happens to radioactive substances in the coelomic fluid. After a meal of radioactive *Macrocystis* we find that radioactivity reaches a peak in the coelomic fluid rapidly and then drops off (see FIGURE 29). There may be a second peak later on, at approximately 100 hours, and then it diminishes. The red coelomocytes, which are cells in the coelomic fluid, accumulate radioactivity rather slowly and then reach a peak at approximately 100 hours and then lose activity. These red coelomocytes are very ubiquitous and are found not only in the surface epithelium of the sea urchin but are also found

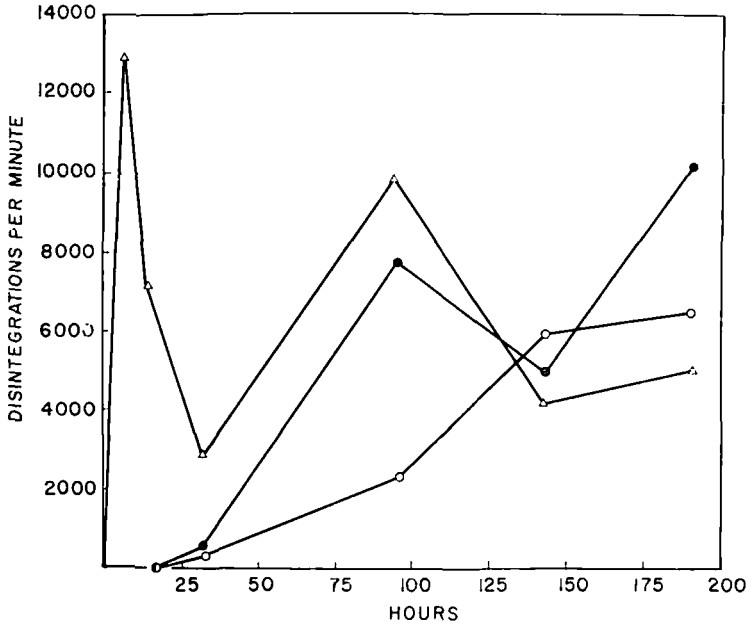

FIGURE 29. Radioactivity of coelomic fluid and its cells after a meal of ^{14}C-labeled *Macrocystis pyrifera.* All samples were corrected for a specific volume of coelomic fluid. *Triangles:* coelomic fluid, *closed circles* red coelomocytes; *open circles:* white coelomocytes. [After Boolootian & Lasker (102).]

in all of the tissues of the body. Furthermore, they are found in the hemal connectives that we find penetrating the gonads. It is very tempting to hypothesize that the coelomocytes are carrying the nutrients with them to the tissues of the animal. There is no denying that the coelomic fluid itself, regardless of the cells involved, gets very radioactive due to soluble nutrients, chiefly mannitol. We are still in limbo here and I would not like to say positively what is going on.

STRICKLAND: How long do you let the algae react before feeding it to the animals?

LASKER: We let it become uniformly labeled. This was one nice thing about Vaughan's thesis(103), in that he determined the time it took for the algae to become fully labeled, and we followed his instructions.

BARKER-JØRGENSEN: There could be no problem of digesting, only absorption.

LASKER: That is right.

BARKER-JØRGENSEN: What about the alginic acid; that has to be digested?

LAKER: Yes, it has to be digested.

BARKER-JØRGENSEN: Is that a special enzyme?

LASKER: It is a special enzyme; it is what we call an algin depolymerase. Depolymerization is the way digestion of algin begins, at least. Algin loses its viscosity rapidly when a little sea urchin intestine is mixed with it.

BARKER-JØRGENSEN: Is the enzyme produced by the sea urchin itself?

LASKER: Of course, the experiments were done to elucidate this point. Unfortunately, these things never show what you want them to show. The gut alone will do this but have we washed out all the bacteria? I do not know. Have we washed off the enzyme due to bacteria? I do not know. It is very difficult to show. You have to grow these aseptically, of course.

I would say that the urchin has its own complement of enzymes, but my evidence is just from a series of observations on many enzymes and many cases. When the bacteria was low the enzyme still seemed to be there, and so on, but we never have eliminated the bacteria completely.

We have another one, a *Limnoria* that lives exclusively on *Macrocystis* holdfast, and there is a student now at Scripps who is looking at algin decomposition.

RAY: In the *Limnoria,* do you know whether or not the ones that live in the kelp holdfast are able to depolymerize the alginase?

LASKER: That is what he is looking at.

RAY: Our wood-living one does not, but they are pretty capable of attacking *Laminaria.*

LASKER: That is a different species.

RAY: I would suspect that they might be living primarily on the *Laminaria* but that is just a suspicion.

SANCHEZ: One often observes in urchins that the feces contain a large amount of untouched algae.

LASKER: That is why this was so surprising. We had been looking at this for years and saying that the plant cells were just not touched. It was quite obvious that the urchins were wasting the algae they had eaten. They are not doing that at all.

BARKER-JØRGENSEN: This was true also of the copepods. They were thought to be utilizing the food to a very low extent and this also turned out to be wrong.

Is kelp losing mannitol to the surroundings—with this high content inside, it would be surprising if it did not.

LASKER: Of course, these kelp do leak a great deal of extracellular material. Perhaps Doctor Fogg can tell you more about that than I can. If you rub your fingers across kelp you will get quite a bit of so-called mucus.

FOGG: Mainly mucilage. I do not think it is mannitol.

STRICKLAND: This could be weighed up. If the thing leaked through the experiment, you would get rather a phony amount, apparently more eaten.

LASKER: Yes, you would, but we were running a control on it. We ran a piece of alga by itself.

YONGE: What size pieces do they take in?

LASKER: The bite is a millimeter, a millimeter and a half in size.

YONGE: There are an awful lot of cut edges, are there not, where something could leak?

LASKER: Oh, yes.

BARKER-JØRGENSEN: Was mannitol 40 per cent of the algae?

LASKER: This is 40 per cent dry weight.

BARKER-JØRGENSEN: This is about 8 per cent of the wet weight. It is still a high content.

FOGG: With unicellular Chrysophyceae you do get high concentrations of carbohydrates in the cells and you do get a lot leaking out, but this leakage does seem to depend on cells breaking. Little seems to escape from intact cells.

BARKER-JØRGENSEN: But you have concentrations as high as, say, 8 per cent of a monosaccharide in solution.

FOGG: In the cells? Yes.

BARKER-JØRGENSEN: Osmotic concentration of 8 per cent mannitol?

FREMONT-SMITH: It is enormous. Does this not have to be based on

the assumption that the cell membrane either is not permeable to water or that the mannitol is in some agglomerated situation polymerized or otherwise inside so that it does not exert its full osmotic pressure?

FOGG: If my arithmetic is correct, it is about 10 atmospheres.

FREMONT-SMITH: It is enormous.

FOGG: Not for a plant.

FAGER: I think one thing to be pointed out is that mannitol is not a sugar, but a hexahydric alcohol.

RAY: Do you have anything further, that you could comment on in relation to this general question?

FAGER: A student of mine, Ray Ghelardi(108), looked at the community of organisms in *Macrocystis* holdfasts and found *Limnoria* was an abundant organism (median density 10/100 cm^3 of live holdfast). He also put out some synthetic holdfasts which were simply half gallon plastic containers which had holes drilled on the top and sides and were filled with plastic-covered clothesline. Almost all of the organisms found in proper *Macrocystis* holdfasts readily colonized these in comparable numbers. *Limnoria* did not. So besides using the *Macrocystis* physically, it is apparently getting something chemically out of it.

RAY: Do you know whether any other kelp holdfast is also invaded by *Limnoria—Nereocystis,* for example?

FAGER: No, we did not look at holdfasts of other species.

RAY: I am interested in the kelp-living *Limnoria* too. There appears to be a rather interesting difference along the coast. We do not find *Limnoria* living in *Laminaria* and *Nereocystis* holdfasts. These two genera of kelp are not very distant systematically and I should think that the composition of their tissues ought to be fairly similar. In any case, I spent a good month one summer examining holdfasts every day, literally hundreds of them, from *Nereocystis,* and finally succeeded in finding one single specimen in one holdfast and a second specimen in a tunnel just sitting on the top of a holdfast. We put those two animals onto wood right away and they were perfectly happy there. It was possible to change some of the wood-boring *Limnoria* over onto some of the *Laminaria,* particularly *Teregophora* which has a very woody stripe. They would go into a *Nereocystis* holdfast but only with some reluctance; however, I don't believe there is any profound difference.

STRICKLAND: How do you measure the reluctance of a *Limnoria?*

RAY: If you take a *Limnoria* and put it into a dish of sea water and let it stay there without anything to burrow into for a period of a few hours or two or three days, and then add a bit of wood, just as fast as it bumps into the wood it starts to tunnel into it if it is good and healthy. If you do the same thing and add a bit of *Laminaria,* a *Nereocystis*

holdfast, or some kind of algal material, it will walk around it and go off and keep coming back, and finally start nibbling a little bit and shake its head every once in a while. It takes quite a long time. Only after a period of a week or eight or ten days will it begin finally to nibble in and begin to invade the kelp.

SANCHEZ: What about the feeding habits in nature of this urchin; is that the algae that the urchin eats more frequently because of the distribution? Is algae frequently present in the habitat of the urchin?

LASKER: Yes.

SANCHEZ: Which one has the larger population?

LASKER: This is one of the difficulties on the West Coast, that the people who extract algin are constantly complaining of the depredation of this particular sea urchin on the kelp. They want to know what to do to get rid of the sea urchins. I would like to see the sea urchins stay.

SANCHEZ: Do you plan to compare the same model with other urchin species? Would it be interesting to see, really, the highest utilization of the algae in different species of urchins for that algae which is abundant in the niche or in the zone of the urchin?

LASKER: I do not plan to do this but it would be an interesting problem.

V. EFFECTS OF QUANTITY, QUALITY, CHANGE OF DIET AND NUTRITIONAL VALUE OF FOOD

Discussion leader:
L. PROVASOLI
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PROVASOLI: I have to confess that Doctor Strickland and I decided to include this topic mainly to satisfy our curiosity; we wanted to find out how much is known about some fundamental questions.

Why have many marine animals one-year cycles? Why do they copulate and spawn only in certain seasons? Do external conditions like temperature, photoperiod and water composition act directly on the animals or indirectly through the phytoplankton food, whose changes in species composition and quantity are governed by these ecological variables? Or are internal factors, like hormones or a physiological clock, the most important factors?

I think that Doctor Costlow has some interesting things to tell us on this subject.

COSTLOW: We have started out with decapods. There are about 160 species at Beaufort. Of those, about 70 are Brachyura. They present a reasonable start on a study of several different species and how they and their larvae are affected in culture by varying some of the environmental factors we have been talking about. So far, we have reared about 30 of them. Of those 30, we have taken about five that are quite different in their niches, and have done much more extensive work on the larval development.

As you know, the crab larvae molt, they go through successive stages of zoea to a megalops stage, and that in turn molts to a crab. The regularity of this molting is something that is really awesome. Under the right circumstances of temperature, salinity, photoperiod, diet, you can almost set your watch by the molting regularity. Ninety per cent will molt at one time into the next stage, so it is a very good indicator of rate of development, physiological processes, and a number of other things.

The conditions that we have used so far have been constant conditions

in a loose sense of the word: temperature, salinity, photoperiod, and for the most part the type of food, and the quantity of food. We are now going on to cycles of these things, controlled cycles within the laboratory, and I will mention that as the last thing, what little we have done on it so far.

The food that we use consists of fertilized *Arbacia* eggs as a start. The reason for some of these different foods is the size range, for one thing. As you know, *Arbacia* eggs are about 80–100 μ and the reason for fertilizing them is that after the first six to eight hours they are a motile source of food and many decapod larvae appear to feed on a motile form whereas they will ignore one which is on the bottom.

The *Artemia* nauplii that have just hatched are another size up and some species larvae cannot handle these, they are just too big, although it is an amusing sight; the larvae of the blue crab in the first stage zoea are about a factor of five times the size of a newly hatched *Artemia* nauplii and yet they will occasionally manage to grab one and they give you the impression of a gentleman who is not very tall running around smoking a tremendous cigar.

Other eggs that we use are *Chaetopterus* eggs, again fertilized; the eggs of *Eupomatus,* and the barnacle nauplii which are, of course, motile to start with.

To present a short summary of a long series of negative results, it appears to be, with animal food, anyway, an all-or-nothing process. They will either eat it and develop and go on to become little crabs, or they will not. There is no in-between stage. That is, there is no delay in development over a long period of time which seems to be caused by food and food alone. Temperature, yes, but not food.

With the unicellular algae or mixtures of unicellular algae and animal food, it is a different story. You do get an increase in time of development with the mixture of unicellular algae and any of these animal foods.

There are other things that crop up with diet but I am not sure it is really diet—it may be tied in with temperature and diet—and that is, occasionally you have a variability in larval stages, that is, in the number of stages and in the picture that it presents to the world, the appearance, the morphological characteristics of the larvae.

SANCHEZ: Does this mean different numbers of intermediate stages depending on the food?

COSTLOW: Yes.

SANCHEZ: It can skip one stage?

COSTLOW: That is right. Recently, I have been taking a beating because laboratory rearing is subject to all sorts of criticism and that is one of them. For a long time now people have been saying, "Oh, that does not

mean anything because you did it in the laboratory. You get all sorts of abnormalities." So just out of curiousity I went back through the literature to see what kind of variability occurs in the natural environment and I do not want to hear too much more of the accusation that it only happens under laboratory conditions, because there are any number of references, where for every crustacean form, virtually every crustacean larva—that is larvae that depend on molting—there is variability in the natural environment.

FREMONT-SMITH: It skips a stage but goes on to the adult form?

COSTLOW: Right. Let me give you an example. *Callinectes* has seven zoeal stages as a rule; sometimes there is an eighth one; and then there is a megalops stage as in all crab development, and then the megalops metamorphoses to a small crab. Up until the fourth zoeal stage in *Callinectes* there is no variability. You never find combinations of a second and third zoeal stage; you never find one that skips from the second to the fourth; but when you get to that point something happens and you may have several possibilities. You can have a molt of a fourth stage zoea which results in a fourth stage zoea—no change whatsoever morphologically. You may have one that skips and you can go right on over to the fifth stage zoea, morphologically.

FREMONT-SMITH: This is going from IV to V?

COSTLOW: This would be going from IV to V in the normal sequence, or you could have one that would go from IV to VI. Then you have the type that does not know what to do and it goes from a IV to a V and a VI, which in this case invariably means that the anterior portion of the animal displays the advanced characteristics; the posterior portion has the retarded development.

BARKER-JØRGENSEN: Is there something like a juvenile hormone involved in molting?

COSTLOW: Yes, I am quite sure there is. It is going to be hard to pin down, but let me finish this and we can get back on that. You never find this reversed.

FREMONT-SMITH: The front end is always the advanced end?

COSTLOW: That is right.

FREMONT-SMITH: This has a sort of broad biological significance, I suspect.

COSTLOW: I suspect so, yes, but just how it is accomplished I am not sure. Those are the three types of variability. This applies to forms other than *Callinectes*.

FREMONT-SMITH: So the only one that is skipped is the fifth one?

COSTLOW: No; you can get this same combination—it will go to a normal fifth and then it would jump the sixth state and go to a VII.

This is where it would normally go to a megalops. Occasionally you have an eighth stage stuck in here and in that case again the anterior portion of the animal is more like a megalops and it is an VIII or a VII stage.

FREMONT-SMITH: But you cannot skip the megalops?

COSTLOW: No. You can accelerate the metamorphosis of the megalops by removing what seem to be the sites of endocrine activity, and we will mention that a little later.

One of the frustrating things about this is that some of the early workers(109) on crustacean larvae maintained that the *Portunid* or the swimming crabs, the ones that have as a rule the most larval stages, are the most primitive. Many crabs have only two zoeal stages; for example, the spider crabs have only two zoeal stages, and then you come right on up the line. One of the small marsh crabs has three, *Sesarma reticulatum,* a close relative to *Sesarma cinereum,* a little wharf crab that has four zoeal stages; and you can get into five. I have never seen six, for some odd reason, but seven is not constant and it is confined to the *Portunid.*

BODEN: How about pelagic crabs, *Pleuroncodes?*

COSTLOW: I do not know. There is very little that has been actually described here other than reconstruction from the plankton and this can get risky, as you know.

LASKER: There has been some work on the rearing of *Pleuroncodes*(110).

COSTLOW: But they did not take them all the way through.

LASKER: Yes, they took them all the way through.

FAGER: The usual development involved five or six stages.

COSTLOW: In an early paper(111), Doctor Boden, you referred to the possibility of what, nineteen or sixteen?

BODEN: Yes, but this is skipping again.

COSTLOW: In those species that have a small number of zoeal stages, you rarely, if ever, find skipping or any kind of morphological changes other than those that are the constants. What it is, whether it is a matter of endocrine changes, whether it is a matter of food which in turn affects endocrine stages—this is something that we do not know yet. There is one thing, though, that is quite obvious, and this, I think, is that molting and development per se are two entirely different processes. Normally they are superimposed, that is, molting is superimposed on growth, and therefore there has been a classical impression that if an animal molts it must come out this way with X number of setae on so-and-so and Y number of setae on so-and-so. This is not true. You can have a molting pattern which is independent of a developmental pattern, and this is apparently what we are getting here, and which, of course, is suggestive of at least two separate endocrine systems, one controlling molting and ap-

parently that one is quite fixed because when you have this type of skipping the molting frequency remains constant. They molt roughly every fifth day in *Callinectes*. The one that skips from the fourth to the sixth will do it after a five-day interval. It does not speed it up, neither does it slow it down.

STRICKLAND: What happens if it has not made up its mind what it is going to be; if it molts does it die?

COSTLOW: It still molts. It remains the same shape.

STRICKLAND: Is this one organism or is this a whole batch that has skipped something—for instance, one whole rearing?

COSTLOW: As a rule, it would be from the egg mass of one particular female, but not always. We have done this on about five different series now within *Callinectes,* and of those five, three skipped and two did not; but in some of the other crabs like *Sesarma* which have only three or four zoeal stages we have yet to find any skipping, and this would represent studies on about fifty different series.

So to get back to this mechanism routine, if you remove the eye stalks of a beast early in development, you will eventually wind up with a situation which is almost identical to this skipping routine where the anterior portion is much further advanced in development than the posterior portion. With a small percentage you will get a megalops which superficially is identical to the normal megalops. You have not speeded up the molting of the animal. The molting sequence goes right along as it always has, but the developmental rate apparently is radically changed.

CONOVER: What happens to the eye, the eye stalk itself. Where they have been removed, have they regenerated?

COSTLOW: They have never regenerated. Occasionally you get an antenna being regenerated in the place of the eye, but as a rule there is nothing regenerated.

CONOVER: Is this true of other parts of the animal?

COSTLOW: No. You can remove, say, any one of the appendages and it will be regenerated.

CONOVER: In one molt?

COSTLOW: It depends on where you do it. If you take the chela of a megalops early enough in development of the megalops—and there are eight days involved from the time of the biozoeal molt to metamorphosis to the crab—if you take the chela on that first day it will appear as a completely functional chela on the ninth day when the megalops goes to crab; and the same applies to the periopods or the walking legs of the beast also; but this, to my knowledge, never applies to the stalked eyes and the same is true for the adults. We know that they can regenerate ad infinitum except in the case of the eyes.

BODEN: Have you tried taking out one eye?

COSTLOW: Yes, and you get á real mixed-up mess. It is most frustrating there, too. Not only does it affect such things as developmental rate but apparently the water balance is completely destroyed. In the later molts you get a much larger animal that is primarily water—the difference in size is primarily water.

We have looked for possible changes in sex because we can maintain these long enough now—with the blue crabs the sex externally begins to show about the fifth molt but if you maintain them beyond that point, they do develop the external sexual characteristics, but I do not know that any of this is functional.

We have gone to the point now of trying to inject back into these things what we have taken out, but so far the results are hopeless. I do not know whether it is a matter of titer, or the time at which it is injected. As you know from the insect work, there is a critical period as to the time at which any one of these parts can be removed and put back in, and apparently the same thing applies in crustacean larvae.

So far there is no real indication of the juvenile hormone that has been established for insects but it has been found in the adult eyes and, very possibly, it exists in the larval form. We do not know yet what triggers metamorphosis in crab larvae. These forms that have an extra late stage eventually metamorphose to a megalops but why they manage to skip this, whether it is a matter of an endocrine system running down or, as was discussed this morning, the possibility of a gradual reduction all the way along and this is what results in the number of larval stages being changed, is not understood.

STRICKLAND: What happens if you take the eye off at stage IV?

COSTLOW: Nothing. In this type of thing, mortality is a mixture of two things: the condition of the operator the day that he does the removing and the condition of the animal following this. Normally, the mortality is highest within 24 hours afterwards. Let us take another form; *Rhithropanopeus* has four zoeal stages and then the megalops stage. If you take the eyes off early, a fifth zoeal stage is produced, sometimes a sixth. The fifth will go to a megalops. So far, the sixth has always died —and they are tremendous. They are twice as large at least as the normal fourth stage.

If you do it early enough with the third stage zoea, you get the same effect, and here the time involved is important: that is, the day that it molts to the third zoeal stage, the day after, the second day after, the third day after—there is a very thin dividing line here. It is right in here. Anything removed prior to the second day of the third zoeal stage gives you these extra stages. If you wait until the third day it does

not. They then go on to be a fourth zoeal stage and megalops and they, in turn, go on to be crabs.

SANCHEZ: 'Is the megalops in the crab that results from skipping zoeals the same as the normal?

COSTOLOW: Insofar as we have been able to tell. We have not gotten into any physiological work yet or any analysis of body tissues, so I really do not know. I am going strictly by morphological characteristics at this point.

PEARCE: It is interesting that in some of the pinnotherid crabs the later postmegalopal or postplanktonic stages are well defined. In at least three species of the genus *Pinnotheres* and in one species of *Fabia, F. subquadrata,** there are five of these stages (112–114). Sometimes interstage conditions are found, i.e., in about 1 per cent of the females. In other words, there would be a form midway between what is called a Stage III and a Stage IV instar. These stages are described on the basis of the width of the abdomen relative to the carapace, and on the development of the pleopods.

The intermediate forms will sometimes have well-developed pleopods but the abdomen remains relatively narrow. There are other anomalies but this might better be discussed at a later time.

COSTLOW: This is in the crab itself?

PEARCE: Yes.

FAGER: Does one of these that goes by three zoeal stages as opposed to six or seven take qualitatively bigger morphological jumps?

COSTLOW: No.

FAGER: They are the same grade only there are just fewer of them; is that it?

COSTLOW: That is right.

FREMONT-SMITH: Does that end up with a small crab? It sounds as though it would.

COSTLOW: The megalops here is roughly the same size within the species. The megalops developing from this is much larger, but back in the other situation under natural conditions where you had a megalops resulting from, say, six zoeal stages rather than seven, there the size is the same.

The only other time we have observed this (and this is why I brought in the cycles), was this past summer when we started working on *Rhithropanopeus* larvae reared under cycles of temperature. You can program

* J. Pearce. 1960. The biology of the mussel crab, *Fabia subquadrata* Dana, from the waters of the San Juan Archipelago. Unpublished M. S. thesis, University of Washington, Seattle.

the temperature to almost any cycle you want within the cabinet and we used about four—15–20°, 20–25°, 25–30°, and 30–35°. One animal out of the several thousand that we had under these conditions did skip stages just as if we had taken the eyes off—actually, it added the stages, it did not skip them—at 15–20° over a 24-hour period, and there we tried to simulate temperature changes as they would appear outside.

We had one zoea that wound up with a fifth zoeal stage where it normally would have four. Next summer we will start perhaps with a 10–15° cycle and see if we get more. In all cases, the food was adequate, everything else was the same, the photoperiod was the same; so whether he just happened to be a freak that had an injured mechanism to start with, or whether it was actually brought about by temperature, we do not know.

As to photoperiod on these, you know there is a lot of talk in some of the earlier work about the effect of photoperiod and light intensity, and we have run through a number of series of larvae of several different species, maintained under different conditions of photoperiod, and as yet we have no evidence whatsoever that photoperiod has any effect on larval development.

I should qualify that right now before you do, and say that one big difference is light intensity. The light intensities that we use from these MacBeth Examo-lights are quite low compared to outside conditions; perhaps 200 foot candles is the maximum, which I realize is nothing compared to outside intensity under normal conditions.

I might mention in passing that we chose the Examolights because they do have a spectral distribution which is almost identical to natural daylight. The so-called daylight fluorescent bulbs are an example of a very poor choice of words. There is very little resemblance between their spectral distribution and that of daylight.

SANCHEZ: How much of that goes into the water?

COSTLOW: Of course, that depends on all sorts of things.

SANCHEZ: I mean in the habitat where these zoea are found.

COSTOLOW: Very little of it, because the area where we are working has a good deal of runoff into the surrounding water and the turbidity is high.

SANCHEZ: So your lamp is probably an adequate imitation of the natural conditions.

MCLAREN: It may be adequate in intensity but it will not be adequate in spectral distribution.

COSTLOW: I think you can make alterations there that would compensate for it but so far we have not done this.

BAYLOR: The trouble with fluorescence or anything that is excited by

ultraviolet is that you have always got the Mercury lines in the spectrum. I do not know whether this is going to bother you or not, but it is something to remember and to keep in the back of your mind.

STRICKLAND: There are no lines in a cold—in the ordinary type of fluorescent light.

BAYLOR: The last time I looked, which was the day before I came here, there were.

STRICKLAND: But not nearly as much relative to the continuous energy, as is found with arc lights.

BAYLOR: No, but they are there, and they are fairly intense.

KANWISHER: I agree with you.

COSTLOW: We do not know what is causing this variability, as I said earlier. It may be a matter of endocrine mechanism; it may be a matter of food, or one affecting the other. We hope to follow up several aspects of this this summer and try to pin it down.

The material lends itself very well to this sort of work; once you get the hang of taking off the eyes there is nothing to it.

STRICKLAND: Your implication is that because it is an eye it could possibly be light, and possibly spectrally activated; is that it?

COSTLOW: Not really, no. The adult mechanisms have been reasonably worked out and they are known to be in the eye stalks.

SANCHEZ: What about food? What is the food in this system?

COSTLOW: In this system it would be strictly *Artemia* nauplii.

SANCHEZ: You do not have any experiments on varieties of food?

COSTLOW: Yes, I do, but the results are virtually negative. You either get development or they die. You do not, as a rule, get any halfway point.

SANCHEZ: *Artemia* has been chosen because of previous experience?

COSTLOW: Or *Arbacia* eggs. Some of these, for example *Callinectes* larvae, are too small really to handle the *Artemia* so we give them a mixture of *Artemia* and *Arbacia.*

BAYLOR: You can't get *Arbacia* eggs the year round, can you?

COSTLOW: With the exception of December and January. We bring them in late in October and November and they will last for another two or three weeks, and about early March they start up again. The fertilization is quite poor in early March but for our purposes 40 to 50 per cent is perfectly all right.

PEARCE: You mentioned the other day that you had succeeded in raising *Pinnotheres maculatus.* Will the early zoeal stages of this crab take *Artemia?*

COSTLOW: No, we use *Arbacia* eggs on both the *Pinnotheres.* Even in the *Paleomonetes,* which Broad showed very nicely is tied in with food, he could almost control the number of stages of the larvae by the

amount of food that he presented. He got all sorts of skipping and intermediate stages and extra stages, depending on the availability of the food and the quality of the food, too. But that is all from the macrurans. There is a good deal of difference.

The thing about it that is puzzling is why the skipping is always late; even in the Brachyura what little we have seen is confined to the late zoeal stages. You do not see it in the early stages.

SANCHEZ: That would not be so surprising, would it, on a general biological comparison?

YONGE: It would depend on what they got from the egg, and later on it would depend on what they got from the environment.

COSTLOW: It would depend on what is causing it. I do not know if I can think of an example that does not. Take ones with five zoeal stages, which is the next closest thing, really; those as a rule never skip. They go from the fifth straight to the megalops. They never show the sixth stage. Is it a question that the diet is adequate and everything is optimum, whereas with *Callinectes* it is not; or is it something that starts much earlier in the development of the beast?

YONGE: If you go on to later stages in the life history—think of caridean prawns on which I have worked—there are intrinsic factors which control the intermolt stages. A female *Crangon* or *Leander* lays her eggs, these hatch and then she molts into a neuter condition with one of the egg-carrying setae on the pleopods. She feeds and molts again into an egg-laying condition. There are certainly intrinsic controls here.

COSTLOW: But how to substantiate it or otherwise is the perplexing part.

PROVASOLI: Have you obtained a complete generation?

COSTLOW: We have, yes. In fact, we have gone to F_1 with some forms.

PROVASOLI: Is it possible to shorten the normal life cycle in the laboratory by changing conditions or by giving plenty of food so that they will be in a different condition than they are normally exposed to in nature?

COSTLOW: Yes. We have not done it on any real scale but with this *Rithropanopeus,* the adults that we have reared are much larger than those we normally find in nature. This may be predation, I do not know, and they spawn earlier the next season without any real effort on our part. Their larvae hatch out earlier and proceed to be larger again, and of course they are fed all the time. They are maintained at more or less constant higher temperatures than the natural environment would be in the wintertime, so I think if we really worked at it we could easily work in three generations a year.

FREMONT-SMITH: Are they responsive at all to thyroid?

COSTLOW: I do not know.

FREMONT-SMITH: Has that ever been tried in the invertebrates?

COSTLOW: I am reasonably sure it has but I cannot quote you any work right offhand.

FREMONT-SMITH: I wonder if anybody has an answer to that—whether they are responsive to thyroid in terms of more rapid molting or metamorphosis.

RAY: As far as I know, in the cases that have been tried, there has been no reaction.

BAYLOR: We have tried it and gotten negative results. I would like to ask Doctor Costlow a question about pedogenesis or neoteny. Does this ever occur; is there any evidence that this occurs in response to a limited diet?

FREMONT-SMITH: What is pedogenesis?

BAYLOR: Sexual maturity of larval forms; and if so, is there anything known about it in something that has lots of larval stages like the crustacea?

COSTLOW: Not under artificial conditions, I think. Most of the cases cited are those picked up in midwater trawls and this sort of thing, deep-water forms. I do not know that anyone has produced it or induced it in crustacea under laboratory conditions.

BAYLOR: Are you saying that sexually mature larval forms have been picked up in midwater trawls?

COSTLOW: Thought to be, yes. There are a number of references to this kind of thing.

CONOVER: What kind of organism?

COSTLOW: Supposedly Brachyura. They never find the crabs, of course, and supposedly they do not exist—and this is the next step as far as I am concerned in one phase of this work, to see if we can get some of these and carry them in the laboratory long enough to see what happens, and conceivably get the larvae of these forms from the larvae where they originate and see if we can change it or see what causes it.

FAGER: Are they in the megalops form?

COSTLOW: There are some that are. I think most of them are in the zoeal form and they are tremendous in size, which again makes you think about endocrine activity. The two usually go hand in hand. With some of them that I have seen, you would swear that there was something wrong. You are familiar with the size of the average zoea, and they would be a factor of 20 times the size of the average.

BODEN: Some subadult euphausiids have been reported(115) to be fertile and able to copulate, although their copulatory organs are not sufficiently developed that a taxonomist would be able to use them as specific criteria.

COSTLOW: Did you ask if this is caused by food?

BAYLOR: Yes; I was wondering whether there is any evidence that it is brought on by lack of food.

COSTLOW: They had no knowledge of what caused the ones that they found outside. Some of Gurney's work(116) talks about this. If you will accept the concept that molting and rate of development, etc., have no real relationship, there is no reason why the animal could not continue right along with the larval form and develop sexually; and if you had a reverse of what we have indicated here, if the mechanism which controls molting is retarded or obliterated completely, then you would have the zoea which has sexual maturity. I would like to check on whether or not the megalops has ever been found. I think it has but I would not swear to it.

SLOBODKIN: In the phylogeny of the crab, I have always been fascinated that in all the crabs the zoea was there and looking like a zoea. It would sort of make sense that somewhere there was an adult zoea as a conceivably primitive form—the reverse of pedogenesis. Is this completely wild?

MCLAREN: Surely you can draw a phylogeny among the other Malacostraca, among the Malacostraca in general, in some of which the zoeal stage does not occur.

LASKER: I would like to ask about the intermolt period. You say they are very constant. Can you alter them by excess food?

COSTLOW: Only with the addition of animal food and vegetative food, cellular algae. This is the only case I know of where this has been changed, and actually one of the little mud crabs is, as a rule, very constant in its rate of growth.

LASKER: Is this skipping a complete stage or just the intermolt period?

COSTLOW: Just the intermolt period, and if you cut 'way down on the animal food it will not make it then. It will go on for a two-week period but it will die.

PROVASOLI: Is there anyone else who wants to contribute on the effects of the diet on reproduction or life span?

EDMONDSON: I have something that I think relates to some of this morning's discussion by McLaren and is directly connected with what you have just mentioned. I will be brief about this because this has to do with an investigation which I talked about at the First Marine Biology Conference(117).

It has to do with the effect of kinds and quantity of food on the rate of reproduction, meaning the rate at which the females can pump out

eggs. What has happened since the first conference is that I have finished the analysis of the qualitative aspects and I can say a little more now about the significance of different kinds of algae.

I am going to talk about the reproduction of rotifers in lakes, and I think this may be more relevant to our present topic than might at first seem clear, because I think that if marine biologists would spend a few dollars on finer bolting silk they would find rotifers everywhere they went. Populations of rotifers have been found in the middle of the Atlantic by people who used fine enough nets. There is something called *Synchaeta atlantica,* and certainly in estuaries there is a rather rich variety of these things.

PROVASOLI: This is very important and reminds me of what Steeman-Nielsen brought up in the second conference. The ciliates also have been very much neglected. They form blooms in the sea, especially in waters near the shore.

EDMONDSON: In lakes, too.

PROVASOLI: I think that the importance of the ciliates and rotifers in the food chain is that they offer a food of an intermediate size between flagellates and new-born invertebrate larvae. This size might be essential for the growth of a number of other invertebrate larvae.

EDMONDSON: The method used takes advantage of the fact that many rotifers carry their eggs, and by it the rate of reproduction can be determined from preserved material. You can look at a fixed plankton sample(118, Figure 1) and count around to get the ratio of eggs per female. If you know the duration of development (and you can determine this for different temperatures), then knowing the temperature of the collection time you can compute the rate of egg-laying per female per day. I simply went to Windermere and spent all day for several months looking at plankton samples and came up with the rate of reproduction. We have data from samples taken every two weeks in four lakes for four years. The rotifers create vortices in the water with the cilia, and cells are thrown down against the mouth area and they are sucked through the mastax into the stomach, sometimes being choppped up and broken on the way through, sometimes not, by *Keratella* and *Kellicottia. The Polyarthra* is a little different. Its mastax forms a pump and it draws things through whole, rather big things, or else pumps them empty. It can pump fairly sizable things through.

The span of the jaws of *Keratella* and *Kellicottia* limits the size of food. They can eat bacteria, *Chlorella* and things about up to 10–15μ. *Cryptomonas* is a little too big for them, although they can sometimes grasp the flagellum and pull the organism to the jaws.

An examination of graphs of the data shows that the reproductive rate

of *Keratella* tends to vary in concert with variations in abundance of edible algae and temperature.*

SANCHEZ: I would like to raise a question for which I do not have the data; perhaps something can come out here. It has to do with asexual reproduction, or better still, with nonsexual reproduction and its relation to quantity and quality of food. I do not know if some people have some recent data. I do not, but I have some field observations on the occurrence of asexual and sexual populations of fresh water *Veneria* which I would like to analyze.

I do not know whether some of the laboratory work on *Hydra* has contributed some information on that.

SLOBODKIN: My animals are sporadically but very rarely sexual. I see no real regularity in that. Loomis and Lenhoff(119) and many others have a great deal of data, and they can induce sexuality by a wide variety of physical and chemical changes in the medium. For example, they can maintain a *Hydra* in a dilute agar medium, almost in a slush, and this induces sexuality in *Hydra littoralis* where the waste products from the *Hydra* cannot diffuse very far and form a halo of waste material.

Loomis also has been able to produce sexuality more or less at will: at one time he considered that he was doing this by adding gaseous carbon dioxide as distinguished from carbonic acid. He thought that carbon dioxide gas, as such, gave rise to sexuality. I believe that a wide variety of other things have now been found to do that. I do not remember the recent standing of it.

In the *Daphnia,* sexuality is never universal in the population but does have a consistent period of appearance during the history of a population, specifically as the population is just growing into its experimental container and the reproductive rate begins to fall. *Daphnia,* you remember, reproduce parthenogenetically. As the parthenogenetic reproduction rate is falling, sexual eggs appear. It occurs just when things begin to get crowded, not when they are extremely crowded, and not when the population is growing at maximal rate.

SANCHEZ: Is this a direct consequence of feeding?

SLOBODKIN: It is the sudden decline of food per animal. The sequence low food, high food will not do this. As the numbers increase in the container, the food per animal drops and finally, as the food per animal

* Editor's Note. At this point Doctor Edmondson summarized at some length the results of a multiple regression analysis of the relation between reproductive rate and the abundance of food organisms, published in full(118). There was considerable but inconclusive discussion of the hydromechanics of the rotifer corona and feeding mechanism as related to selection. Other points mentioned were the relative digestibility of *Stichococcus* and the inhibitory effect of *Chlorella.*

passes some critical point, sexuality happens—not in all the animals but in a greater percentage than at any other time.

What I would like people to think of is the situation that up to now we have by and large been discussing the physiological reaction of an organism to an environmental factor and I suggest to you that if conditions are optimal, the thing that the organism has to tolerate is members of its own species. Quite often one finds physiological changes associated with the relative abundance or concentration of animals of the same species in one place. What I would think we might reasonably do is try to collect whatever cases people have of interactions between the numbers of organisms and the physiology of the individual organisms, the point being that if there is such a thing as a population as something to study, it arises from this kind of interaction.

I want to present two ideas which are not quite obvious. In *Daphnia,* if you plot the amount of food fed a population against the amount of nitrogen in a population, you get a straight line.

KANWISHER: Is this dynamic balance here?

SLOBODKIN: Yes. If you have the kind of population which comes to numerical equilibrium, in the case of *Daphnia,* at least, you again get a linearity with food supply, none of which is surprising.

In the *Hydra* population, also, the more food you give the more animals you get—no surprises.

This brings us to a somewhat surprising thing. In *Hydra littoralis* population size tends to approach a value approximately the same as, or not significantly different from, in any case, the number of food particles per day provided. What is magic about one *Artemia* nauplius and one day?

SANCHEZ: You add daily?

SLOBODKIN: So many particles per mouth.

SANCHEZ: Per dish and the population can then adjust itself to the number of particles per day?

SLOBODKIN: That is right. That is, I have a food regimen. I have a culture medium, I put in a few animals and the animals can then do what they want to with this; and what they seemed to want to do was to come to the situation where each *Hydra* mouth eats approximately once daily.

In separate experiments where we maintain isolated *Hydra,* Griffing(120), working in my laboratory, showed that if you fed one *Artemia* per day to a *Hydra oligactis* mouth, it is not quite sufficient to permit budding. If you fed two *Artemia* per day over an extended period of time, the *Hydra* comes to a fixed size and fixed budding rate. This rate is more than sufficient to maintain a population and results in an in increase.

I switched to using *Daphnia* as food for the *Hydra* rather than *Artemia,*

the argument being that if an *Artemia* nauplius weighing around 2 micrograms is sufficient to hold a *Hydra* for one day, if I fed a young *Daphnia pulex,* which weighs around 4 micrograms, or a young *Daphnia magna,* which weighs around 9–11 micrograms, I have various possibilities. I might expect to find that the number of *Hydra* that I have, using a smaller number of larger food particles, is still the same as the number of food particles per day provided, but if this is so then the *Hydra* should get bigger, or the alternative is that I get the same number of *Hydra* in the population as I did before, essentially, but each one eats less often.

What actually comes out is the following: If I feed *Hydra oligactis* 100 baby *Daphnia pulex* per day or 100 *Daphnia magna* an approximate 1:1 relationship seems to hold.

If I take an isolated green *Hydra* I can feed it and maintain it for a period of around four or five months on baby *Daphnia magna,* but if I try to raise a population of green *Hydra* on *Daphnia magna* they starve to death.

This is the kind of thing I was talking about before, where you get a difference in the physiological reaction related to the fact of being in a population. The green *Hydra* can be very large and also can be very small with the same genotype, depending upon the nutritional state.

If you take a large green *Hydra* and feed it on *Daphnia magna* it stays big. If you skip a few feedings, the green *Hydra* goes ahead and reproduces anyway, just as if it were well fed, but it gets smaller and its progeny gets smaller and they get so small they can no longer eat a *Daphnia magna.* If you have a green *Hydra* which is so small that it cannot quite eat a *Daphnia magna* and feed it on *Daphnia pulex,* it will eat the *Daphnia pulex,* and when it gets too small for that it can live on *Artemia,* and if you feed it enough *Artemia* you can get it big enough so that you can go back to feeding it *Daphnia magna.*

The point (and this is related to the point that came up in another context earlier) is that the green *Hydra* are playing a different kind of strategic game with their universe than are the brown. The green *Hydra,* confronted with a closed container or any sort of sealed system, become numerous and very small. The brown *Hydra* reproduce less rapidly, but maintain their body at a somewhat larger size.

The advantage of staying big is that the size range of food organisms that it consumes is quite wide. The disadvantage of being big is that should the world be full of very small food particles your food-catching ability is relatively small in terms of the volume of material you are trying to maintain; that is, the mouth per body ratio becomes unfavorable, or the converse; the advantage of being small is that should the food particles be of a small and reasonable size you have very many little mouths

all waiting to catch them. The disadvantage of being small is that should the food particles not be of small size, or should a small food particle never appear you have a rather short time before you starve to death.

STRICKLAND: Could you clarify a little bit about *Hydra?* Can you consider them as virtually lots of little isolated mouths, or do these things have some sort of intercommunicating channels.

SLOBODKIN: When a *Hydra* is fed a fairly large amount, the body grows somewhat larger and buds appear on the sides. From one to a maximum, in our cultures, of six buds may be maintained off the side of a *Hydra,* and these are essentially miniature *Hydra* which eventually drop off. They come in a ring almost around the body.

PROVASOLI: And you count them as new mouths?

SLOBODKIN: When they are feedable; when they are feeding I count them as three individuals. At a time when they have no tentacles I would not, but from most of these histories we are dealing primarily with this type of animal. There are relatively few buds; maybe one out of every fifty animals would have a bud.

STRICKLAND: When it makes a new mouth is that the process you were showing us?

SLOBODKIN: Yes. A bud appears on the side which then grows out somewhat further, and after around two days there is a new mouth.

STRICKLAND: This is what you call the smaller mouth?

SLOBODKIN: Now, this is the reproductive process. From a well-fed population of *Hydra* you get a weight distribution of from zero to 300 micrograms, and in nature they tend to be heavy, as determined by skindivers collecting brown *Hydra.*

In the laboratory, in the early stages of population history they come from well-fed cultures and the mean body weight is on the order of 100 to 200 micrograms. As the population history goes on, the weight distribution shifts toward low weights. At an intermediate stage, in the green *Hydra* fed on *Daphnia pulex,* you get a bimodal weight distribution. This is all being repeated and this is what I think we get. We have done it once and it is starting again.

Large animals are the animals who have always fed, who by and large have been lucky in their feeding history, and have been eating fairly regularly every day. Occasionally they get a bud or someone misses a meal. These small animals cannot eat very well and once they get below the size range of their food supply they are on their way to zero to 5 micrograms. You can still get live *Hydra* at a weight of between zero and 5 micrograms and you can very carefully shove *Artemia* nauplii into their mouth and nurse them back to full size.

SANCHEZ: Does budding reduce the size of the individual?

SLOBODKIN: No. The bud is a share of the body increase in the brown *Hydra.* If you take well-fed green *Hydra* and give them no food at all, they will go ahead and bud, and in that situation the body size will be reduced.

FAGER: This means, then, if you are willing to consider *Artemia* and the two *Daphnias* as equivalent energy sources per gram dry weight,—

SLOBODKIN: Which, essentially, they are.

FAGER:—that the growth efficiency is strongly dependent upon the size of the food you feed them even though you are feeding them the same kind of food.

SLOBODKIN: That is right.

FAGER: It seems unlikely.

SLOBODKIN: I am sorry but this is how it comes out. Remember, we were talking about the strategy that an organism plays in facing the world. The green *Hydra* can afford to play the strategy of reproducing heavily and being very small because it has the ace in the hole of a light energy source. As we pointed out, we can keep green *Hydra* for as long as 91 days that I know of so far, in the complete absence of food if they have light.

A brown *Hydra* in the same circumstance is gone by around 25 or 30 days, depending on temperature—sometimes as long as 50, but they are on their way out. The brown *Hydra,* therefore, must play it safe by being at an intermediate body size and cannot afford to risk the problems associated with being very small, even though smallness does have advantages under certain circumstances.

We have seen here a situation in which the physiologically suitable food supply for an individual animal is not a suitable food for the maintenance of a population of animals of the same type. That is, the same thing that will feed a member of a species will not support a population of that species.

The second point is this: In the situation where we get dichotomies in the weight distribution, that is if you have a situation where the *Hydra,* in order to maintain the animal's body size, must eat regularly and if they do not eat regularly they begin to shrink and then become less and less likely to eat in the future, you get an adjustment to nutritional circumstances which is quite different from our normal picture of population control mechanisms. Normally, you think of a population having a mean physiological characteristic or a mean set of physiological characteristics in a relatively empty environment.

As the population increases and fills that environment, we normally think of the mean physiological properties deteriorating to some degree until we get to the stage where they can just reproduce and replace them-

selves and then we have some sort of a dynamic equilibrium, and all the printed theories of population growth are of this form.

But I would like to suggest, as Errington suggested fifteen years ago, at least, and I just caught onto last summer, that you can have an alternative set of population theories in which instead of having a single mean physiological condition, which then shifts with degree of crowding, you can divide your population in a sense, into two categories: one category of animal that is doing fairly well and continues to do fairly well; another category of animal that, as a consequence of not having done well in the past due to some statistical factor, if nothing else, continues to do more and more poorly. These animals, the ones that are fairly heavy in their bodies and are still feeding well, represent in a sense the population's investment in staying where it is. The others are waiting for change.

Errington cited it for the mammal population where on almost all the highways of America in the autumn you have a thin layer of dead young mammals. These are the mammals that do not have territories, that do not have, in his sense, a place in the social structure of their own population and wander off, and these are the ones that essentially get hit by cars or are taken by predators.

How general this is, I do not know, but I pass it on again as a kind of phenomenon.

FAGER: This is the same sort of thing that Nicholson(121) was talking about when he suggested that there were two kinds of interactions within populations. In one case a few individuals win and survive in good condition; in the other case everybody gets something but it is insufficient and the population as a whole declines.

SLOBODKIN: Yes, that is essentially it. I would be very curious to know what information other people have on the integrative mechanisms, if you will, of populations, since here we go from an individual level to quite a different set of phenomena when we deal with a group of organisms held together, and in essence all organisms have to be held together.

SANCHEZ: If I understand correctly, the green Hydra will reproduce even if not well fed; is that right?

SLOBODKIN: That is right. Let us go further; even if not fed at all, they will reproduce for a while.

SANCHEZ: It seems to me, then, that the increasing number of mouths has an adaptive value since the probability of catching scarce food will be greater for a given genotype if it were represented by many phenotypes, by many individuals.

SLOBODKIN: Yes, this is valid. The extra point that has to be added, however, is that during the process, since each individual becomes smaller,

the kind of food he can catch changes. He can no longer catch a large food particle.

STRICKLAND: I am not sure this is so. Might not your big fellow be able to get a potential set of small ones?

SLOBODKIN: In this case, the large *Hydra* do quite well when fed even on the small pieces.

STRICKLAND: I see. It is rather a specific case?

SLOBODKIN: That is right.

STRICKLAND: The whole *Hydra* system seems to be a rather unreal business from the standpoint of a population dynamics theory.

MCLAREN: To the extent that you are able to generalize this to squashed muskrat, this approach does have significance, but I think a good deal of what you have said does depend upon this curious system of degrowing, and so forth, which *Hydra* represents.

BAYLOR: Do you not find something similar to this in one of the local lakes around Ann Arbor, Michigan?

SLOBODKIN: In the lakes we have found that there are three species of *Hydra* in residence in Pickerell Lake—*Hydra oligactis, Hydra pseudoligactis,* and a green *Hydra,* and that *Hydra oligactis* constitutes a rather heavy fur of material on the sides of the lake and that underlying this is an undercoat, if you will, of *H. pseudoligactis,* and in between a very small green *Hydra,* which I think is what you are referring to.

BAYLOR: Is there not a similar variation in size of prey available to them throughout a summer?

SLOBODKIN: Normally there is a generation of, say, copepod nauplii or copepods. It varies from lake to lake and with the latitude, but the typical kind of picture you get might be Cladocera appearing in the spring and being replaced by copepods later in the late spring and summer, and perhaps a second appearance of the *Cladocera* in the fall; so there is a shift in the size distribution and the *Hydra* population seems adapted to it but I cannot go too much further.

One thing I can add is that, in nature, the *Hydra* population is not food-limited—at least the *Hydra oligactis* was not, in the situation we examined. They stayed abundant until midwinter and then were wiped out, essentially, by a population of *Hydraemoeba,* an epidemic of amoeba eating on the outside of the *Hydra,* and as soon as the *Hydra* begin to be chewed up by the amoeba the normal little hypotrichs, Hydrocoeles and Rhabdocoeles begin eating great chunks of *Hydra.* You find them wandering around the lake with nematocysts imbedded in their flesh.

There is also a Cladoceran, *Anchistropus minor,* which feeds on *Hydra,* which is like reporting that a rabbit eats lions.

They hook the spines into the body of the *Hydra* as a lineman hooks

his boots into a telephone pole and they get a lump of *Hydra* tissue between the valves and they seem to be feeding on it, judging from the colors.

EDMONDSON: In the range of sizes, will the green *Hydra* take such things as *Chydorus,* rotifers, ciliated protozoa, and such things, or are they interested?

SLOBODKIN: Hydra does not seem, in general, to be interested in protozoa and I have not been able to feed them on rotifers. Chydorids, they will take. Whether an animal is caught by a *Hydra* depends on the relative size. *Daphnia magna* bumping against a *Hydra* will be stunned, typically, but if it is a relatively small Hydra it does not seem to be stunned that badly and can pull away. There is an intermediate stage between being able to eat *Daphnia magna* and not being able to eat *Daphnia magna* in which the *Daphnia magna* are not actually caught and swallowed but are stung badly enough so that they drop dead in the bottom of the dish.

EDMONDSON: One other point. Does this connect with the observations of Rose(122) about the growth of tadpoles and antibiosis?

SLOBODKIN: We have been completely unable to repeat Rose's results. A group of graduate students tried it this year and it does not seem to work.

BAYLOR: Lester Barth,* in the Department of Zoology at Columbia University, has repeated these.

SCHMIDT-NIELSEN: Would you mind telling us what this particular work is?

EDMONDSON: The reason I brought it up is that in crowded tadpole populations, the growth rate is suppressed, and according to this work it is an antibiotic effect, at least mediated by something liberated, that is, a rather specific substance dissolved in the water.

SLOBODKIN: By the largest tadpole?

EDMONDSON: The point is that the largest tadpoles grow well; the little ones get stunted and it makes a very clear bimodal separation.

SLOBODKIN: We have tried giving known quantities of food to a group of tadpoles and we do get one largest tadpole and you eliminate that tadpole and, according to Rose, you ought to get another one largest tadpole, but we do not. This has to be done again.

BAYLOR: Frederick E. Smith and I* repeated this accidentally—we did not intend to do it—on a population of *Xenopus laevis* larvae. This is the African clawed toad that we were keeping in the laboratory for other reasons than this particular study. For our purposes it was especially nice because there was always one big tadpole and a couple or

* Unpublished observations.

three that were a little bit smaller, and after we had experimented on the big tadpole then the next largest one would grow up and take his place. I currently have a similar population of tadpoles in my laboratory that show this phenomenon now.

FREMONT-SMITH: It would be very interesting to compare notes and see what was different in the two experiments. There must have been some difference to account for the difference, for the fact that the results were different. Frequently, what happens is that one says, "I have tried to repeat the experiments and could not confirm them," and it is because one did a different experiment, a little bit better or somehow modified.

BAYLOR: I have raised mine dirty.

MCLAREN: I do not think what I have to show will bring out as much population interaction of the sort Doctor Slobodkin has been suggesting we stick to, but I will show some figures anyway and we can discuss them as alternatives to Doctor Slobodkin's comments. This (FIGURE 30) Doctor Slobodkin would say, is something like his *Daphnia* populations, namely a sort of linear relation between the amount of food expressed as the mean number of *Pseudocalanus* remaining at the end of winter (per meter squared—extremely crude) and the numbers of predators remaining—*Aglantha digitale,* a very common Arctic, holoplanktonic medusa.

Actually, the exact position of these points in terms of cubic meters (a more proper density expression) is a little less simple, but I can tell you that point number 4 (FIGURE 30) represents a very critical level indeed. You can see that it is approaching the zero line. In fact, this population failed to reproduce itself in the following summer. There was a probabilistic gap of population there, I think.

There is obviously a relationship between the number of prey and the number of predators, but it may not work both ways. The number of prey is not necessarily dependent on the number of predators. I am not suggesting this is a two-way relationship at all, but it is at least a one-way relationship. The number of prey does not in this case depend upon the number of predators. The number of prey certainly is a function of a good many other things in this lake, including productivity of the various basins involved, and so on.

EDMONDSON: What happens if you plot the abundance of the predator against the abundance of the food organism early? Do you see what I mean?

MCLAREN: Yes. This is the outcome of the overwinter game, as it were. This is what remains at the end of the season just before the pred-

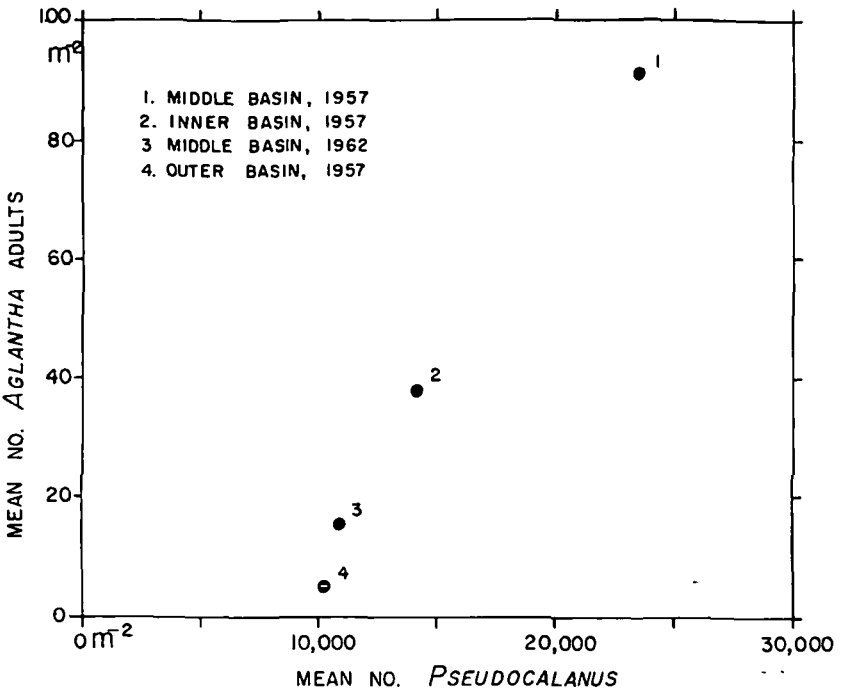

FIGURE 30 Relationship between number of *Aglantha digitale* remaining at the end of winter and the number of *Pseudocalanus minutus* remaining in Ogac Lake, a landlocked fjord on Baffin Island. The number of *A. digitale* is the mean of all June samples in each basin, and the number of *P. minutus* (females only) is the mean of all samples taken up to the time of the setting of the second brood of young in each basin; in both species these mean values avoid postreproductive mortality.

ator generation, and the prey generation for that matter, is about to reproduce.

SANCHEZ: Is that the main food of the medusa?

MCLAREN: Yes, almost the exclusive food. There are other predators in the lake which respond entirely differently. For example, in FIGURE 31 we see at best an extremely loose relationship between the number of prey remaining at the end of winter and the number of predators, but it is an inverse one, such as it is.

I can say this, that points 2 and 4 were taken from the same basin in two different years, so that apart from the predators, the same general influences—the same general productive influences—were acting on the prey: point 1 is from a much richer, and point 3 is from a much poorer basin, so the deviations are more or less in the expected direction.

Anyway, that is not what I want to stress particularly. Here we see

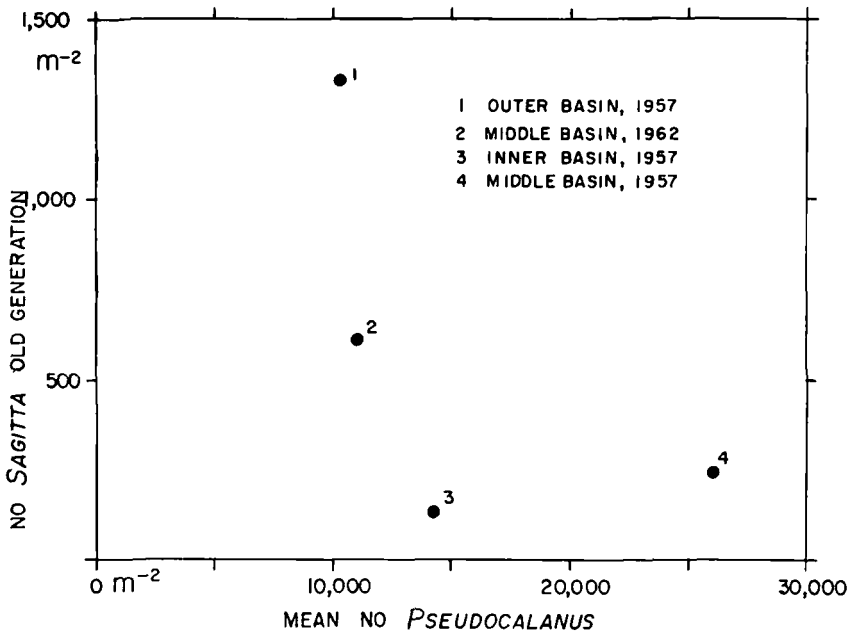

FIGURE 31. Relationship between number of *Sagitta elegans* remaining at the end of winter and the number of *Pseudocalanus minutus* remaining in Ogac Lake, a landlocked fjord on Baffin Island. The number of *S. elegans* is the number in the first sample of the season in each basin, and the number of *P. minutus* is determined as for Figure 30.

that whether you accept this or not, at least there is either a negative or no correlation between the number of prey and the number of predators at the end of a winter.

This situation appears in the same collections as the ones in FIGURE 30, in which the data are obviously adequate.

SLOBODKIN: I am not sure of that.

MCLAREN: There are explanations I will not go into for deviations from any negative population relationship that does exist, but the FIGURE 32 shows, I think, a more acceptable relationship between the number of this second predator, *Sagitta elegans,* in the lake and something else. It is a relationship that you see has an origin of zero. The number of *Sagitta* present in the later summer depends on the number of reproducing *Sagitta* which were present at the appropriate time. The appropriate time is the time when there are a large number of small nauplii available for the newly produced *Sagitta.* Thus with this predator, unlike *Daphnia* as you saw earlier, everything seems to be a matter of timing. For *Daphnia* there does seem to be a more direct and simple control of some sort.

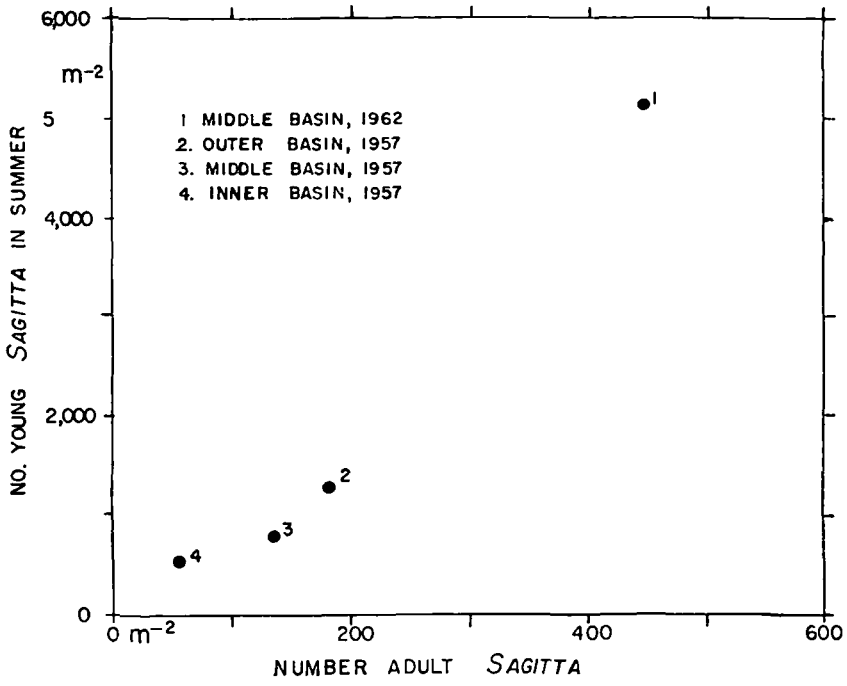

FIGURE 32. The relationship between the size of the *Sagitta elegans* population in summer (mean of all samples during summer), and the size of the reproductive generation at the time when the summer generation was 50 per cent recruited.

I am sure that both of these situations are multiplied 100-fold in the sea and represent two different kinds of relationship from the ones which Doctor Slobodkin has presented.

FAGER: Do you think you would get the same curve as this last one if instead of numbers of *Sagitta* at the time of the spring influxes you had plotted the number of *Pseudocalanus?*

MCLAREN: The absolute number of *Pseudocalanus* at that particular time is enormously variable between the basins (see FIGURES 30 and 31). Again this is a threshold effect; once the number of nauplii reaches a certain point, this is good for young *Sagitta* and all that are born at that time manage to get through; virtually all.

FAGER: Because if it is going to tie in with food for young *Sagitta* (and its relationship looks like a good strong one), then it would seem that your explanation requires that it also tie in with the *Pseudocalanus* abundance at that particular time.

MCLAREN: Yes. I think there is a considerable wearing down of this summer generation over the ensuing winter, possibly due to a shortage

of *Pseudocalanus* as prey. But the initial size, in summer, is set by timing

There are some very special things in this lake which could explain this in much more detail but I shall not go into it except to present the crude relationships which I have shown.

SLOBODKIN: I think it should be emphasized that there are certain species which clearly pay attention to each other in nature, as, say, Crisps' barnacles or limpets or breeding territorial birds; others which do not seem to, and there are general characteristics of the reproductive potentialities of these animals, of the general life tables of these animals, which almost permit you to divide one from the other.

I think Doctor Edmondson may want to talk about reproductive rate calculations in this sense. If not, there is a Figure which I think is relevant. This indicates the maximum rate at which a population may increase under optimal conditions as a function of various things. The data are from Smith(123), and J. T. Bonner* at Princeton has collected more, and it all fits the same pattern.

In general, in FIGURE 33 we see bacteriophage, miscellaneous bacteria —*Tetrahymena, Paramecium, Chlorella,* malaria parasites, the body louse, various of the flour beetles, etc. The vertical axis represents the intrinsic rate of natural increase—that is, if you grow a population so it is growing at a Malthusian rate, I have plotted that rate—

STRICKLAND: You mean the highest rate you found in the literature?

SLOBODKIN: The rate is not found directly from the literature. It is a function of the fecundity and life expectancy. It is a well-defined equation which is a sort of standard item in an elementary ecology course.

EDMONDSON: But it still represents the maximum, does it not?

SLOBODKIN: It represents the maximum.

FOGG: Is it temperature-dependent?

SLOBODKIN: They typically are temperature-dependent, but this is overshadowed by the range of differences we actually find here. You will find that they fit an inverse relation between size and increase rate fairly well.

Generation time and reproductive rate are not logically connected. That is, you may have a generation that is extremely long. You are born now, you do not reproduce until you are 20 or 30 years old, but then you reproduce 4 million eggs. This does not happen. It sounds ludicrous because no one does it, and this is interesting.

The rate of reproduction on the average would be quite large but in general the generation time is inversely related to the rate of reproduction. This general pattern can be interpreted as meaning that certain organisms, in particular small ones, have a strong selective pressure to be

* J. T. Bonner, Princeton University, personal communication.

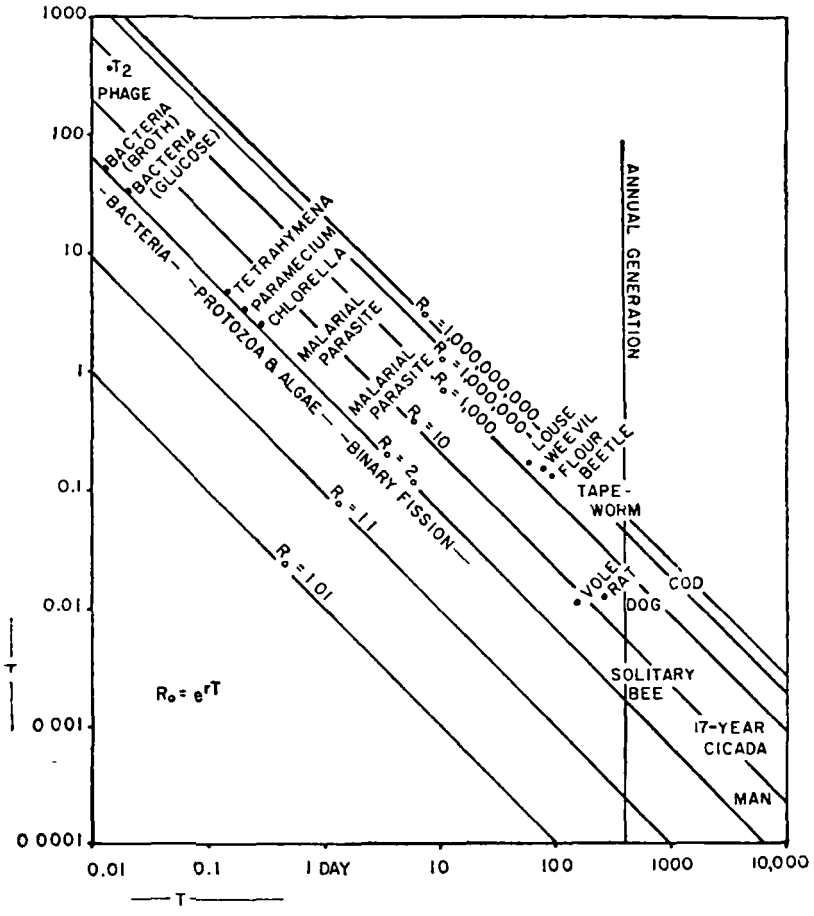

FIGURE 33. The relation between r and the generation time T. Note that larger animals tend to be in the lower right hand region.

able to reproduce rapidly and the large ones are not necessarily able to reproduce rapidly.

STRICKLAND: But there is a terrible "fudge" around that, is there not? You can get small algae apparently at their optimum that are about the same size as larger algae, because this is all swamped out on that log scale, is it not?

SLOBODKIN: Yes, it disappears on the log scale. The implication is a peculiar one, but you can consider that an animal that is extremely highly adapted to getting into new places is not particularly highly adapted or does not often find itself in a circumstance where it behaves as a popula-

tion—that is, where it is crowding itself. There is an incompatibility in a sense between staying in one place and invading new places.

SANCHEZ: Niche or geographical place?

SLOBODKIN: Geometric unit—geographical place.

STRICKLAND: What were those various lines? You did not explain them.

SLOBODKIN: This family of lines indicates the rate of increase per generation, not per unit time, so the binary fission situation is indicated by the line marked "2".

SANCHEZ: Increasing numbers?

SLOBODKIN: The number in this generation divided by the number in the previous generation.

STRICKLAND: You have put man in as having ten children, have you?

SLOBODKIN: No, on the order of two or three.

I suggest to you that most of the organisms in the sea are the kinds that are in transit, that are not staying in one place, and that part of the absence of data on the effect of crowding derived from nature may be, and probably is, due to the animals being the kind of animals that rely on the ability to increase rapidly when opportunities are good rather than on the ability to hold onto a particular situation in which they find themselves. There ought to be exceptions in the sedentary animals; there ought to be exceptions in animals in vary stable environments.

MCLAREN: I do not understand this. *Daphnia* presumably is one of those animals which does reproduce extremely rapidly when the going is good and then removes itself from the scene when the going is bad.

SLOBODKIN: Yes.

MCLAREN: That is not true, I think, of the majority of marine animals. It is not true of the majority of marine zooplankters which occur, in some cases, throughout the year.

SLOBODKIN: In *Daphnia,* in the course of population growth in a container, sexuality occurs at an early stage. When *Daphnia* are sexual the eggs that are produced are encased in a tough container and can be dried or frozen or anything else you want, and then you sort of have instant *Daphnia* that you mix with water and out steps a *Daphnia.* At that point, in a sense, the *Daphnia* has escaped from this container.

The time that a *Daphnia* population requires from the initiation of the population to reach some sort of a numerical equilibrium is on the order of 90 to 100 days, even in a very small container. This is longer than any period of temperature and food constancy that a *Daphnia* population is likely to encounter in nature, so that the curve from day 20 on is something that happens only in the laboratory. Does that relate to what you are asking?

MCLAREN: Yes.

YONGE: I would like to get Doctor Slobodkin's reactions to the problem of population dynamics on the coral reef. We are only considering corals. These *Madreporaria,* or *Scleractinia* as we now call them, are carnivores. The zooxanthellae are not concerned with nutrition.

You have these sheets of living matter. You can cut out the calcium metabolism; we are not concerned with that although probably the zooxanthellae are concerned with it(124). There are probably in the Atlantic up to 70 species of corals and in the Pacific more than 200. You can count the number of animals in every colony if you are prepared to do so. They will run into millions and thousands of millions, of course, but at any rate you can estimate.

You find, of course, that you have some corals where the polyp is large; maybe the size of your hand in some species but in many the individual polyp is minute. These creatures are all feeding on zooplankton, although the biggest ones could presumably take a small fish. Quite obviously, the smallest one can only live on the very minute members of the zooplankton.

Nobody has ever even begun, so far as I know, to tackle the problems of population dynamics that arise here. Near the surface of reefs, coral colonies are normally branching or rounded, giving a large surface for feeding purposes but lower down they tend to form flat sheets.

These colonies certainly vary, particularly in the speed of growth. There is no indication or no very obvious indication that they become exactly senile. They are, of course, in constant battle with the environment, the actual force of the sea which will break them up, or the effect of boring organisms of a wide variety from sponges to bivalves, and so on. But I wonder what thought this sort of picture of a population raises in your mind.

I do not think anybody has ever tackled the matter at all in terms of population dynamics but here is something that in a sense you can count; here are the number of polyps, the number of feeding individuals which are corresponding to the mouths in your *Hydra.*

SLOBODKIN: I think perhaps an interesting thing to do, and I do not know if anyone has done this, is to practice experimental predation on the coral. That is, if you have a coral bed with a whole series of small polyps, what happens if you burn out every other polyp? Would you then get a differential growth rate of the remaining polyps? If the polyps are competing with each other, which is, I think, in a sense what is happening—

YONGE: Not within any colony, surely. They are completely within a colony, are they not?

SLOBODKIN: Or even adjacent colonies.

YONGE: Adjacent colonies obviously do compete.

SLOBODKIN: It would be of some interest if you have a field of coral, to pick up half of them and substitute wooden pots or wooden blocks or stones or something. Would you then get a more rapid rate of settling of new corals than in the controlled area where you had left them all intact—that kind of thing? I do not know.

YONGE: Yes, I do not doubt that you would, and if you could isolate a part of a reef, if you could build a wall all around it so that within that area of water you could control the zooplankton, both the nature of it and the quantity of it, then you might—

SLOBODKIN: That would be lovely but that is very difficult. The difficulty with this kind of thing is that if you have a field situation and you manipulate it, it becomes an extremely expensive and extremely difficult situation which has all the equivocal properties of the laboratory, and if you have a field situation and you simply observe it, what has happened has happened and you are left with all the equivocal properties of the field, and what is required is occasionally going through some sort of theoretical argument of the sort that Doctor McLaren has been going through which permits you to look at the field situation in a new way and perhaps try out a laboratory-developed or mathematically developed theory in the field, but it requires a rather long-range ingenuity.

You saw FIGURE 33 which indicates that small animals have a higher rate of intrinsic increase or higher intrinsic rate of increase than large ones. On other grounds, which I would rather avoid going into now unless I cannot avoid it, we believe (meaning the Ann Arbor group in a sense) that herbivorous animals in most, at least terrestial, situations are controlled in their abundance largely by the effects of predation, while carnivorous animals are more likely to be controlled by being crowded—that is, internal controls of the sort that we get in the *Daphnia* populations or in the *Hydra* populations.

If these statements are valid (and whether or not they are valid need not concern us at the moment), it ought to be the case that if you look at a population chosen in nature, there ought to be a relation between body size and abundance for herbivores but not for carnivores. I will come back and pick up the ambiguities in that sentence. The nice point about this is that working with the soil-mite population of Michigan where it is fairly clear who is a pure herbivore and who is not from the mouth structure, Hairston(125) shows that the smaller herbivorous mites are more abundant than the larger herbivorous mites but there is no relation at all between body size and abundance in the carnivorous mites.

Whether this is of major significance ecologically or not is almost beside the point. The interesting thing about it is that we have gone

through a series of statements, none of which seemed *a priori* that probable, and ended up making a rather unlikely prediction about the world, and it checks out, in a sense lending strength to the statements that went into the argument.

PROVASOLI: Unless the different steps taken nullify one another.

SLOBODKIN: No, that they did not. They may be wrong but mutually contradictory, they are not.

The reason I bring this up is that it is an example of how one can use a field observation to check out a theoretical structure, and the kinds of things you are looking for are otherwise unlikely statements about nature. For example, I have made, in the last several days, extremely unlikely statements about nature, one of which, for example, is that if an animal has a caloric content per ash-free mass of more than 6000 it is a well-fed animal. I just say this and I will stick by the argument that went into that until someone shows me a contrary case in nature, and this is the kind of thing that might actually be checkable in the field.

BAYLOR: It is certainly true that *Leptodora* is the largest of the Cladocera and it is certainly the carnivore of the Cladocera. Does it follow from your argument that the tiniest Cladocera is the most herbivorous of all?

SLOBODKIN: No, it would not follow at all.

BAYLOR: But this is what you said about Hairston's data.

SLOBODKIN: No, within the class of herbivorous mites, it ought to be the case that the smallest mite represents the largest total biomass. Within the class of carnivorous mites there ought to be no relation between body size and abundance of biomass, and this holds.

SLOBODKIN: I think I might go through the chain of argument as just an example of the kind of argument that is involved. We start with the assumption that the rate of accumulation of organic sediment on a global scale is negligible compared to the rate of photosynthetic fixation, implying that the entire biosphere, if you will, is energy-limited, and this would also be related to the caloric value per gram data that I presented previously. It also leads to the same general conclusion.

STRICKLAND: You are saying this now, but this does not apply to the carboniferous?

SLOBODKIN: During the carboniferous, I believe the whole parcel is possibly true; that is, it does not take very much of an imbalance to give you a coal deposit. Over a sufficient length of time, on the average, any organic molecule will be eaten up almost completely.

When you looked outside, not now, necessarily, but in the fall, you found that the trees were green and if the trees are green there is a lot of organic material sitting on the trees and therefore the herbivores that are

feeding on the trees are leaving something. If they are leaving something and if energy is in short supply, something must be making them leave something, and we believe that this is due to predation. This is related to the fact that when you find trees denuded of their vegetation completely, it is typically an imported pest that has denuded them. It is almost never a member of your local herbivorous fauna that has wiped out a tree.

YONGE: They are in balance normally, are they not?

SLOBODKIN: Yes, and the fact that if you take a European tree pest and bring it to the States and it wipes out the leaves, it implies either that the European tree-eater was preadapted to the American climate in a fantastic way, which seems unlikely, or that the European tree-eater's predators had been left behind in the Old Country.

The argument then runs that where herbivorous material is permitted to accumulate the herbivores that ought to be eating it are predator-limited. If they are predator-limited then the predators must be limited by their food supply.

If the herbivores are limited by their predators then their abundance is related to how rapidly they can reproduce; that is, they are reproducing at close to their intrinsic rate of natural increase because they are being kept uncrowded in a rich food environment—not deliberately but by the effect of being preyed on or pushed down away from food limitation they are always in the process of increasing in some manner related to their intrinsic rate of natural increase.

We do not know the intrinsic rate of natural increase of most herbivores but we do know that larger animals have a smaller rate of natural increase than small ones. We, therefore, would think that where animals are limited by intrinsic rate of natural increase, the smaller ones should be more abundant than the big ones, and whatever you may think of the detailed steps, this is the way it comes out.

KANWISHER: More abundant in numbers?

SLOBODKIN: In total biomass.

KANWISHER: The mosquitoes equal the elephants, you know, in the African grasslands.

SLOBODKIN: The elephant is a peculiar herbivore in the sense that it does not have a predator acting on it. We are sticking to the soil-mite system.

KANWISHER: You do not want to discuss the shore, for instance.

SLOBODKIN: I do not have the data on it.

KANWISHER: I am just upset by your reluctance to manipulate nature for your own experimental ends. There is a lady from the University of Liverpool who worked on the Isle of Man; it has always been a bit of a

mystery why certain green algae are not more plentiful there. Things like *Enteromorpha* can double their mass in 24 hours by photosynthesis and yet they are relatively scarce along the shore. She had a group of students take several hundred meters along the shore, remove all the limpets, and in two weeks this was a green field. I thought it was a very illuminating thing.

SLOBODKIN: Yes, this is lovely. I am certainly not condemning that kind of thing. I am saying that the way you do it differs with the local situation and it requires a certain amount of ingenuity.

FAGER: In that particular case it appears that the herbivores were limited by their food.

SLOBODKIN: Yes, I limited my argument to a terrestial situation when I began it.

STRICKLAND: And eliminated elephants and cows.

FREMONT-SMITH: In that the elephant needs no predator.

SLOBODKIN: The reason I limited it to a terrestial situation is that there do seem to be many circumstances in both fresh water and marine situations where no vegetation piles up; that is, where the herbivores do seem to be directly food-limited.

YONGE: I thought that was true in the coral reef region. It is awfully difficult to get down to brass tacks here, but the primary production must be, of course, the diatoms and the flagellates, and so on.

SLOBODKIN: I believe that primary production may be limiting in the ocean but the fact of seeing a great accumulation of dead leaves on the ground in the fall implies that at least as far as those things which feed on green terrestial herbiage are concerned, something else has happened.

YONGE: Yes, except that something else comes along and eats the dead stuff.

SLOBODKIN: The whole system is energy-limited. There may be local subareas in it that are not. One of these areas we believed was the soil-mite situation, the herbivorous soil mites. We believed this only because you have a tremendous number of soil bacteria that are wandering around cleaning up what the soil mites leave, implying that the soil mites themselves are not doing the whole job, and it is for this reason that the test case was made in this situation.

FAGER: What does this say about the relative numbers of the different predators? Does it say they should be equal, or that there should not be any relationship that makes any sense?

SLOBODKIN: There should not be any relationship that is predictable directly from intrinsic rate of natural increase. The argument on this, which may not be obvious, is that if you go to the old, more or less standard equations of population growth, and you deal with the situation of two

species in competition or N species in competition, you find that except under certain circumstances (and there are circumstances where this does not apply), the intrinsic rate of natural increase drops out of the equations as a term and you are left with a system in which the rate of increase should make no difference.

This is where we get the argument that if many species in a particular community are competing with each other for some energy limitation, in particular carnivores, we would not anticipate a direct relation with the intrinsic rate of natural increase.

FAGER: What did turn out in Hairston's study(125) in terms of predatory mites? Were they all of about the same abundance?

SLOBODKIN: No, there was a greater variance of abundance among the predator mites than among the herbivorous mites, as I remember, but there was no relation at all to body size.

YONGE: You mean the predatory mites are feeding on their herbivorous relatives?

SLOBODKIN: That is right.

EDMONDSON: This comes back to something you started with, which was that if a population means anything it is because they do something to each other. It seems to me that all through this discussion we have been asking, what are the various things that happen when animals get jammed together? In almost everything that has been said here we are talking about effects, and when Doctor Yonge says there is obviously competition on the reefs, this means some particular kind of interaction. Many situations seem to permit interactions that are not dependent upon food relations but antibiotic ones. I am wondering just how widespread this kind of thing is that must be considered in such systems as soils and water.

SLOBODKIN: The antibiotic relations are particularly prominent among the soil bacteria and among the fungi, these organisms that are clearly limited by their energy supply since they are the ultimate degraders of anything that anyone else leaves, and they have particularly developed mechanisms of lousing up the adjacent species. Among the herbivores these are not found typically.

EDMONDSON: But let us go back a step. How about plants? Many plants seem to have developed rather nasty tasting substances, hairs and spines. How about the effectiveness of antiherbivore devices in plants?

SLOBODKIN: There is a difference between an antibiotic as found in a soil bacterium or animal and the antiherbivorous device of the plant, namely, the antibiotic of a bacterium is specifically designed to combat organisms on exactly the same trophic level as the organism that is producing the antibiotic. It is designed to stab competitors in a very elaborate

way. Putting up an evil taste or spines or something of that sort in a plant is designed to avoid being eaten directly by someone who is not your competitor, actually.

MCLAREN: Are seals outside marine biology?

SLOBODKIN: By no means.

MCLAREN: This is the other end of the scale from the bacteria, but the fact is that they demonstrate within themselves, the phocid seals, two further interesting influences on rate of increase, sociology and intelligence, in a very revealing way. Because seals are highly social and because they are slow breeders, they have been used by people like Wynne-Edwards(126) to support arguments about group selection. But, in fact, if you examine the situation closely, quite the opposite seems to be involved. The very primitive seals anatomically, the seals closest to the ancestor of the hair seals, include the ringed seal and the habor seal of our East Coast. Both are solitary animals, wild and wary. The one only comes out on ice; the other comes out on offshore skerries, distant rocks, and is generally a beast which seems to keep away from terrestial carnivores at all costs.

The aquatically most advanced seals include the elephant seal at the extreme, which are highly social and live on land away from any potential predator, of course, in the Antarctic. You might expect, in fact, that with an increase of sociology and an increase in size, which is involved here, too, that is, with advanced evolution, the elephant seal being about 25 times or more as heavy as the primitive seals, that r would be negatively correlated with this, but in fact it is positively correlated with it.

SLOBODKIN: Do you mean r or do you mean fecundity?

MCLAREN: I mean r, intrinsic rate of increase. The fecundity of the seal is one per year after maturity. The elephant seal matures in two or three years. The ringed seal matures in six or seven years. Thus, the more social, more advanced species seems to be practicing less "self-control."

What seems to be happening here is that the elephant seals, as an extreme case, are social but highly stupid, who gather together on an island and through a great deal of wear and tear and hard struggling manage to construct themselves a harem (that is, the bull which of course it possesses utterly). They have great success in propagating broods of their own particular dimensions and will.

The ringed seal, on the other hand, is a much more subtle animal, the harbor seal particularly, which in a sense needs intelligence. It finds itself, through many years, the best possible places to produce a pup. This is certainly true in the ringed seal which, with increasing age, is likely to be found in much more suitable pupping localities. There

would be, then, a selection for perhaps a later age of maturation, since the oldest ones—not the oldest but the middle-aged ones—would be most successful in reproducing their pups.

This does seem to be rather revealing because it does go opposite to the trend you have in fact described.

SLOBODKIN: Yes, this was just a general trend. I am not overwhelmed by things shifting over. We might look at two things: One, the discussion this afternoon in a sense has been quite unsatisfactory, I am quite aware of that. This is partially because Doctor McLaren and Doctor Edmondson and a few others are talking on the end of a long chain of theoretical arguments which we could not really start from scratch in a meaningful way now because there has been a long literature which has been almost separate from the literature of marine biology—I think that is a fair statement—that has grown up on this. Various theorems are understood or at least accepted with reference to populations; then you start talking at the far end of it and it is almost as if you started talking about chemical equations without ever discussing elementary chemistry. Perhaps the discussion has a value in pointing out this problem.

It is also the case that most of the previous discussion that has occurred, has been concerned with the straight-forward physiological properties or behavioral properties of the various marine animals, and the least of your worries, confronted with complete ignorance, is what the animals think of each other, and this is almost where all of the theory of population dynamics has focused. Would you want to comment?

FAGER: Not except to agree that an individual not trained in ecology at Michigan, Yale or Chicago, is likely to have found this afternoon hard to follow.

SLOBODKIN: For this, I am sorry. Would anyone care to come to my rescue?

EDMONDSON: This will not rescue you but I will ask two questions. In view of all the antiherbivores, how can you be sure that all the green matter is left over in nature because of the reason that you say? Some animals will starve to death in the presence of leafy plants because the leaves are no good; they are nutritionally deficient and the good parts have been nibbled off.

GONOR: I have specific examples of this.

SLOBODKIN: The koala bears will not eat anything except old eucalyptus leaves.

FAGER: Of a particular species.

EDMONDSON: The other question is, What would happen if, after you had gone through this long chain of arguments, the mites had not done the right thing; you would not have told us about this, would you?

SLOBODKIN: How many other examples of this sort have we tried?

EDMONDSON: How many have been tried and discarded?

SLOBODKIN: We have not tried others. It is a fair question. In point of fact, we have not tried any others. This was the best data, census data of this type, that we had where there was a clean distinction between herbivores and carnivores. It is equivocal for some animals.

FAGER: I think another thing should be put in here. You referred to it in passing but I think it should be stated specifically. In many of the best studied examples of herbivores, that I know—and this is mostly rodents—it looks as though they may be regulated by intraspecific processes. In fact, your *Daphnia* also has this mechanism of regulation although it apparently never or seldom comes into play in nature. Therefore, the real flaw in the argument presented by you, Smith and Hairston(127), is that it suggests, without any qualifications, that herbivores as a class are all limited by their food.

I think this is a bit broader than is justified by the data in the literature. Many of them may in fact be limited by intraspecific interactions and not by the food. If this is true, then, of course, the argument for predator limitation of them falls down, and the whole argument about predators falls to pieces.

SLOBODKIN: Yes, I think you are right. If we find a situation in which a particular organism is not food-limited, it ought to be predator-limited, and what you are suggesting is that it may not be. I suspect one can find local deviants, yes. This does not change the global thing.

FAGER: No, it is a question of how many species populations are regulated which way.

GONOR: What is the validity of a generalization like that which breaks down with every specific example? I do not mean to be nasty.

SLOBODKIN: That is quite all right. It is specifically a denial of the following statement: namely, that the abundance of organisms in nature is controlled by the climate. This is what we are specifically denying and we believe this, in essence, is impossible. What this came out of, this general argument, was Smith, Hairston and I trying to decide (a) was there anything in ecology we agreed on and (b) is there any reasonably irrefutable way to counteract the sort of nihilist position that there is no way of doing population dynamics and what you do is become a weather man?

SANCHEZ: I would like to make a comment on your idea of herbivores being limited by carnivores. I do not know, in fact, what the data are and it may well be that in some cases such is the case, but suppose a situation where there are no carnivores.

SLOBODKIN: Then herbivores ought to be food-limited except if they are socially limited as Doctor McLaren indicated.

SANCHEZ: But what does food-limited mean? If they go out and eat all the leaves they probably will not have any left to eat next year, so there would be some limiting factor prior to the extinction of all the plants available.

SLOBODKIN: This is the kind of situation we have in our laboratory containers where the physiological properties of the individual organisms deteriorate to the point, one way or the other, at which you have a balance in the rate of change of time. This typically or quite often does not happen in nature. Other things come in.

CONOVER: I have a feeling that the ocean is full of "koala bears," too.

VI. ALGAL MUTUALISM

Discussion leader:
C. M. YONGE
Department of Zoology
University of Glasgow
Glasgow, Scotland

YONGE: I feel that I should discuss this question of imprisoned phytoplankton, of symbiosis between unicellular algae and invertebrates. I will try to be as brief as I can on what is rather a big subject.

Among marine invertebrates (and you can also include quite a few fresh water invertebrates), you will find innumerable instances of intimate association with unicellular algae(128). The algae vary, I would say, almost as widely as the animals. They are usually 5 to 10 μ in diameter. There are green zoochlorellae and brown zooxanthellae (129).

The nature of the relationship varies enormously so that what may be found to be the case in one group of animals, even in one order of animals, may have no application to what occurs in another group, or even another order within the same group. In other words, what is undoubtedly the case in the *Chlorohydra* which Doctor Slobodkin mentioned yesterday has no application to the conditions in corals which are another group of coelenterates. All reef-building, or hermatypic, corals contain astronomic numbers of these algae in the endoderm.

There are, in my opinion, two general ways in which this association may come about. In herbivorous animals whose normal food is alga, it is the algae which must become specialized to resist digestion by the animal. That is certainly what happens in the fresh water sponges where there is a rather temporary population of algae. The plants seem able, temporarily, to resist digestion, but after a time they succumb and their place is taken by newcomers.

On the other hand, if the animal is carnivorous (and this would apply to coelenterates and Platyhelminthes), then the onus of specialization lies with the animal. It has to acquire the capacity to take in algae and tolerate their presence in the tissues. These are two clearly different ways in which the association may have come about.

This association becomes rigid in many of these groups. Instead of the normal cycle of events, the excrement of the animal being utilized by the

phytoplankton in the surrounding water and the animal feeding eventually on these plants, all takes place in a tight circle within the one organism.

In the endoderm of any reef-building (or hermatypic) coral, there are vast numbers of these algae contained, it seemed to me, not within the actual endoderm cells, but within wandering cells. Recently, Tom Goreau has shown by means of the electron microscope that this is indeed the case, that these algae are always contained within wandering cells.

This association has been known for a long time. What is the purpose of it? Many of the older workers and later the very distinguished Dutch zoologist, Professor H. Boschma, considered that the algae provided food for the corals and that was the position when I went to Australia in 1928.

However, I was unable to find that the algae have any obvious nutritive value to the animal. If you starve the coral, the first thing that happens is that algae are ejected. The coelenteron of a coral is subdivided by many mesenteries and the tips of these mesenteries consist of trilobed filaments. These are what matter. The central lobe secretes the extracellular enzymes responsible for the breakdown of the purely animal food.

The lateral regions on each side make up the one region where particular matter can pass into, or alternatively *out of,* the tissues of the coral. Boschma had observed that disintegrated algae occur in these regions. This was one of his arguments that the corals do feed on the zooxanthellae.

In point of fact, if you inject foreign matter of any kind into a coral with suitably stout tissues it is all ejected from this region. And when you starve a coral or subject it to low oxygen tension or to a sublethal high temperature; whatever you may do to lower the metabolism of the coral, algae are ejected in the same lateral lobes of the filaments.

I maintain that this imprisoned phytoplankton plays no part in the nutrition of the coral. What does it do? If you put a coral into a jar of sea water, having first estimated the phosphate content, and leave it there for a while, you find the phosphate content has fallen to zero. You can increase the normal phosphate content of the water a hundredfold and after several days find that all or a large proportion of the phosphate has been removed. In other words, the zooxanthellae have removed phosphate, and without doubt also ammonia(124, 128).

The products of protein breakdown; phosphate, ammonia and, of course, carbon dioxide, are automatically removed by these plants. I finally decided that whereas the presence of algae is not necessary for the maintenance of an individual coral colony (they can live without them under conditions of darkness), they are essential for the maintenance of a coral reef. They provide an automatic excretory system, thereby increasing the efficiency of the colony.

What Tom Goreau has discovered more recently is that the algae

undoubtedly play their part in calcium deposition (130–132). They are of fundamental assistance in the processes which enable corals to form this enormous mass of calcium carbonate which represents a reef. His evidence and arguments are well presented in a series of papers which many of you may know. There are thus two aspects of the problem. As automatic organs of excretion, the algae promote coral growth but they also increase calcium metabolism. The two are quite distinct. There is no good laying down more and more calcium carbonate if the tissues are not growing at the same time, and perhaps *vice versa*. Two processes are proceeding, they should go on at the same speed, and I think the algae are undoubtedly concerned with both. The algae are assisting the coral to grow, to increase its tissues, and at the same time they increase the speed with which it secretes calcium carbonate.

FREMONT-SMITH: May I ask a question? Are they still intracellularly when ejected? You said they are in the cells.

YONGE: Yes.

FREMONT-SMITH: If there are many algae there, there must be many cells.

YONGE: There are indeed.

FREMONT-SMITH: And these cells are ejected with the algae?

YONGE: I could not give you an absolutely certain answer on that, but I think they are ejected from the cells when they pass from the lateral lobes of the filaments into the coelenteron.

FREMONT-SMITH: And the cells are retained there?

YONGE: I think the cells are retained.

PROVASOLI: Is there any digestion of the algae once they reach the coelenteron which contains enzymes?

YONGE: The coelenteron contains proteolytic enzymes which act purely on animal proteins.

KANWISHER: There must be zooxanthellae being discharged in a non-starved animal if they act as a mop for all of the particles.

YONGE: Yes, I think that is true. I do not think you will ever section this region without finding a certain number of degenerating zooxanthellae.

STRICKLAND: Is there binary fission of these things?

YONGE: Yes. Sheina Marshall, who was with me in Australia, tried unsuccessfully to culture these zooxanthellae by the then known methods. It has been left to workers in Doctor Provasoli's laboratory in New York to find out what they really are, and although I do not think they have ever actually used zooxanthellae from corals, they have used them from anemones which are essentially the same thing.

PROVASOLI: Yes.

YONGE: And from jellyfish. These algae turn out to be dinoflagellates.

STRICKLAND: Yes, but they do divide when they are in the beast.

YONGE: Yes. They have a free-living phase, but they seem to have an indefinite vegetative phase.

STRICKLAND: That is what I mean, if they divide in there something has got to give.

YONGE: But remember that the coral is growing; more and more space is becoming available.

GONOR: Was it space or nutrients that you were worried about?

PROVASOLI: Nutrients. After what Doctor Fogg has said, certainly the algae leach some nutrients.

YONGE: I realize I did not say what is the major evidence that corals do not digest the algae, namely the effect of starvation. Clearest results are obtained with *Fungia* which are round or oval in shape, consisting of a single polyp with a mouth in the center and thin tissues stretching over the flat disc. Within days of placing specimens of *Fungia* in filtered water, and keeping them in light, the tissues begin to retreat and at the end of about ten weeks the disc tissues have withdrawn to a narrow ring with all the skeleton bare in the middle. All the time, vast numbers of algae are being ejected from the tissues into the coelenteron and so away from the animal.

STRICKLAND: Is there any reason to think this can be completely generalized? Could not a gradation of behavior, according to the type of coral, be postulated?

YONGE: I do not think so. As far as one can make out, the Scleractinia are quite consistent. If you are speaking about the Alcyonaria (and I do not intend to introduce these into the discussion), then I would agree that you do get a gradation.

PROVASOLI: Are you excluding only that they do not eat the algae or are you excluding also the fact that the algae can contribute soluble products which are serving in some part as a nutrient?

YONGE: I am certainly not excluding that. It is obviously possible, as Doctor Fogg has shown, that material passes out of the intact zooxanthellae into the surrounding tissue. This may, as you say, provide ammonia or some vitamin.

PROVASOLI: Or even sugar and some carbohydrates.

YONGE: Yes, that is obviously so, but the fact is that you *do* get an immediate effect of starvation.

PROVASOLI: Probably not, it all depends on the food. However, it has been also said that there is not enough animal food in the zone to account for the enormous growth of coral. There should be then some other source, which may not be the most important source but, nevertheless, is a source.

YONGE: That point has been made and there is a real gap in knowledge here: How much zooplankton is there in these waters? In tropical waters the replacement rate is very great and many of these corals with very small polyps are adapted for feeding on correspondingly small members of the zooplankton.

PROVASOLI: And if the nanoplankton has been neglected, we might well have missed the part of the biomass which has not been included in the calculation.

YONGE: You normally tow for plankton in bright sunshine when it simply is not there. It has descended into deeper water or on to the bottom.

SANCHEZ: Doctor Yonge, it is surprising to find cited in the literature on metabolism and digestion in lower invertebrates that one finds proteolytic enzymes in the gut as you have referred to these mesenteric filaments, and never, or rarely ever, enzymes that would break down carbohydrates.

YONGE: The carbohydrates seem to be broken down intracellularly. The carbohydrates in this case would be largely glycogen.

SANCHEZ: Could it not be that the algae are providing the carbohydrates?

YONGE: Yes, it could be. I am not excluding that.

FOGG: You always get surf around coral, I think. Could they be regarded as machines for converting soluble organic matter into particular organic matter?

YONGE: It has been found that bubble formation promotes conversion of soluble organic matter into particulate organic matter(133), so, therefore, could a coral reef be regarded as a machine for converting soluble into particulate organic matter? Would a coral tentacle react to these particles that you postulate?

PROVASOLI: That is a very good question.

SANCHEZ: Would not the animal's respiratory current?

YONGE: We are back again to the old questions of why does an animal have a highly complicated and most efficient feeding mechanism if it does not use it?

EDMONDSON: In this case they were particles.

BAYLOR: Branch worms feed on such particles.

PROVASOLI: But they are filter feeders, while the coral has a capturing mechanism.

EDMONDSON: But suppose zooplankton fed on these particles, then they are fatter and better sources of food themselves.

SANCHEZ: The point is that although these animals are carnivorous and would not be considered as filter feeders, there is a permanent

current of water going into the gut and out, so that anything that is in the water will go into the gut and be usable for digestion.

YONGE: No, it would not. In the presence of plant material, diatoms if you like, the mouth will close tight and will not let them in. It will remain shut until they are removed by the cilia.

SANCHEZ: I do not know what the range of size is, but particles smaller than a plant cell?

YONGE: Yes. There is a great deal to speculate about here and I would far from wish to be didactic on this subject.

EDMONDSON: I have thought of an interpretation of this ejection of algae, and I would like to ask you if it makes sense on the basis of the natural history and behavior of corals. You have given a picture of a small continued liberation of algae into the coelenteron all the time. When you then starve the corals, you have a massive liberation. One would think that if these algae were really a source of nutrition the coral would not throw them away at a critical time like that. But if the continued liberation does result in doing something definite for the coral, mediated by the algae, then would not massive liberation be regarded as a stress reaction to starvation—just an exaggeration of a normal process that is nutritionally helpful?

YONGE: We are not merely dealing with starvation here; we are dealing with anything which lowers the metabolic rate, raises the coral to a sublethal temperature, places it in water of very low oxygen tension, and the same consequences follow.

EDMONDSON: So it is a generalized stress reaction. Does this make sense?

YONGE: Yes, that is all right—a generalized stress reaction.

BARKER-JØRGENSEN: Is there any difference in the rate at which the animals are reduced in size in light and in darkness?

YONGE: Effectively not. They were starved in light and darkness—parallel experiments.

BARKER-JØRGENSEN: Would not this settle the question whether the algae are of nutritional value or not?

STRICKLAND: No, because protein might be the limiting factor or it might not.

FAGER: Everybody keeps talking about the corals ejecting the zooxanthellae. Could not one look at it in a different way; namely that the zooxanthellae are so adapted that when the nutrient concentration within the corals reaches a certain level they leave because this is an indication that the coral may die?

YONGE: No. The coral is not necessarily going to die. The zooxanthellae come out, many of them obviously dead; others not so obviously dead,

because it is often difficult to say whether an alga is dead or not, but they are all masked in mucus.

PROVASOLI: Some of the zooxanthellae should come out alive because this is the resting stage from which the dinoflagellated cells, which infect other corals, are produced. Somehow this stage has to be secured.

YONGE: It does seem most probable that new coral colonies are infected by way of the egg. The fact remains, as your people have shown, that they are dinoflagellates.

PROVASOLI: Really it was Kawaguti to show that first.*

YONGE: Yes, he had before, that is quite true.

FOGG: If they come out dead, does this not suggest the coral had sucked them dry?

YONGE: A good point, but all I can say is that they have time to suck much out of them because you get this immediate effect of starvation.

FOGG: You can take a lot of soluble material out without altering the cell form.

YONGE: There are lots of loose ends here. But after standing still for a long time, this problem is coming to life again. Tom Goreau has developed new techniques(130–132). I feel we should now go ahead with the Tridacnidae. This is a family of Indo-Pacific bivalves. Compared with a normal bivalve, the mantle and shell swing round so that the hinge comes to lie on the underside beside the foot and the siphonal region has spread right over the middorsal side of the animal. Hence, if you look down on them, you see a great expansion of siphonal tissue which spreads forward and also laterally. More or less in the middle lies the rounded exhalant aperture with the elongated inhalant aperture remaining at the posterior end(128, 134).

Anyone who has studied Indo-Pacific reefs will have noted these animals because their tissues are most brilliantly colored. Tridacnids are surface-dwelling animals and no matter how shallow the water and how brilliant the light, hardly screened at all by a few inches of water, these animals are always fully expanded. These hypertrophied siphonal tissues represent areas used for "farming" of algae. The zooxanthellae appear very similar to those of corals but are probably distinct. That might come out in culture. They are present in thousands of millions.

The brilliant color of the tissues is undoubtedly a means of screening them from the harmful effects of the light. Here also the algae are contained within cells, in this case in phagocytic blood cells. There they obviously increase; you can see them in stages of division. Nothing is known about their life outside the animal, but their life within the ani-

* Kawaguti, S. 1944. On the physiology of reef corals. 7 Zooxanthellae of the reef corals is *Gymnodinium s.p.*, Dinoflagellata; its culture *in vitro*. *Palao Trop. Biol. Stat. Studies.* **2**: 675–679

mal, superficially, resembles what it is in corals. Sections through the visceral regions reveal these blood cells, a feature of all bivalves, containing algae which are obviously being digested. You examine the kidneys and you find the largest such organ in any bivalve. Why? Because these algae are being digested, not in the gut, but in the blood system and the only way of disposing of the indigestible material is by way of the kidneys, hence these enormously hypertrophied kidneys. This, I think, makes metabolic sense.

That, very briefly, is the story except that the Tridacnids do also feed normally. They have the usual gills which collect phytoplankton. But some species, notably the giant clam, do become far bigger—Doctor Barker-Jørgensen could comment on this—than any animal could surely get just with an unaided ciliary feeding mechanism. I think there is a limit of size to which an animal can attain just with a ciliary mechanism, and yet these animals must get up to a weight of more than a quarter of a ton.

SCHMIDT-NIELSEN: If filter feeding is a surface function, and photosynthesis certainly is a surface function, they should be limiting in the same way.

YONGE: Yes.

KANWISHER: Maybe in a different size range, though.

FREMONT-SMITH: This is the weight outside or inside the shell, not the shell?

YONGE: No, with the shell. If the animal is a really very big one it must weigh up to half a ton and the bulk of that is shell. There is also much meat, the adductor muscle is 6 inches in diameter.

FREMONT-SMITH: Seven or eight hundred pounds of organism?

YONGE: Yes. That, very briefly, is the position. Tom Goreau worked on these animals as a result of an invitation to join an Israeii Expedition to the Red Sea. Having done a great deal of tracer work with corals (130–132) he tried the same techniques with small Tridacnids. By using carbon-14 he showed that this is immediately taken up by the algae as would be expected. Later it passes into various secreting surfaces in the animal but beyond this I should not go, at any rate in print, because his work is unpublished.

PROVASOLI: Once the routes of migrations of the radioactive substances are known in greater detail, it will be extremely interesting to follow the biosynthetic pathways from the fixation of the radioactive carbon dioxide by the algae to the algal products leaching out in the blood, their accumulation in the mucous glands, in the areas secreting byssus and the crystal-

line style, and finally to their excretion in sea water. This might not be too difficult. Since the *Tridachnas* are large animals, it should be possible to work with large quantities of the different tissues and fluids. By the type of organic compounds found in the blood it will be easy to assess how much the gardens of zooxanthellae contribute to the physiology of the *Tridachna.*

VII. PLANKTON

Discussion leader:
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YONGE: The theme I have to supervise is very general although it has certain specific implications with which I am personally concerned. When speaking of phytoplankton and invertebrates you are really considering the relationship between primary and secondary production.

I am not quite sure what the present position of the argument is, but not so long ago there was a great debate between those who believed in grazing and those who considered that overconcentration of phytoplankton excluded the animals. I am sorry that Gordon Riley is not here because he is obviously the person who can say a great deal about this. I think it should be discussed by anyone here who has feelings on the matter.

FAGER: I think it might be of some interest in connection with this question of zooplankton exclusion by phytoplankton that I carefully analyzed some of the evidence upon which Hardy(135) based his original idea. I biased my sampling of his sampling by considering the examples he suggested were the most convincing (data in Tables LII, LIX, LXVI, LXVII). Not one of the examples provided statistically significant (at the 5 per cent level) support for the idea of exclusion of zooplankton by phytoplankton. In fact, in the case of some of the zooplankton which he picked out as the best examples of exclusion, there was an indication of a positive correlation between phytoplankton concentration and zooplankton numbers when all the data were considered. I also looked into the suggestion that zooplankton abundance was positively correlated with intermediate phytoplankton concentrations and negatively correlated with both high and low correlations. There was no statistical support for this idea in the data. He has more recently(136) indicated that, on different grounds, his faith in the validity of the exclusion principle has been weakened.

This is something that disturbed me a great deal because I have the highest respect for Sir Allister and yet, the numbers simply say that his intuitive guess was based on no evidence at all, or negative evidence, although I do not think he knew that; I am sure he did not.

I must however remind you that there is work by Lucas(137) and also by Bainbridge(138) which does show that in the laboratory some phytoplankters at certain concentrations do seem to be distasteful, if you want to put it that way, to certain zooplankton. Most of the zooplankton used were, unfortunately, near shore organisms and not deep-sea zooplankton at all. There might very well be differences in their reactions.

KANWISHER: Do the laboratory counts of Lucas have realistic concentrations as far as the open sea?

FAGER: Lucas used 1000 cells/mm.^{2}; Bainbridge used 1–18 cells/mm.^{3}

CONOVER: Probably not awfully high when compared with areas in which mysids are found under certain conditions.

YONGE: You do have great concentrations from time to time in the North Sea of *Rhizosolenia,* which do produce conditions unfavorable to zooplankton.

BAYLOR: The same could be said of a red tide.

YONGE: Of course it could.

BAYLOR: I would like to say I have done the same thing but I never trusted my own conclusions because my statistics are sort of home-grown, self-taught, and I always thought, "Well, probably I am wrong," but I certainly came to the conclusion you did on reworking the same data.

YONGE: It has always seemed reasonable that, as the zooplankton must depend on the phytoplankton, they presumably graze on it.

EDMONDSON: This is one of the questions: the effect on the population. Has anybody measured over these areas the mean crop of grazing animals multiplied by some realistically derived average figure for clearing rate per individual to see what reproductive rate had to exist to maintain a population in the face of this?

BAYLOR: Doctor Slobodkin has done this ad nauseam.

EDMONDSON: Not with these data, though, the marine data.

BAYLOR: Not with these data, no.

EDMONDSON: Steele and people like that have done some of this.

CONOVER: I do not think it has been done. I think it probably ought to be done.

SANCHEZ: I think it has been considered qualitatively by people like Menshikoff, has it not?

YONGE: I think that Sheina Marshall and the late A. P. Orr, the pioneers in this field, would have some comments. I gathered from them that the sequence of events never quite fits. The increase in animals starts sooner that it ought to do.

BAYLOR: That is all right. If you assume they are eating the particulate organic matter which is produced by the Langmuir circulation pattern

and wave action in the lake, then they have an almost adequate supply of food to get started on.

YONGE: That is in the sea?

BAYLOR: Yes, but in the lakes, also. I really think this is the answer to the missing food paradox.

PROVASOLI: Naturally we should also consider that some organic solutes can be used directly by invertebrates. Stephens found that soft-bodied marine invertebrates representing 10 phyla removed significant quantities of glycine from a sea water solution. The only invertebrates which failed to do so were the six species of arthropods tried, perhaps because their chitinous envelope is poorly permeable. This confirms our findings on the poor use of solutes by *Artemia*. He found also that other amino acids and sugars are equally absorbed.

It is too early to assess how much is the contribution of these absorbed solutes to the nutritional balance of the marine invertebrates. Even if they prove to have only a subsidiary role, quantitatively, it might be relevant nutritionally and ecologically if the substances thus acquired from solution compensate for nutritional deficiencies or imbalances, as in the case of the vitamins and *Tigriopus*. The uptake of organic solutes may also spare the more conventional feeding mechanisms and might make the difference between survival and death in the periods of scarcity of live particulate food when the animal has to depend almost solely on its reserves.

The enormous store of organic solutes in waters, which after Krogh(139) seemed an unused resource, may yet prove to be an important step in the food chain either through direct uptake or as a source of amorphous particulates *a la* Baylor and Sutcliffe(87) and Riley(88).

STRICKLAND: What did he study this on, what sort of beast?

PROVASOLI: Among the 40 or so species tried, several invertebrates as *Microciona prolifera, Nereis virescens, Littorina littorea,* and *Asteria forbesi* stand out for their exceptional ability to remove in 22 hours from 80 to 100 per cent of the glycine in solution (150 mg. per liter). The other soft-bodied invertebrates absorbed 25 per cent or more(140). This concentration is about 100 times larger than that occurring in seawater. After this exploratory work, Stephens employed(140)C-labeled amino acids and sugars at the more realistic concentration of 10^{-5}–10^{-6} molar. The uptake of sugars, glycine, and other amino acids was fully confirmed even at these concentrations and is very rapid. The animals apparently absorb the solute through the body surfaces because the rate of uptake is an exponential function of the weight of the animal; it is independent from the apparent mode of feeding of the animal and is not reduced in animals whose digestive tract had been occluded in various ways.

FOGG: Is it quite certain that the substance is being taken up by the

animal tissues or might it be by the associated bacteria. These were aseptic organisms, were they?

PROVASOLI: No, the work was not done under aseptic conditions, but seems quite reliable. Antibiotics have been added when the experiments lasted a few hours. Later on, the use of labeled compounds allowed shorter exposures and showed that the rate of uptake was not modified by the antibiotics used previously. More detailed work done on the worms, *Clymenella* and *Nereis*(141, 142) shows that the radioactive amino acids are accumulated in the body at concentrations 4 to 10 times higher than in the external solution after only 15 minutes uptake. The radioactive amino acids were recovered in the alcohol soluble extractives from body tissues. It is also interesting that *Climenella,* which had previously accumulated radioactive glycine and phenylalanine, placed in seawater containing these amino acids, but unlabeled, did not release in the medium any radioactivity, indicating a one-way accumulation.

BARKER-JØRGENSEN: I have no personal experience in this field but I have a feeling that it is difficult to get a coherent picture, and that the picture contains many contradictory traits. For instance, if you maintain the theory that in the oceans the primary production of phytoplankton is controlled by the grazing of the zooplankton you will run into difficulties if you will, furthermore, assume that the same zooplankton should also live on organic detritus or on the dissolved organic matter, because ultimately the detritus and dissolved organic matter must also be derived from the primary production. We know that the concentrations of organic detritus and especially dissolved organic matter in oceanic waters are much higher than the concentration of phytoplankton. The turnover times of detritus and especially dissolved organic matter must therefore be much longer than the turnover times of phytoplankton.

STRICKLAND: But you do not have to postulate that they all come from the same spot.

BARKER-JØRGENSEN: But do you not think if you take the conditions in the middle of the ocean, that we have a system where what is dissolved and present as detritus must be derived from the primary production in this area?

STRICKLAND: But not necessarily the total amount of dissolved organic material. That could have come from the coast.

BARKER-JØRGENSEN: In the middle of the ocean?

KANWISHER: Come from where?

STRICKLAND: From the coast.

BARKER-JØRGENSEN: How did it arrive there?

STRICKLAND: By circulation.

BARKER-JØRGENSEN: One thousand miles from the coast you have circulation?

STRICKLAND: Yes, certainly; you see kelp floating past there.

BARKER-JØRGENSEN: I thought that a volume of oceanic water would behave as a unit that could not be enriched specifically by dissolved organic matter of coastal origin.

STRICKLAND: I think that there is plenty of evidence that the coastal waters of British Columbia find their way out several hundred miles offshore fairly rapidly and we know that the crop and the dissolved organic matter in this coastal water is often very high.

STRICKLAND.* I have one observation which might be interesting. It was new to me. There is some indication of the distances that detrital material can travel from the observation that radioactive "fallout" material enters the sea around latitude 50°N in the Pacific and is detected in appreciable quantities in mussels on the shores of the lower parts of Baja California.

The fact that these organisms concentrate radionucleotides which presumably have been swept down the east Pacific several thousand miles attached to filterable food, is quite interesting and underlines the permanent suspension of such material.

BARKER-JØRGENSEN: What do you mean by radioactive nucleotides? Is this Goldberg's work?

STRICKLAND: No, this is work that has been done recently by T. R. Folson of the Scripps Institution of Oceanography with ^{54}Mn and ^{65}Zn.†

FREMONT-SMITH: Sodium?

STRICKLAND: No, no, this is fallout. In the studies of coastal America where the California current impinged on Baja California, you get this terrific increase, which I found rather staggering. It implies that whatever is on the surface waters very far North and West has stayed in that system over a considerable distance.

BARKER-JØRGENSEN: Another thing, how much of this patchiness is dependent upon the methods—what is the accuracy of the various measurements?

STRICKLAND: Quite accurate enough to detect patchiness. In a 10-mile track you can detect phytoplankton very easily, and patchiness which is not due to *in situ* growth. The *in situ* growth rates are not sufficient to produce the patchiness found over any reasonable period.

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* Editor's Note. The following comments were made later in the conference in reference to this problem.

† T. R. Folson, Scripps Institution of Oceanography, La Jolla, Calif., private communication.

BAYLOR: May I suggest a method by which you can account for this patchiness? If you consider laboratory experiments in which it is possible to adsorb phytoplankton on bubbles and bring them to the surface of the water, and then if you consider the Langmuir circulation pattern in the ocean, you see that there would be a concentration of phytoplankton at the downwelling areas.

STRICKLAND: But not of the silicate or nitrate.

BAYLOR: Possibly not that, but all I am trying to do now is account for patchiness of phytoplankton and if you recall, it is always very uncomfortable to make a plankton tow crosswind so it is always done downwind and, therefore, parallel to the rows of Langmuir circulation. Hence, you may be towing either in a downwelling area or you may be towing between two, and I believe this is the sort of thing that will account for the fact that you may think you have made one tow downwind and the following tow upwind through the same course when in point of fact you have not.

STRICKLAND: You are talking about zooplankton patchiness?

BAYLOR: No, I am talking about phytoplankton patchiness as well.

MCLAREN: The same thing occurs—you might be inside a row or outside a row for any drop.

BAYLOR: If people do not make plankton tows, on the basis of what evidence do they assert that patchiness exists?

STRICKLAND: I pick it up in a bucket.

BAYLOR: You are thinking of Cassie's data(143) now?

STRICKLAND: No, I am thinking of my own data—a bucket over the side of a ship at sea.

BAYLOR: Essentially, you are making a tiny little tow every time you throw the bucket over—but how do you know you have the bucket in a downwelling row at one time and between a couple of them the next time?

STRICKLAND: I only know if you plot up chlorophyll concentrations in samples taken by a bucket lowered over the side, taken at half-mile intervals around a seven-mile square and across both diagonals, too, you get a picture of a discrete patch of phytoplankton, whereas I think if the samples taken were completely random or results arose from errors, we would not get a picture of one or two distinct large patches.

BAYLOR: Yes, that is quite all right. You can have a patchiness on a larger scale.

STRICKLAND: I am sorry, I was thinking of patchiness as of the order of half a mile—that sort of thing—not micropatchiness, which I am sure does exist there.

BAYLOR: I have no idea how you can account for larger-scale patchiness.

STRICKLAND: I think it is differential grazing.

McLAREN: Doctor Yonge, may I come back to the point you made which precipitated all this organic matter? You in fact stated that in Loch Striven there was some difficulty explaining the reproductive rate of the resident copepods.

YONGE: It just does not fit in as you think it ought to do.

McLAREN: As I remember it, this does not seem to be true. Certainly *Calanus* and *Pseudocalanus minutus,* two copepods found in the Loch—their reproductive periods are perfectly correlated with the presence of diatoms throughout the season. As I remember, Marshall(91) concluded in her "small copepod" paper that things like *Microcalanus* are not predictable in terms of primary productivity as measured by the net diatoms, but these other things were. Am I correct? Doctor Conover, you know this work as well as I do.

CONOVER: I would say you are more or less correct in that. I also want to point out that in the organism that I have been working with, the correlation is not so good because these animals have evolved so that they can reproduce just opportunely before the bloom. What they need to accomplish is to put on a large biomass during the bloom.

The breeding cycle of *Calanus hyperboreus* is such that it breeds about a month before the phytoplankton really gets going.

EDMONDSON: What is the signal?

CONOVER: I have no idea but I feel that there is a clock, I just guess it is metabolic, as I do not know what else it can be, which runs the whole system from the time the animal gets this stimulus from the food. It runs the whole system all the way around the year back to this point again.

BAYLOR: More a calendar than a clock, is it not?

YONGE: It does vary from year to year. The spring increase with us comes on with the most dramatic suddenness and it does vary. It seems to be light. It certainly is not temperature.

CONOVER: No, I am sure it is not temperature.

YONGE: Two weeks in fifty-two is quite a bit, is it not?

CONOVER: I see no way that the animals that are in the deeper water, in this particular case *Calanus hyperboreus,* can know that it is time to come to the surface again. The light stimulus must be rather limited at depths perhaps greater than 1000 meters. I have some evidence on this from the point of view of molting. The molting cycle of this animal also seems to be seasonally controlled. Even if you take these animals out of the ocean and put them in a dark refrigerator, the animal still knows it is time to molt to an adult in the fall to get ready to breed in the winter, and how it does this I do not know. They sometimes get a month out of phase if you have them in the laboratory for quite a long time, but

nonetheless they come rather close to the actual molting cycle that you can observe in nature.

GONOR: This sort of phenomenon has been observed in the spawning of barnacles. The release of barnacle nauplii is correlated not with the beginning of phytoplankton increase in the spring but just before it. The female barnacles (well, all of them are females), the barnacles with the load of nauplii, know ahead of time that it is now time to release the nauplii so that they will be able to feed on the incipient increased phytoplankton. This has resisted analysis so far.

STRICKLAND: It cannot be just the light because what governs the spring bloom in say, Georgia Straits, British Columbia, is not only light increase but local meterology. You can start a bloom for a day or two and then get a storm that pretty well returns the sea to winter conditions. I cannot see how any barnacle would predict things better than the Vancouver Weather Bureau, which does not say too much.

EDMONDSON: What are the actual statistics of the records? Could you account for this by saying that they come out at some particular time, and on the average this usually brings them out in good conditions?

STRICKLAND: I think you get good herring years, good barnacle years, and good everything else years, mainly as a result of the timing of the spring bloom fitting in ideally with the early feeding of the organism in question. This is to some extent a creed and there is no satisfactory data to support or refute the hypothesis, but it seems the most reasonable explanation.

FOGG: Johnston(144) has shown for some phytoplankton species that the water needs to be conditioned, presumably by organic growth factors. Why should this not apply for the zooplankton, too—when the concentration of certain substances in the water is built up to a certain level then everything starts off?

STRICKLAND: But you have not very much there to start building up.

MCLAREN: That is not true of all the copepods. *Calanus hyperboreus* is a rare copepod compared with *Calanus finmarchicus,* and in the latter there appears to be no question—it breeds and produces eggs, when the diatoms are there in abundance. This seems to be the general rule among copepods, and the others are interesting special cases.

COSTLOW: The barnacle nauplii are really something. You can see the nauplii ready to hatch, you take them out of the mantle cavity of the female, put them in sea water and they will hatch, and yet if you open barnacles for the next month if the bloom has held off, the eggs begin to rot and yet they will not be released into the water.

EDMONDSON: When you evaluate the relationship between breeding and abundance, how are you looking at the phytoplankton abundance? What

I am thinking of is that with the spring bloom in Windermere, the maximum growth rate of the *Asterionella* population, which presumably has some metabolic significance, occurs at least three weeks before the maximum population density.

Maybe this is some kind of signal to the animals that are eating those few active cells.

GONOR: I do not believe that the people who have worked with barnacles have pushed their analysis to this point. I think they simply looked at, or judged it, on the time when there was the maximum amount.

EDMONDSON: This can be very deceptive.

YONGE: I would have thought we probably have discussed this matter about as far as we can take it. I threw this at you, rather, without any knowledge to guide any discussion, but certain points have come up. Now Doctor Gonor will talk about algal food specialization, in certain gastropods.

FOGG: I am sorry I missed my cue earlier but I would like to go back to soluble organics for a moment and show the results of the only experiments that I have ever carried out with zooplankton (FIGURE 34). Gly-

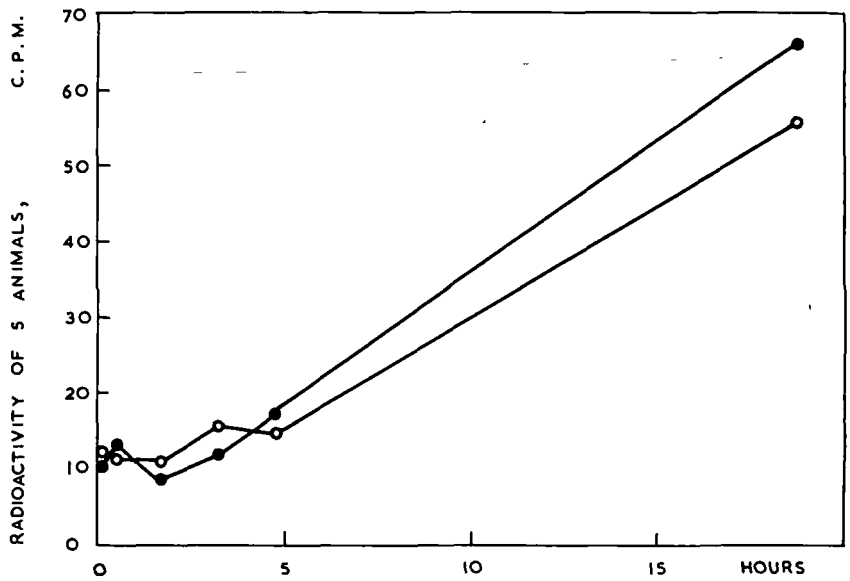

FIGURE 34. Uptake of ^{14}C-labeled glycolate by starved female *Temora longicornis* (Müller) in subdued light. *Open circles:* in the absence of any food organism; *closed circles:* in the presence of *Skeletonema*. The total concentration of glycolate in the sea water was 0.5 mg./liter, its activity 5×10^7 cpm/liter. (Unpublished data of Å. Berner, C. Nalewajko & G. E. Fogg.)

colic acid ($CH_2OH.COOH$) is an extracellular product of some algae under at least some conditions and it has been detected in sea water, so I thought it would be interesting to supply zooplankton organisms with this substance and see whether they took it up. We used the copepods *Acartia* and *Temora* and put the starved animals in sea water containing glycolate labelled with ^{14}C and then at intervals we picked out five animals, washed them thoroughly, and measured their radioactivity. With both species there was definite and continued uptake. Just as a check, we did a parallel experiment in which the animals were supplied with ^{14}C-labelled bicarbonate. We found that they did not take that up to anything like the same extent. With both species, then, we got definite uptake of ^{14}C-labelled glycolate from a solution of about the same concentration as one would expect under natural conditions.

FAGER: This does not say that there is net uptake.

FOGG: No, it may be exchange and it may, of course, be due to bacteria on the surface.

STRICKLAND: There could not be exchange unless you assume there was glycolate in the animals.

FAGER: What did you measure, just the ^{14}C content of the animals or the ^{14}C content of glycolate extracted from the animals?

FOGG: The ^{14}C content of the whole animal. It could have gone in, reacted somehow or other, and an equivalent amount of organic material, not necessarily glycolate, could have come out. I do not mean physical exchange; I mean physiochemical exchange. What I am trying to say is that this may or may not constitute a food source in the sense that there has been any net addition. I do not think it does constitute a food source because from a rough calculation, the uptake of glycolate which we found would amount to only about 0.001 of the carbon requirement of the animal. I think that direct uptake is probably quite negligible, but I wonder whether there may not be other pathways. There does seem to be a tendency to equilibrium between intracellular and extracellular glycolate in *Chlorella,* at any rate. It is well established that the substance is taken up by cells as readily as it is liberated from them(145). When you have steady-state conditions, with photosynthesis running steadily, then glycolate, which is an intermediate in photosynthesis, is elaborated into cell material in the alga, but if growth is interfered with—if, for example, you give an inhibitor which prevents protein synthesis—then glycolate comes out from the cells(146). It represents, as it were, an overflow product of photosynthesis. Similarly, if outside the alga you have a strong sink for glycolate—if, for example, there are bacteria which absorb it very readily in the vicinity—then this, too, would be expected to divert a higher proportion of the photosynthetic production into glycolate.

So if there were bacteria utilizing glycolate—and there do seem to be in sea water—you might imagine that a part of the photosynthesis of the phytoplankton would be diverted to glycolate, utilized by bacteria, and bacteria might be eaten by the zooplankton.

Another possibility is that glycolate might be adsorbed on particulate matter. We find, as a matter of fact, that it is adsorbed rather strongly on the membrane filters we use in this work, so a possible link in the food web might be production of glycolate by phytoplankton with adsorption on the particulate matter. This might then be eaten by zooplankton, but it remains to be seen how important that may be.

KANWISHER: You say it is adsorbed on things like a millipore filter?

FOGG: Yes.

KANWISHER: So that in the usual productivity measurements, if a fair amount of the photosynthesis during the period of measurement had gone as glycolate, it still might end up on the filter and enter the counter.

LASKER: But it would not be counted very well.

PROVASOLI: In the conference on phytoplankton the effect of the glycolate leaching on the precision of the productivity measurements done with ^{14}C was discussed.

GONOR: This gives me an opportunity to ask a question that would perhaps be better answered this afternoon. We are going to try again to find some large Pogonophores to study uptake of food materials. These animals have no gut. There is no question about swallowing things. It has to come from outside through some other mechanism. We want to try soluble materials. The question I want to ask is: Can you suggest an experiment of this sort which will get around the difficulty that Doctor Fogg mentioned and Doctor Fager raised, the question of how to determine that a material which can be taken up from solution is indeed being utilized as an energy source?

FOGG: You have got to supply it as the only energy source and demonstrate a gain in the weight of your animals.

GONOR: That is probably going to be impractical. The time in which we can work with healthy organisms will probably be very short.

FOGG: In that case, as Doctor Fager suggested, you have to recover protein, for example, and show that carbon from your source has been incorporated into it.

LASKER: I did an experiment years ago in which we took the animal and soaked it in antibiotics. The antibiotics are very mild. They do not hurt the animal. Your soluble, radioactive nutrient is in the medium with the antibiotic. The animal then respires and you collect the CO_2. It is a kind of evidence, I think, that points in the right direction.

CONOVER: What is known about the development of these Pogonophores? Have they no gut at some time in their development?

GONOR: Very early in development, there is an area of the embryo that can be considered to be endoderm and a solid cord of what would be the gut in an animal that has a gut. This does not develop a gut structure so that in the very earliest embryology there is a reminiscence of gut and that is the end of it for the animal.

The eggs are very yolky and are brooded in the tubes so that you cannot say that the animals feed as larvae and then simply subsist as adults on what they got when they were larvae. There is no time known in which the animals have any gut to feed with. They get along just fine without one.

BARKER-JØRGENSEN: I do not know the Pogonophora personally, but I have heard about their habit of coiling the tentacles so that they would be able to make a trough in which there might be uptake of particulate matter that might be digested extracellularly, so I think this still remains as a possibility.

YONGE: This happens in *Balanoglossus;* there is digestion in a sort of mucous covering of the animal.

GONOR: Those animals have an extracellular amylase in the mucus of the proboscis, which puzzles me a great deal.

YONGE: Doctor Lasker now would like to contribute.

TABLE 6 shows work done on the maintenance of *Euphausia* in the laboratory in which we were able to keep this species for as long as 50 days. This is a planktonic form found occasionally at the surface but usually at the point of around 300 m., weighing anywhere from 1.3 to almost 5 mg. dry weight.

The table shows the molting frequency of this species in cases where we got at least two molts, so we have at least one intermolt here. We have had them up to eleven molts. These are all adults.

The molting frequency can be anywhere from four to seven days for a mean frequency of five days in the laboratory. The temperatures ranges were not rigidly controlled. They were kept in 1-liter plastic containers in sea water.

At any rate, this frequency did not change very drastically. We fed these one drop of *Platymonas* every day. The water in the container was changed daily. The interesting thing here is the dry weight of the molt as compared to the dry weight of the animal when it was finally killed. We assume that the animal was not growing tremendously in 50 days.

TABLE 6

MOLTING FREQUENCY OF THE DEEP-SEA CRUSTACEAN *Euphausia pacifica* (147)

Euphausiid	Temp. Range	Final Animal Dry Wt. Mg.	Number Molts Produced	Ave. Wt. Molt	Time (Days) Alive In Lab.	Ave. Molting Frequency (Days)	Molts = % of Animal Dry Weight
1	9.5–12.5	2.333	2	.247	10	5	10.6
2	9.8–11.2	2.143	2	.182	14	7	8.5
3	9.8–11.2	4.810	2	.479	8	4	10.0
4	9.8–13.7	4.800	3	.416	18	6	8.7
5	9.8–13.7	—	3	—	15	5	—
6	10.8–14.5	1.541	2	.198	10	5	12 9
7	10.8–14 5	1.975	3	.167	12	4	8.4
8	10.8–14.5	—	2	.187	14	7	—
9	10.8–14.5	—	2	.109	12	6	—
10	10.8–14.5	1.244	2	.157	9	4	12.7
11	12.3–13.2	—	3	.249	13	4	—
12	12.3–13.2	—	2	.263	12	6	—
13	12.5–13.2	4.798	2	.327	9	5	6.8
14	12.5–13.2	—	2	.161	7	4	—
15	12.6–14.3	1 300	11	.128	50	5	9.8
16	12.8–14.2	3.476	3	.380	12	4	10.9
17	15.4–17.5	—	2	.146	8	4	—
18	15.4–18.9	1.305	10	.211	36	4	16.1
19	15.4–18.9	1.326	8-	.121	40	5	9.1
						Av. 5	Av. 10.4 ± 2.4 (S.D.)

S.D. = Standard deviation.

We find that these molts average out to be about 10 per cent of the dry weight of the animal.

I thought this was fantastically high. These were done with a microbalance and I believe that all of these values are accurate.

KANWISHER: This is each molt?

LASKER: Each molt was 10 per cent of the dry weight of the animal. This is a fantastic figure, but it held up, as you can see here, and we had as many as eleven molts. We weighed each one separately(147).

If one considers the amount of molt material being dropped to the bottom of the sea based on this 10 per cent, one comes up with a rather large figure and I made some calculations. Doctor Edward Brinton, at Scripps Institution of Oceanography, has been studying *Euphasia pacifica* for many years and he has what I consider to be a very good estimate

of what the numbers are.* His biomass estimate for the entire geographical range of this species, which is 5×10^{13} square meters, is 6.5×10^{13} grams. Because this estimate is based on summer figures I will restrict my remarks to that season.

McAllister, Parsons and Strickland(148) made some measurements in this range of the production of carbon. The mean daily production was 205 mg. of carbon per square meter. If one multiplies that by the geographical range, one comes out with 1.02×10^{18} grams of carbon per day.

STRICKLAND: Let us be fair. This was done a thousand miles further north.

LASKER: This takes in the entire geographical range where *Euphausia* occurs. If we take 10 per cent of the *E. pacifica* biomass, which is the molt, we get 0.65×10^{13} grams of molts every five days. Each day then, approximately 0.1×10^{13} grams is lost by these animals. Let's take 50 per cent of this as being carbon—0.05×10^{13} grams/day. Therefore 5 per cent of the carbon production is put back into the sea daily by one species through its molting alone. I examined these molts for nitrogen and found 3 to 5 per cent of the ash-free dry weight is nitrogen.

CONOVER: Do they have much ash? Is there much mineral content still in there?

LASKER: Fifty-four per cent of the molt is ash.

CONOVER: However, this 54 per cent here is high.

LASKER: That is right, this would be relatively high. However, just for sheer mass of material falling down, I think it is a large quantity. Put it this way: in 50 days we will have one biomass coming down. That means in a year we will have seven biomasses coming down.

YONGE: Presumably the chitin-splitting bacteria get to work on these almost immediately, do they not?

LASKER: Yes, they do; these molts will not last longer than a day. If you do not retrieve them the day they are produced, the following day they are very fragile.

STRICKLAND: That is not necessarily disappearing.

LASKER: No, they are not disappearing.

YONGE: But they are going back into circulation quite quickly.

LASKER: I would not be surprised.

KANWISHER: If they are put into a fine enough form, gravity cannot act on it very effectively to get it out of the local scene.

LASKER: They are very light. They will stay up there.

CONOVER: I can say that one copepod has a chitin-utilizing bacteria in its fecal pellets. The molts of *Calanus hyperboreus* are not anything

* Personal communication.

like the biomass of *Euphausid* and they occur twelve times—a cast skin appears twelve times in one generation. I do not think you can attribute anything like these kinds of numbers to copepods in general, but it certainly is an interesting study.

LASKER: Am I right that *Euphausia* makes up in some of these areas a very large percentage of the population?

BODEN: Oh, certainly, it is the dominant organism.

KANWISHER: This is in biomass and not in numbers?

LASKER: This is biomass.

FAGER: It turns out to be somewhat of both, according to Brinton. You get larger numbers of this animal which itself is quite large and therefore you get large biomass. Excluding microcopepods and other very small organisms, this is numerically one of the major plankton organisms in the eastern north Pacific.

KANWISHER: When you read Brinton's paper, unfortunately, it is just on *Euphausids* and he does not give you a perspective on the rest of the community.

SANCHEZ: Is that 10 per cent of the wet weight?

LASKER: Ten per cent of the dry weight, not wet weight.

BARKER-JØRGENSEN: Can you be sure they are not eating their molts in nature?

LASKER: If they are molting; they seem to be doing well. They are molting every five days. They have been kept in the laboratory for almost two months. Of course we get the molts out for analysis, but they do not appear to eat their molts. However, in the sea they do feed on detritus.

COSTLOW: I am surprised that temperature did not seem to bother them.

LASKER: That was another interesting feature of this. We had the whole range and the molting frequency did not change.

KANWISHER: Most of these are obligatory vertical migrators, are they not; so it is rather nice to think that they are not too much a Q_{10} victim of their environment. They are going down through a 15° difference every day.

LASKER: That is right.

COSTLOW: Did you find any reduction in the carbon with time, in the late molts versus the early molts?

LASKER: No.

KANWISHER: I hope you can scale the productivity upward and the molts a little bit downward, because if we imagine the nitrogen at 10 per cent of the atrophic level, such as Doctor Slobodkin had very convincing data for, then we have almost nothing left for anything else in the ocean here.

LASKER: I might just add here that Gustaf O. Arrhenius saw this information at the Scripps Institution* and was very interested in whether there were trace elements in these molts. For example, if indium were found or something similar, then all the indium in the sea would be in cast molts. There was no indium or anything of that nature.

* Personal communication.

VIII. VERTICAL MIGRATION

Discussion leader:
I. A. McLaren
Department of Marine Sciences
McGill University
Montreal, Canada

McLaren: It has been suggested by Doctor Strickland that we get on to questions of vertical migration and I agree it certainly interests me. I think Doctor Boden has something to say on this subject.

Boden: I hate to toss in the subject of vertical migration at this point because it usually means a fight which will go on for three days. Anyway, I am going to keep it to one aspect and one species to try to limit this.* It is the same species that Doctor Lasker mentioned a little earlier, *Euphausia pacifica*, and I am glad he brought this up because, as he said, in the pelagic circumstances around San Diego *Euphausia pacifica* is usually found, the adult at any rate, very seldom at the surface. I would say that the normal depth of the adults is certainly below 200 m.; it is generally about 350 m. The reason I am mentioning this in San Diego is, that it came to our attention that up in Canada (this is Strickland's back yard), in Saanich Inlet there is a scattering layer. The *E. pacifica* tend to stratify at depths of sonic scattering there. I am not saying and never have said that this is the cause of the scattering, but it is found at these depths.

As I say, it came to our attention that there was a layer up in Saanich Inlet, a layer in which the Canadians considered *E. pacifica* was a very conspicuous component, and it existed at a depth of about 100 meters. Saanich Inlet actually is a fjord and it is about 24 kilometers long and about 6–8 kilometers wide. The depth of the fjord is only 200 meters at the deepest part and it has a sill, which separates it from the Straits of Georgia, which is only about 75 meters deep and about 3 kilometers

* This work was supported by Public Health Service Research Grant NB–02841 from the Division of Neurological Diseases and Blindness. It was also undertaken under contract between the U.S. Office of Naval Research and the University of California.

wide. The exchange of water between the outside straits and the fjord is extremely slow.

Below 100 meters, 80 to 100 meters, there is an oxygen deficiency which extends to the bottom, and this forms a sort of oxygen floor. It seems that the scattering layer there sits on the floor all day and it is divided into two components. One component sits there day and night but the other component is extremely sensitive to fluctuations in light intensity, so much so that even a passing cloud will cause it to migrate vertically just a few meters, perhaps 10 to 15 meters even.

On a clear day it is merged with the bottom component. On a darker day it is stuck a little bit above. At twilight it will go up or down toward or from the surface. It goes up at nightime and comes down in the morning.

The Canadians have been examining this scattering for a long time and they have made a lot of tows in it and they considered it was a rather simple situation in which the lower component was composed largely of Gammarid amphipods which appear to be quite insensitive to light—they just stay there all the time, sitting right on top of this oxygen-deficient layer, whereas the upper part was composed of *Euphausia pacifica.*

It is not quite as simple as that, it turns out, and investigations have shown that there are an awful lot of fish tucked in there and you can see these on Precision Depth Records but they are quite discrete, they have the little crescent shape that fish usually have on photometer records. These are hake, dogfish, etc. I do not suppose the identify of the fish matters but they are fish and they appear to be sandwiched between these two components of the layer but it is apparent that it is the *E. pacifica* which migrates and our interest then was to determine the ambient light conditions. It seemed that this was the first parameter to investigate, why *E. pacifica* in a closed situation should be 150 or even 200 meters above the condition which it normally inhabits in pelagic conditions.

So we took our light meter up and had a look and we found that indeed the light conditions are quite different in the two situations. This is an irradiance meter, incidentally. We were not looking at scattering; we were not looking at anything except near-monochromatic light of a known intensity.

In Saanich Inlet we found that the wave length of the light that we were looking at, peaked between lambda 494 and 502 millimicrons whereas the same species in the San Diego area is living in a much bluer light between 475 and 480 millimicrons. The intensity of the light in Saanich was 2 or 3 orders of magnitude greater. It was about 10^{-1} microwatts per centimeter squared, whereas in San Diego it is about 10^{-4}.

Obviously, then, the animals were trapped between this oxygen mini-

mum and the surface. They cagily would not go down into the oxygen-deficient layers but they were stuck with this brighter light.

STRICKLAND: I think you might add that it is absolutely anaerobic, too.

BODEN: It is, yes. Apparently you get hydrogen sulfide down at the lower depths occasionally and there is very little flushing. Occasionally you get a sporadic overturn.

LASKER: And this scattering layer goes into this H_2S? Perhaps I should interject here that I determined the lower limit of oxygen tension for *E. pacifica* and it is 0.7 ml./1.

BODEN: It is what Herlinveaux(149) has called an oxycline. I object to this for philological reasons but that is irrelevant.

(The point then was to see if there had been any adaptation in these animals and how they had adapted.) There is the inference that because there is such a slow interchange between the Straits waters and the fjord waters, this may be an isolated community, so I caught some of these creatures and flew them back to Scripps. I caught them in the morning and we did the experiment that night.

There was no sort of temporal adaptation state there. (We tested their spectral sensitivity.) This we do by strapping the animal down and sticking an electrode in his eye and then exposing him to all sorts of humiliations: flashes of known time, known wave length and known intensity. By going through all sorts of mumbo-jumbo, you can come to a sort of spectral sensitivity curve,(and it turns out that the inshore representatives are more sensitive to the light in which they are living, this greener light of greater intensity, then they are to the light in which the parent community lives.

It is difficult to tell quite how they have done this. Both forms have a spectral sensitivity peak at 460 mμ, which corresponds with the peak of euphausiopsin(150). This is the visual pigment which was originally extracted, incidentally, from *E. pacifica* and these peaks coincide so that there is no doubt that this is the same peak. However, the ratio between the peaks further along toward the red is different and the only thing we can think of is that this may have been accomplished by a greater deposition of astaxanthin in the eye in the inshore forms. The role of astaxanthin is not very clear in visual processes. It may be simply a screening pigment. Wald* figures that it may possibly be active actually in the visual process but Duke-Elder(151) figures that it is not at all, so there is still a little bit of fussiness about that.

However, it does seem apparent that with the inshore forms there is

* G. Wald, Personal communication.

a greater deposition of astaxanthin. We have not actually made extractions of this but it seems from histological evidence that this is possible, and so let battle commence.

STRICKLAND: I am surprised that in Saanich Inlet, with which I have had some experience, you could make very much of a statement about intensity because it is subject to enormous blooms and for erratic periods of the year I should think that the light could hardly penetrate at all.

BODEN: Let me qualify that. This is a short investigation which we made at the same time of year in San Diego.

STRICKLAND: Which time of year was this?

BODEN: About April, I think.

STRICKLAND: Yes, you could be anywhere between the first spring bloom and the next, and the statement of absolute intensity at depth I would think was much less meaningful in that situation than it would be in pelagic waters.

BODEN: Of course, that is true. I do not know, the figures that we came to were quite different from Utterbach's figures in the Strait of Juan de Fuca(152). Our spectral sensitivity was quite different. Whether this was a matter of difference in method, I do not know. He was using broad band filters. We used interference filters.

STRICKLAND: I think it is terribly varied.

BODEN: You mean naturally? Yes.

STRICKLAND: The terrestial runoff, degree of blooming is so large and erratic in that area that there is hardly a meaningful mean figure.

Were you stressing the intensity very much, or mainly the spectral?

BODEN: This is mostly spectral stuff, actually. It was the spectral stuff that we were interested in most but it does seem logical there, that if an animal is living a good 200 meters higher than it is elsewhere, it is going to be subjected to higher intensity most of the time.

STRICKLAND: You don't have to have much of an extinction coefficient to wipe out that difference.

BAYLOR: What is the rate of change of intensity which will initiate migration?

BODEN: I am not at all sure that it does. The one thing that we also have noted, in San Diego and I noted it there, too, is that at twilight you will get a shift in spectral composition. Whether it is the shift in the spectral composition that triggers the migration or whether it is the actual change in intensity—

BAYLOR: Do you notice any difference then in the apparent time at which migration is initiated on a day that has a very red sunset so that the color temperature of the sky is essentially very low compared to

other days when you have, say, a nice meteorological high overhead so that the color temperature is exceedingly high?

BODEN: When you are dealing with such gross things, how do you do this?

BAYLOR: You measure the color temperature with an ordinary photographic device.

BODEN: At depth?

BAYLOR: Yes; there is no reason why not. All you need to do is to measure the intensity of two different wave lengths and compare them. They should be on either side of green.

MCLAREN: To get back to the animal for a moment, is it not true that these pigments are ecophenotypically adapted on a rather short time scale? Cannot the balance of pigments change within an organism by nongenetic means?

BODEN: I am not saying that this is genetic adaptation.

MCLAREN: It really could be something which was established in the previous week or something of that sort.

BODEN: Yes, except this is an isolated community as far as we can tell.

MCLAREN: But this in itself might constitute an argument for the isolation of this community.

KANWISHER: Can we go back to the open ocean for a minute where there is a bit more of an area to interest us? What is the vertical history of *Euphausia pacifica* off San Diego where you studied it, you said at 400 meters: daytime or nightime, does it come up to the surface?

BODEN: No, Doctor Lasker said 400 meters. Normally I would say about 350 meters. The adult is seldom found above 250 meters in the daytime. It does come to the surface at night or toward the surface, within the upper 30 meters or so.

KANWISHER: These figures Doctor Lasker has presented on these tests—

BODEN: They were daytime figures, were they not?

LASKER: Yes.

KANWISHER: If they do not selectively throw out their tests at night when they are at the top, this represents a tremendous vertical pumping of organic matter and one of the intriguing factors of the scattering layering itself is the fact that they possibly feed at the top and metabolize down below and again are aiding all of these gravity processes in pulling neutrals away from the surface layer. I am trying to get your feeling on how *Euphausia pacifica* might contribute to this.

BAYLOR: Could we get back to the rate of intensity change? I was not clear about why you thought it was not the thing that initiates migration.

BODEN: I am not saying it is not. I am just saying that this shift may be the thing that triggers it. Actually, as it happened in Saanich Inlet, the scattering layer—well, let me explain our experimental procedure.

BAYLOR: I am essentially sympathetic with your point of view because I think *Daphnia* works the same way.

BODEN: What we did was to lower the irradiance meter to the depth of the layer. We noted the irradiance value through a reference filter. We can select our filters from the deck, and this was at about 502 millimicron which we took as an arbitrary figure.

Then we just kept the meter at this irradiance level and then we compared that with the fathometer record later, so we ignored the fathometer record from that point on until we checked them out together. It turned out that, actually, the top part of the layer, once migration is started, will overtake this for a little bit. It will start up with it and then suddenly overtake it—not to a great extent but to a certain extent anyway.

YONGE: There was one point I did not quite understand. You said there are two scattering layers but one never leaves the bottom?

BODEN: No, this one just sits there.

YONGE: How do you know it is there if it is always on the bottom?

BODEN: It is not on the bottom. It is at the oxygen level.

YONGE: I understand—at the effective bottom?

BODEN: Yes. It is an oxygen floor.

KANWISHER: The eastern tropical Pacific from the area off Costa Rica and Panama out for possibly half a million square miles has from 100 meters on down to 1000 meters extremely low oxygen water, from .1 down to .05 ml., well below the .7 ml. that you have measured as a critical PO_2 value or content for *Euphausia*. I have spent months cruising back and forth across that, never seeing a scattering layer at this innerface, and one suspects it might act as an oxygen flow.

BODEN: Were any collections made?

KANWISHER: Yes.

BODEN: You found *Euphausia?*

KANWISHER: I do not know.

LASKER: *E. pacifica* stops somewhere around Baja.

BODEN: I am not talking about *E. pacifica* at this point. I was just wondering if you found any *Euphausia* at all.

KANWISHER: We found some *Euphausia* and fish and a whole new paradox, because I cannot understand how any of these would still be in such a small amount of oxygen. It is not anaerobic.

BAYLOR: You say there was or was not a scattering layer?

KANWISHER: There were scattering layers hung on the sharp break in oxygen which occurs at a 10-meter depth range.

SCHMIDT-NIELSEN: How is that established?

KANWISHER: It is established possibly by a combination of physical factors, one upwelling, and the other radiant energy, tending to produce a thermocline, and these will react in a dynamic fashion to form a two-layer model with a sharp break between them.

CONOVER: What is the depth? I missed it if you mentioned it.

KANWISHER: Off Costa Rica it is as shallow as 30 meters; further out it is as much as 1000 meters. There are fish within this low oxygen water with 50 atmospheres of oxygen in the swim bladders, which should not be there.

STRICKLAND: I understand that the idea of migrations following isolumes is now a little passé but is it still reasonable to assume that intensity and perhaps spectral shift initiates something in the animal which then possibly carries on migrating irrespective of the isolume—or is that too simple?

BODEN: There is a very close correlation between the intensity between the isolume and the movement of the layer. It is not as close as we figured originally.

BAYLOR: That animals should follow an isolume has always been physiologically untenable because it requires you to assume that there is an absolute energy receptor, and that you have discovered some marvelous way of avoiding all the difficulties of adapting to the stimulation.

STRICKLAND: No, I think this may not be as difficult as it might seem. If you have a newspaper or something similar to look at and adapt in an ordinary twilight, there comes a time, as the darkness sets in, when you can no longer see the newspaper. The "cut off" is reasonably sharp and reasonably constant when measured by a meter. If a Euphausid has something it is looking at, it may find it quite easy to recognize the time for migration.

BAYLOR: That is 10^{-2} foot candles.

MCLAREN: This expression of isolumes always logarithmically does tend to mask what would appear to be a greater physiological potential. Surely, the order of magnitude or two which is sometimes involved in the correlation of isolume and migration is a very fuzzy one compared to what Doctor Strickland suggests, and once the newspaper disappears it is a fairly precise loss of illumination; not within an order of magnitude.

BODEN: But it becomes very uncomfortable to look at the newspaper sometime before it disappears. If you took a long tube and you had it black at this end, and you show a light at the other end, I think you would find the animals would tend to congregate somewhere where it was fairly comfortable, and I think this is what Doctor Baylor is talking about.

BAYLOR: The thing I had in mind is that ordinary daylight intensity changes from noon to, say, three o'clock in the afternoon by two or three orders of magnitude, but you are not aware of it.

FREMONT-SMITH: You make pupillary adaptation and other adaptations.

STRICKLAND: You mean in the middle of winter?

BAYLOR: Yes. It is a little less in the summer. In fact, in the summertime you are not aware that there is much of a change until around seven or eight o'clock at night in these latitudes.

STRICKLAND: I agree and your eye responds roughly logarithmically. The fact remains that within the precision of measuring isolumes and the rate at which this is changing, the animal would still seem to be following an isolume and one does not have to assume that it had to have awareness of absolute energy.

BAYLOR: It has to be very close to it if the animals are to follow an isolume.

BODEN: Yes, but I do not have a fuzzy light meter.

STRICKLAND: But the rate of change at that point is getting very rapid, is it not? I was not suggesting that you have anything but the best light meter. The fact remains that experimentally to determine where an isolume is in an instant and where migration starts in an instant all involves time periods and such.

BODEN: We were lucky here in a way because this is the sort of oceanography that I rather like to do. We were tied up at a buoy in very, very calm water. The skipper used to go home and do his gardening.

But the wire angle was absolutely like that (gesturing vertically) and when you compared the fathometer traces, you could actually see our instrument on the trace, and as the layer came up so did the instrument, although at the time we were simply looking at the irradiance value on our recorder.

When we came to look at these miles of data that we collected (and it was a short period, about three days but we were working continually), just as the layer came up so did the instrument. As the layer went down so did the instrument, and you could see the intrument in the layer all the time except at twilight—at a certain period in the evening twilight, it would overtake the instrument and then you would get this diffused nighttime scattering.

YONGE: Is this an instrument that is maintained at a level according to the illumination at that level?

BODEN: Yes.

STRICKLAND: But what is your precision of measurement?

BODEN: Oh, heavens, I could not say what percentage.

STRICKLAND: A few per cent of the absolute?

BODEN: Yes. The instrument, you see, is calibrated against a standard lamp.

STRICKLAND: But on a boat needles swing, etc., and there are limits of precision with the best equipment.

BODEN: This will depend on the instrument. We were using a Leeds & Northrup instrument and I do not know what the constants are.

KANWISHER: It is within a few per cent of saying the light now is the same as it was 30 minutes ago. If not a fraction of a per cent, it is very close.

STRICKLAND: This indicates a really precise ability to judge an absolute intensity, if it is doing it.

BAYLOR: No, there is one alternative explanation that you could possibly advance and it requires you to make two assumptions: first of all that there is some initial rate of change of intensity which will be the initial threshold, and that the threshold then continually adapts to some higher level and it does this at some logarithmic rate. If you make those two assumptions, then the explanation is almost trivial.

KANWISHER: This really seems much ado about nothing. The scattering-layer animals respond primarily to light in a most remarkable fashion. Doctor Boden's work is the only work I know of directly on the physiology of animals in the open sea doing this. The British records of narrow-angle sound-scattering devices show as many as six, eight, or ten separate components of scattering layer, all coming up separately, never crossing over each other, and he has here an isolated case of remarkable situations where light has to fit with oxygen as the "motivating" parameter. Hillary Moore has done the same thing with other parameters in the Gulf Stream.

BODEN: It is the only chemical barrier that I know of.

BAYLOR: I do not think it is much ado about nothing. I think there is a real question to be answered there, but I do agree that this is really the most exciting work I have heard of about vertical migration.

KANWISHER: Some of the *Daphnia* scattering layers which come part way to the surface are operating at light levels so low that one really has a difficult time assigning enough quantum to any kind of visual method that eventually would have triggered this movement.

BODEN: These are the creatures I want to get hold of.

KANWISHER: It may be that perhaps they have essentially light motivation riding along with a clock mechanism being kept just occasionally in synchrony.

EDMONDSON: Is that work on *Daphnia* done in an area that tends to be relevant here?

BAYLOR: No, it is not cricket to bring the illumination in from the side; it should come in from overhead.

EDMONDSON: But the fact is that the animals went in the right direction.

BAYLOR: Oh, yes, they certainly did. However, he was changing color temperature at the same time.

KANWISHER: These animals in the deep sea, at least in the deep scattering layers, cannot know of each other's presence. The average concentration of *Euphausia* is about 1–10 to 4 cubic meters. This is 30 meters or 100 feet cubed, and obviously the animal cannot see the next one and know what it is doing. The fish are at the same or more dilute concentrations, so we must think of it not as a social migration the way you think of lemmings.

BAYLOR: No, I am sure they don't say, "Come on, fellows, it's time to go."

MCLAREN: Has anyone any further comment on the suggestion thrown out by Marshall and I think by Wiborg at the Plankton Symposium in Denmark(153), on reverse migration in deep-sea forms? Has that been looked at since?

BODEN: I do not think so. There are cases on record, certainly, of scattering layers going down instead of up, even at twilight, but these are simply photometer records. I don't think anybody has ever collected from them and we do not know what is in them.

Another thing that comes up in scattering work is the matter of bioluminescence where they seem virtually to foul up their own light, the ambient light conditions, by flashing brilliantly. You will find occasionally that you have an increase of light with depth when you get down to the layer, and that is simply because of bioluminescence.

CONOVER: Is it clear that it is natural bioluminescence? I realized the bioluminescence might be a problem but it is probably not the *Euphausia* that are responsible for it, not for the major portion of it, and further, what is the spectral intensity here? It is a very narrow range.

BODEN: The spectrum of bioluminescence at that depth corresponds very closely with the spectral sensitivity of the euphausiids.

KANWISHER: It is always broad band, never monochromatic.

BODEN: It is not monochromatic. People are starting to talk about this window in the sea. You are getting spectral sensitivity, bioluminescense, and transmitted light, sun and sky light, all in the blue-green. This is at depth. The peak is sharper as you go down, of course, because the water itself is a monochromator.

STRICKLAND: Do you have a device to stop organisms hitting the instrument and being stimulated artificially to give off light?

BODEN: No, we do not. This is one thing we are working on at present. We want to get a coincidence circuit with two photometers looking out at some distance so that we do not physically disturb the creatures. This may give us a completely different picture.

EDMONDSON: To go back to Doctor McLaren's question, a good many species have been reported to change migration behavior as they age—either they start migrating or they quit, or they go in a different direction. Can any of the changes you mentioned of different layers and things be interpreted in terms of seasonal changes in the age structure of the population?

BODEN: We do not have enough information on that yet. All we can say is that, for instance, in *E. pacifica,* we think the larval forms are usually found nearer the surface. Whether they stratify according to their age or not, I do not know. Then we get back to methodology and how you catch the things.

EDMONDSON: Maybe if this works out you could use an echolocator to study the age composition of populations and changes in growth rates and things like that.

BODEN: If you can get one to tell you what it is looking at.

KANWISHER: There is a seasonal vertical migration, well documented, in the Antarctic southern summer with the surface water going north toward the convergence, and then, with the start of winter, riding back at lower depth. By having a seasonal vertical migration, it manages to keep itself in one place—a very interesting suggestion advanced by Sir Allister Hardy.

MCLAREN: And also Mackintosh(154).

BAYLOR: There is some interesting evidence that larval forms in fresh water have a reversed vertical migration from that of the adults, and the tentative explanation for it is that this prevents the young from being eaten by the adults because often they are nice bite-size.

STRICKLAND: There is evidence for this, you say?

BAYLOR: Yes. Smith(155) is the authority for this, I believe.

MCLAREN: In the marine setting there are comparable examples. In the Black Sea, Petipa(156), showed that in *Acartia,* the *Acartia* which was there, the adults undergo normal vertical migration, while the young seem to leave the surface at night, and his data suggest that the young do not actually leave the surface but, as it were, spread out and in fact do not concentrate at the immediate surface. This might explain some of the larval migration in fresh water as well.

COSTLOW: Bousfield has some nice work on barnacle nauplii and their vertical distribution in relation to circulation patterns and how this

affects their distribution within an estuary. This is not quite the same as vertical migration, I know.

SANCHEZ: The larvae migration is happening once. It is not happening daily.

COSTLOW: With barnacle nauplii it does. It changes with the tide as a rule, which conceivably means it is twice daily. I do not really remember.

KANWISHER: It remains a mystery to me why so many of the smaller animals in the ocean essentially climb out almost every day. It cannot be just a prey-predator escape.

BODEN: I cannot imagine it.

MCLAREN: Perhaps I may present my explanation later today. I do not want to push the idea. I think it should sit for a few years until a few examples are checked out.

SCHMIDT-NIELSEN: I should like to ask one question in connection with Kanwisher's remarks and that is, what does it cost a small organism to move up and down in the water?

MCLAREN: Very little. Professor Hutchinson has worked this out. He certainly told you, Doctor Kanwisher, and he told Doctor Conover, and although he never published the figures he says it is something of the order of 1 per cent for a 100 meter migration for a small cladoceran—1 per cent of the daily budget.*

CONOVER: It is going to depend a lot on the organism. The densities of some of the vertical migrators get food, assuming it does, then it just goes down on its own weight. It is having half the way with kinetic energy and the other half not.

MCLAREN: Not fast enough.

KANWISHER: It is feet per minute. They do not go that fast.

YONGE: It has to move to eat.

SCHMIDT-NIELSEN: If they are small they have to swim down as well. The small one would not sink fast enough.

MCLAREN: This *hyperboreus* of yours, Doctor Conover, does it ever get more dense than water?

CONOVER: It appears that way, yes. It certainly is just about neutrally buoyant when first captured, but this may be because I am changing its environment slightly. After a time in the lab they become more dense and sink.

MCLAREN: But this is only when it is oily. A starved calanoid is much denser.

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* On reading my notes from Professor Hutchinson's limnology course, I find this should be 1 per cent of the animal's weight—a rather larger but not unmanageable figure.

CONOVER: That is true, yes.

BAYLOR: There is an explanation of one adaptive value for vertical migration about which I feel somewhat skeptical but, nevertheless, there is some evidence in favor of it, and this explanation says that the adaptive value of vertical migration is to prevent fouling of the carapace by Epiphytes. This sounds patently ridiculous on the face of it. However, there is the matter to consider that most of these things have a rather hydrophobic surface on their carapace which would make the wetting angle difficult to achieve for any sort of fouling epiphyte that wanted to attack.

The other evidence is that it has been observed occasionally in estuaries and similar places that when a population of offshore pelagic plankters get blown in by a storm. Conditions are somewhat unsuitable in the estuary for them so that they do not undergo their ordinary vertical migration or possibly they go to the bottom but they cannot go deep enough, let us say, in this case they do become fouled up with epiphytes. The notion is that if an epiphyte did succeed in attaching itself to such an organism in the open ocean, relying on photosynthesis as the epiphyte would, it would be out of luck because it would be at the bottom in the daytime where the light is too low and it would be at the top where the water is warm and where it is rapidly respiring itself away.

I just offer this as a tentative explanation. There is better evidence in fresh water that this mechanism does operate.

EDMONDSON: There is another consideration, too. So often the food organisms turn out to be highly stratified and a species that stays still has a high chance of never getting a meal, whereas seesawing up and down increases the possibility of getting fed.

YONGE: That is the basic thing. You have to know where to feed, do you not?

BAYLOR: Why not move sideways? It costs less.

MCLAREN: I was discussing questions of growth, fecundity, and so on, in zooplankton, and the effects of temperature, and I showed that length is a negative function of temperature;—that is, the higher the temperature the smaller the animal.

That sort of thing is behind the analysis which I attempted to make for zooplankton, and from this analysis I attempted to generalize to vertical migration in general.

I used an equation which is based on an extremely general equation

$$\frac{dW}{dt} = A - K$$

This is simply an expression of what must happen—one of those open system equations which by themselves are useless, but nevertheless irre-

futable. It simply says that the rate of change of weight (W) with time, whether negative, zero, or positive, is a resultant of everything which causes change in a positive way (A) and everything which causes change in a negative way (K). This is trivial.

But you can always express A and K in terms of W, or whatever you are measuring with time, and express it as I did as

$$\frac{dW}{dt} = a \cdot f(W) - k \cdot g(W)$$

were $f(W)$ is some function of weight, and likewise $g(W)$. Or you can substitute nitrogen for W, or carbon, or energy, or anything you choose. It is an extremely general equation.

What I suggest is happening in vertical migration is this: that the positive forces of growth, that is anabolism or whatever, are affected by temperature—taken all together are affected by temperature—at one rate and the negative coefficient is affected by temperature in another way. That is to say, expressing A and K as functions of weight, we can then express A and K as functions of temperature.

If that is the case, then it is perfectly possible that if an animal can in its life separate these two functions, that of anabolism in the broad sense and catabolism in the broad sense, separate them in time or space, and subject them to different temperatures, it will affect the weight equation on the left-hand side, of course.

What I have supposed that organisms are doing when they migrate vertically is, in fact, feeding at warmer temperatures and metabolizing in part, that is to say, catabolizing in part, at another average temperature—the temperature which exists in the deeper water. Almost universally in any natural body of water, the deeper waters are colder.

I have deduced the consequences of this kind of thing for specific animals from which I have evidence—*Sagitta elegans* and *Pseudocalanus minutus,* and it seems to work, Whether temperature is universally involved or not, I do not know, but I might point out that not only temperatures need be involved, but oxygen; your oxygen-minimum layer could have effects on metabolism, and perhaps could have a differential effect. If the animal spends the daytime on the bottom resting, this too could prove useful, by saving energy.

Provided the temperature or other relations are correct, are of a particular form, the whole system may provide an energy or a matter bonus to the organism. I have shown that this can perhaps in some cases be converted into the realized or intrinsic rate of increase of the organisms involved and this, by definition (if my analysis is correct), would be a sufficient advantage.

SANCHEZ: This is anabolism and catabolism of cellular function?

MCLAREN: They are functions of the whole animal. They are simply defined in terms of mass.

SANCHEZ: But they are cellular functions; it is not overt behavior, such as feeding or movement?

MCLAREN: Anything could be involved here.

SANCHEZ: Metabolism and catabolism would be going on at least at a minimum rate, the whole time, and let us look at what are those small energy-consuming processes. One would be migrating, itself, so that process could take place through all the range of temperatures or oxygen concentration in which the animal displaces itself during the migratory voyage.

MCLAREN: That is right.

SANCHEZ: Another energy-consuming process would be eating. That would take place at one level, and probably digesting would take place at another level, so I do not see very clearly that you can separate, really, a phase where the animal is anabolizing and another where it is consuming.

MCLAREN: Anabolism in the last analysis has to be the uptake of food. This is the only source of increase in weight, whether it is dissolved organic material or diatoms.

SANCHEZ: Yes, but that is not ingestion.

MCLAREN: So that expresses the whole of A in the equation. Everything else goes in K. To the extent that you can get an at least approximately analytical expression for all these processes lumped together, K as opposed to this rather more narrow process A, then the results suggest in the paper which I have written—

SANCHEZ: Yes, I understand what you say. I do not see, though, how these two processes are separated in time or in space in an animal which is displacing itself vertically.

MCLAREN: I perhaps did not make myself clear. The animal is assumed to do all its feeding near the surface; that is to say, it is feeding in warmer water, thus driving anabolism, driving the intake of food—everything—to a higher pace than it would be if it lived all day in the cooler water and still got a similar proportion of food.

SANCHEZ: I get a feeling that you are identifying anabolism with catching of food.

MCLAREN: I am identifying it with the incorporation of food.

SANCHEZ: Yes, the incorporation of food into the gut.

MCLAREN: The tissues of the animal.

SANCHEZ: I do not see that anabolism stops there. It only begins there.

MCLAREN: No, but that is because in physiology the terms "anabolism" and "catabolism" are used in a much different sense. I like to call every-

thing, that you are discussing, intermediary metabolism and leave it like that. I should have called it uptake and output; you know there is a very simple input and output equation by Von Bertalanffy(157) who invented the specific equation upon which this general one is based, and who referred to these two portions of the equation as anabolism and catabolism, respectively.

This annoys physiologists who maintain you cannot say that. We are not talking about the same thing, that is all. You are defining anabolism and catabolism in terms of the—

SANCHEZ: Metabolic; biochemical.

MCLAREN: Yes, while Bertalanffy defines them in terms of W simply increase or decrease of mass.

STRICKLAND: You mean it would also be advantageous for it to have a very short eating period and a long, cold digesting period?

MCLAREN: Not necessarily. It has at least to eat to surfeit. It has to get within a certain portion of the day all its daily metabolic needs, which I think may be rather smaller than calculated for a lot of organisms, although there has been a lot of evidence at this meeting of the fact that there is an asymptote or upper limit to the rate of digestion. Whether it is regulated instantaneously or by some sort of 24-hour rhythm is another question.

STRICKLAND: Do you think that it is tied in with following isolumes by some evolutionary coincidence?

MCLAREN: No, I think the animal has no means of detecting conditions at a distance; that the food is up there and the cold water is down there. It has simply got to develop some regular system of finding both situations and light offers the obvious cyclical pacesetter for this whole complex system. Light is a trigger and a director but not *the* purpose, as it were, of migration. It is hard to see a purpose in light reactions in most of these.

STRICKLAND: What about the ones that do not migrate?

MCLAREN: This equation can exist in such a form that there is no advantage to migration. You can make it so that it would be advantageous to migrate in a reverse fashion, and there are organisms in nature, for example, in which the relationship between temperature and length is not negative but positive, and in these organisms the whole system should logically, I think, work backwards. I have not found this positive relationship in the plankton, but some fishes seem to work this way.

No argument, you see.

KANWISHER: That does not mean there is no disagreement.

MCLAREN: I do not suggest this does not mean there is agreement, but I have said this in extenso in the publication and that is the proper

thing, I think, to consider(90). Several people here have new things to say.

SANCHEZ: It seems very adaptive, but I do not see how, in a metabolic sense, you can separate in time anabolism and catabolism.

MCLAREN: Let us not call them that.

SANCHEZ: Suppose a copepod eats and digests and assimilates and deposits immediately before it goes down?

MCLAREN: Then it spends the rest of the day in colder water.

SANCHEZ: Does it do all this while it is up there?

MCLAREN: Does it rest in cold water?

SANCHEZ: No; does it do the whole of digestion, assimilation and deposition before it goes down?

MCLAREN: Considering the rapidity with which this sort of thing occurs, I assume most of it is done that way.

SANCHEZ: I would assume it catches it up there and then gradually metabolizes it as it goes down.

MCLAREN: Most migratory animals in which this has been examined seem to have relatively empty guts in the deep water. I think that is true. So that assimilation is done at least in part before they begin spending their time down there. The differentials involved may be very slight. A difference of half a degree Celsius may give an enormous advantage in intrinsic rate of increase, according to some rather arbitrary solutions that I have worked out.

SANCHEZ: The given conditions of your model do occur, really, as you have suggested?

MCLAREN: Oh, yes.

YONGE: You say a difference of half a degree Celsius will really have a major effect?

MCLAREN: It could have, yes—a several-fold increase in intrinsic rate could result. Because of the curious nonlinearities which are involved in the real cases which I have been able to examine, you get exponentials divided by exponentials, and when you get this situation almost anything can happen. The changes in the powers are great.

STRICKLAND: How about organisms reputed to migrate over several thousand meters?

CONOVER: You mean daily?

STRICKLAND: For not too long a period, the Russians(158) have reported plant material in the gut of animals present at several thousand meters depth.

MCLAREN: There is no reason why the system could not work over any scale.

STRICKLAND: There would be a considerable temperature change if an animal came from 3000 meters to 500 meters.

MCLAREN: There is, in fact, in the Atlantic quite a strong differential.

STRICKLAND: But not a very marked rate of change. The animal might have to rise 1000 meters to feel a warming of 1°C.

MCLAREN: I will not defend it any further except to say there has got to be an adaptive reason for vertical migration and that problem enters into any adaptive reason that you suggest.

SANCHEZ: There could be several, though.

MCLAREN: I am not suggesting this is universal.

SANCHEZ: It could be valid and, yet, there could be other reasons.

MCLAREN: I am certain there are, yes.

KANWISHER: Or the adaptive advantage may have disappeared; this might be a hangover.

STRICKLAND: Do you get evolutionary hangovers in that sort of situation?

MCLAREN: I think you do. There are vertical migrations in Lake Mendota, for example, on the order of half a meter or one meter a day near the surface, which does not strike me as being a particularly useful or a particularly useless type of activity.

FREMONT-SMITH: Will big pressure differentials make any difference in chemical rate?

MCLAREN: Yes. This is something I know nothing about but perhaps Doctor Baylor could give us a word on that.

FREMONT-SMITH: This might apply to the Russian reports.

MCLAREN: Yes, it would apply in a reverse way. Of course, this whole equation can be expressed in a reverse way, too.

BAYLOR: Since you asked about this, I have looked in Johnson, Eyring, and Pollisar's textbook(159) on the subject and I no longer feel the same certainty that I used to bluff you with at the last meeting we attended. The fact is that I do not believe that I would even like to comment on it.

FREMONT-SMITH: What was your certainty before?

BAYLOR: Of course, I had Johnson's course a long time ago and I simply could not find the same information in the book that I thought I remembered having had in the course.

FREMONT-SMITH: In which direction did you think it went?

BAYLOR: In general, the effect of pressure is to increase the rate of reaction if it is depressed by high temperature.

FREMONT-SMITH: If the temperature remained constant it would increase the rate—you get an equivalent—

BAYLOR: That is, provided that—Well, the only real handy rule of

thumb that you can hang your hat on and feel fairly comfortable about in pressure studies is to say that, if the organism is operating at its optimum temperature, then pressure will in all likelihood have no effect at all.

FREMONT-SMITH: You are talking now of biological systems but in a straight chemical system, pressure alone will increase activity, will it not?

BAYLOR: It depends on what kind of straight chemical system you are talking about. If you are talking about an enzyme system, this is not true.

FREMONT-SMITH: It could be or not, that is right.

BAYLOR: In ordinary metallic ion reactions it would be true.

MCLAREN: Just to close with a cut at my own theory, I gather Ted Napora * at Yale has empirical evidence that the euphausids off Bermuda would have any temperature advantage of the sort I envisage more or less wiped out by a pressure disadvantage. But at any rate there are differences between deep water and shallow water in their effects on the two basic processes of uptake and output in animals which may be involved here in the adaptive value.

STRICKLAND: What about change in salinity when they go through the North Sea and they have a reasonably big halicline to go through?

MCLAREN: It could happen. Salinity has an effect on metabolic processes.

KANWISHER: What is the nature of the pressure disadvantage that euphausids of Bermuda have?

MCLAREN: Simply that their metabolism increases with pressure.

KANWISHER: Has he measured this?

MCLAREN: Yes, apparently in his pressure system.

BAYLOR: This was the thing that I found so upsetting.

MCLAREN: This is a very long-range migration, I might point out, over a rather small temperature range.

BAYLOR: It is possible to find an explanation for this effect in the book by Johnson, Eyring and Pollisar(159), but it is such a very long, involved thing and I am not really competent to discuss it. I would prefer anyone who is interested in it to look it up for himself.

COSTLOW: Since we can cycle temperature there is no reason why we cannot simulate parts of this and see what happens to decapod larvae.

MCLAREN: I hope you do that, Doctor Costlow, because I think it would be a very important clue.

COSTLOW: I am going to. We will plug it in and see what happens.

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* Unpublished observations.

IX. BENTHOS

Discussion leader:
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Editor's Note: It had been the intention to spend a considerable part of the third day discussing Factors Affecting Benthic Communities; however, the discussion of the earlier topics kept the attention of the group until half an hour before the end. A brief discussion of the topic was undertaken. Edmondson's introductory remarks included a plea to take a comparative view of ecology and to make full use in marine ecology of all relevant existing theory which has been developing rapidly in certain other areas of ecology. Reference was made to concepts of species diversity, and it was pointed out that at many times in the conference it had been useful to refer to work done with birds or with soil arthropods simply because certain principles or concepts had been particularly well developed there or challengingly stated. Some of these problems are not easily approachable through the "factor" route Furthermore, it was urged that particular attention be given to the characteristics of populations as opposed to mass extension of individual physiology, and this would mean specific analysis of the ways in which individuals react to others, either directly or through modification of the environment The latter is easily subject to the factors approach, the former is not. Finally, introductory comments were directed at the problems, repeatedly brought up in the conference, of establishing the adaptive value of particular behavior and features of life history as contrasted to the analysis of the physiological mechanism. Much of the short but compressed discussion that followed these introductory remarks were concerned with pointing out areas in which considerable progress had been made in marine ecology along the lines emphasized in the introductory remarks. The comments below have been somewhat abbreviated.

MCLAREN: Perhaps we could suggest to Professor Hutchinson that he write an "ornithology for copepodologists." He wrote a provocative little paper called "copepodology for the ornithologist" a few years ago(160).

EDMONDSON: That is a very good example, because there has been a lot of work in evaluating clutch size in birds and how this relates to food supply, and there are many observations that relate to some of the things that have been said here today about how the animal seems to

anticipate what is going to happen. I think much of what was discussed there is directly applicable to strongly periodically breeding animals.

COSTLOW: Doctor Yonge might like to comment on the takeover by *Elminius modestus*.

YONGE: I thought there was a similar invasion now proceeding in Florida. This barnacle, *Elminius,* appeared along the south coast of England during the last war, probably having come from the antipodes through the Panama Canal on the bottom of a ship. It very soon established itself and is now in many areas the dominant barnacle.

COSTLOW: And largely because of its reproductive rate.

YONGE: Yes, and then the time of reproduction involving the time of settlement. By the time it has fixed itself to the rocks, other barnacles appear in the plankton but all settling space has been taken by *Elminius*. This may also apply to oysters.

EDMONDSON: But evidently the other species are not able to undergrow.

YONGE: No, *Elminius* seems really to have taken over. It has now spread beyond England to the south coast of Ireland and widely along to the north coast of Europe. Crisp(161) and others have followed the process. It worked north as far as Millport some ten years ago.

SANCHEZ: I might cite a study which is not finished but which I think should prove to be interesting, which is being carried on at present in southern Chile by a German zoologist, Professor Koehn. After the earthquakes of 1960, the coastline was sunk for 3 to 10 meters so the whole area that made up the intertidal was completely sunk and wave action has denuded the new soils there and a settlement has begun of all the organisms that were observed there. That is a case of the value of experimental situations in nature. I think there they are making very good use of this experimental situation.

I wish to express one point by coming back to a Slobodkin comment made earlier, which was summed up by Doctor Costlow when he spoke of the philosophical approach. I think that what Doctor Slobodkin was stressing, was something very real and that is to ask oneself always when one is studying particular mechanisms, What is the meaning of such things to the animal? "To the animal" does not mean the individual animal but the community of animals, the species of the community in which it lives, and I think that possible questions on mechanism acquire tremendous significance when one starts at the same time through a comparative approach, for example, to try to make out really what does it mean to this community to have this or that particular mechanism.

It is the type of thing that I get the feeling physiology is very often lacking in, and it should not be; it should be physiology applied to ecology, which is really the result of an evolutionary makeup.

McLAREN: Doctor Schmidt-Nielsen is taking this approach. Not all physiologists ignore the adaptive value of physiology. In fact, there is a class of ecological physiologists or physiological ecologists.

STRICKLAND: Why did I get a certain amount of disapproval when I asked why was the *Sagitta* transparent? This seems to an amateur to be a reasonable thing to ask.

McLAREN: The answer was that *Sagitta* is not transparent.

FREMONT-SMITH: The answer was that some other organisms are transparent.

SANCHEZ: "Why are we not transparent?" Perhaps it is the same question.

COSTLOW: Doctor Edmondson made reference to sudden changes and I believe he cited the odd 30-year hurricane that can provide circumstances which allow the increase of one population over another, and it can work the opposite way, too. At one time they had at Beaufort *Balanus tintinabulum,* which is found primarily offshore, one of the large acorn barnacles. It had, when I first went there in about 1957, worked its way up into the estuary in a salinity that was ranging from perhaps a low of 20 up to oceanic salinity.

Following the first big hurricane in thirty years, the salinity dropped for about a week to 10–15; the next winter, which was perhaps another month later, it was extremely cold and the intertidal area that this barnacle had been found in was completely denuded, and since that time I have yet to find a *Balanus tintinabulum* within the estuary. How long it will take for it to reestablish itself is something else, but if I had come along the year before and started a study on *B. tintinabulum* in the area I would have had to correct my figures.

EDMONDSON: I think the bottom fauna is where this kind of thing is magnified.

GONOR: People have studied the effects of life history on distribution of marine organisms to a considerable extent. Maybe we ought to mention these things. They are not necessarily new but they are well known. Most of the studies involve selection of substrate by the larval animals which puts them in the right adult habitat. Knight-Jones(162) has studied the worm *Spirorbis,* the larvae of which are sensitive to the substance of the substrate and select it and will not settle successfully on substrates that are not the adult habitat. This is furthermore conditioned by the previous presence of adults.

Crisp(163) has gotten quite a long way into the analysis of this situation in the barnacles. A substance is impregnated into the rocky substrate by the presence of adult barnacles. It resists boiling, and so forth. This substance conditions a substrate for the settlement of larvae; larvae in turn are sensitive to its presence and settle preferentially in this preconditioned area. This is true not only for filter feeders that settle on inorganic substrates. Some nudibranchs, for example, will do the same thing. It has been generally demonstrated that the adults of carnivorous nudibranchs are positively attracted to their food organisms. So are the larvae in certain cases. *Adalaria* larvae(164) require the presence of live *Electra,* a bryozoan, in order to metamorphose. This is the prey of the adult. The larvae settle only in the presence of the specific prey, which is also its substrate. The association of carnivorous nudibranchs with specific prey would indicate that this is a common adaptive phenomenon, except in one case studied by Michael Hadfield(165) in Doctor Thorsen's laboratory. He studied *Onchidoris,* a nudibranch that eats barnacles. When the larvae are put into a dish with the adult prey organism, they are eaten as they buzz around the barnacles. Even recently metamorphosed barnacles can catch these small larvae. The selective factors here should be very interesting.

COSTLOW: From an evolutionary standpoint, I guess, at what point in the life history of an animal is it better adjusted to make these changes if it is called upon to make them? Where you have six larval stages, is there one point—say for the sake of argument the third zoeal stage—that is the point that is better adjusted to make a change, or is this a sliding-scale-type thing?

EDMONDSON: That comes close to the point I was trying to make. These are things that have to be evaluated, but the kind of thing that I was thinking about, was a famous paper on population consequences of life history that Cole wrote(166). Many people have tried to evaluate success of populations in terms of the rate at which they can produce eggs, and the like. This includes a systematic study of how much difference it makes in different stages whether more eggs are laid or whether the organism adds an extra year to life or starts reproduction a year earlier. Which is more important in establishing balance? The point is that to get at this you have to know a lot about the schedule of mortality and the schedule of reproduction, and this information is not available in adequate quantitative detail for many animals. It is not available because people do not look for the data unless they have a motivation for doing it. The point you make about what happened in the different stages is important. Events at different stages will make a tremendous difference.

MCLAREN: Jack was making another point as well. There is a tendency

to suggest that two or three alternative hypotheses which can be found in the literature are equally probable when any reasonable man can often make a decision. This can be expressed as "generally," and then can be argued against, but at least it solidifies the situation.

This question which you raised of the necessity for getting the raw data on the life table, the balanced life table—the literature is full of this sort of material. I have used it myself in working out the vertical migration paper. That material has been in the literature for years, ready for analysis. There is a great deal more of the same sort ready for analysis and it is not being done. People are saying, "We don't know enough about this kind of thing."

EDMONDSON: Generally, at least in many of the things I have looked for, there is just something important missing.

MCLAREN: Very often, yes. There is no shortage of material for anybody who is not choosy of his group, but we generally choose our animal first and then try to find information on it. A marine biologist who is interested in populations in general can depend largely on what is in the literature and what is being produced now at an enormous rate.

FREMONT-SMITH: Is it not rare, when one does compile this sort of thing in the literature, not to find a key thing is missing?

MCLAREN: Yes. But Doctor Gonor was saying there are a great many, a great variety of answers.

EDMONDSON: I am not suggesting that we are starting marine biology today. It is just that a conscious examination of what you have to know will lead to more secure results.

GONOR: You are quite right. I am afraid many times you would look for missing information. You could look and find key information missing. In trying to compile lists of food organisms of Opisthobranchs, I have found a lot of this. I find that people did not do this or that, or in my work I did not do this or that, and it is hindsight operating. I now know what I really should have asked.

YONGE: But the crucial stage in development is surely the end of the planktonic stage with the assumption of the adult form and adult habit of life. We now have a good deal of knowledge about this. Late larvae can suspend metamorphosis until they encounter, by chance, the right environment.

COSTLOW: Not the crustacea.

YONGE: But even then, when does it acquire the adult form and habit? That is surely the crucial point.

COSTLOW: I would tend to argue.

YONGE: All the other ones are developmental stages but there comes this crucial stage, when the organism changes from the larval to the adult form.

COSTLOW: Yes, that is a very crucial point but are there, in the case of crustacea larvae, again previous points within larval development when it is more receptive to environmental changes which will enable it to live to that point of metamorphosis?

YONGE: I agree that there is longer spacing-out.

COSTLOW: Yes; so far, to my knowledge, there is very little evidence for the type of thing you have in mollusks.

YONGE: It applies in annelid worms as first worked out by D. P. Wilson at Plymouth. But it is equally true of a variety of bivalve and gastropod mollusca.

GONOR: Some interesting figures were given by Thompson(164) in his paper on the larvae of *Adalaria,* a nudibranch. He compiled data on mortality of larvae hatched and kept in laboratory vessels during development. He got about 11 per cent mortality during early developmental stages, while the mortality of larvae during settlement and metamorphosis was about 84 per cent of those surviving early development. During the first six weeks of benthic life the mortality of those surviving metamorphosis was down again to about 11 per cent. These mortalities occurred in the absence of predators, and these larvae do not require food during pelagic life.

COSTLOW: Let us assume that we have four zoeal stages prior to the megalops. Let us assume within an estuary, that the optimum for the first stage is 20°C. and 20 parts per thousand. The second stage then is swept into an area where the salinity is much lower and perhaps the temperature is much lower, too.

Let's make it about 10° and 5 parts per thousand. What per cent survival will you expect under these conditions? If these conditions are imposed on the second stage, do you have a higher survival than if the conditions are imposed on the third stage? What happens if these conditions are imposed on the fourth stage, which brings you to the point which is critical, the metamorphic point?

If one of these larval stages can survive better at these conditions it leaves you a greater number to metamorphose in the end.

YONGE: Have you any evidence that these various stages have greater capacity for standing extremes?

COSTLOW: From laboratory work, yes. It is beginning to fit into some sort of a jumbled thing and it is very species specific, too.

PROVASOLI: Also *Artemia* has some stages that are more sensitive than others to the imbalances or toxicities of our artificial media.

One of the most sensitive stages is the first metanauplius which has just consumed the yolk reserves and needs food to go on. Other sensitive stages are when the first three thoracic appendages are articulated, and later on when the metanauplius has at least seven appendages articulated.

The least sensitive stages are the juveniles, i.e., the animals whose thoracic appendages are almost completely grown.

We have profited from this knowledge and now, when the first metanauplii die in some of the experimental tubes, we reinoculate the same tubes with metanauplii of a more advanced stage; if these too die, then we inoculate juveniles. In most cases the juveniles survive, but not always will they be able to grow to young adults, or to sexually mature and fully grown adults. These differentials in growth permit us to assess the toxicity and nutritional value of many variables even if the medium is severely unbalanced.

When we started to identify the need for single vitamins, we obtained a usable vitamin mixture by eliminating the vitamins which were not needed, like inositol, vitamin B_{12}, choline, and carnitine. Then we proceeded to eliminate, one at a time, the needed vitamins. When we omitted either thiamine, nicotinic or pantothenic acid, not only was the speed of growth retarded, but development was arrested at the stage in which the thoracic appendages start to differentiate into articulating phyllopodia. If pyridoxine or riboflavin are missing, development proceeds further until the stage in which seven thoracic appendages are fully articulating and some of the abdominal buds are growing.

If folic or para-aminobenzoic acids are lacking, the animal develops to the stage in which most of the appendages are fully motile—the animal typically swims on its back. Finally if we remove either biotin or putrescine, we obtain young adults which lack secondary sexual characteristics, i.e., well-developed claspers in the male and the egg pouch in the female.

KANWISHER: This is leaving out vitamins?

PROVASOLI: Yes, leaving out one vitamin at a time. Even though we omit a vitamin, our media are not so pure chemically that we necessarily have a complete lack of it. Yet the results in freezing morphogenesis at a certain stage are dramatic. The animals just do not develop further, though they remain alive for 10–20 days.

A similar arrest in development is obtained when the nucleic acids are removed one at a time. The lack of adenylic acid stunts development more than the lack of any other component of RNA or DNA. Adenylic acid accounts for almost 80–90 per cent of the action obtained by RNA so far as development is concerned, but the speed of growth in adenylic acid alone is low; other nucleic acids such as uridylic, cytidylic, and thymidylic are needed to speed growth.

The quantities needed to satisfy the requirement for vitamins are enormous in comparison to what is used in microbiology, but are similar to the values employed for insects. This is probably due to the low perme-

ability of chitin which covers the body of insects and crustacea. It might also mean that they drink very little.

YONGE: Does this mean the animal is taking this in by drinking?

PROVASOLI: I do not know if they actually drink or not. I wish I knew. I was arguing that since all the solutes are needed in high concentrations, the intake of liquids, by whatever way (i.e., drinking or absorption), should be very poor. Since the medium is composed of organic solutes and starch and protein particles, many of the solutes are likely to be absorbed by the particles—this would facilitate their intake. But the absorption on the particles is probably preferential; some substances being absorbed more readily than others. This seems to be true, because when we change the starch/protein ratios, or we employ larger or smaller quantities of particles then we have to readjust the ratios or the quantities of the amino acids supplied by the amino acid mixture to avoid either deficiencies or toxicities.

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marine biology

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PROCEEDINGS OF THE THIRD CONFERENCE ON MARINE BIOLOGY HELD AT PRINCETON, NEW JERSEY ON JANUARY 19 TO 22, 1964 UNDER GRANTS FROM THE OFFICE OF NAVAL RESEARCH AND THE ATOMIC ENERGY COMMISSION

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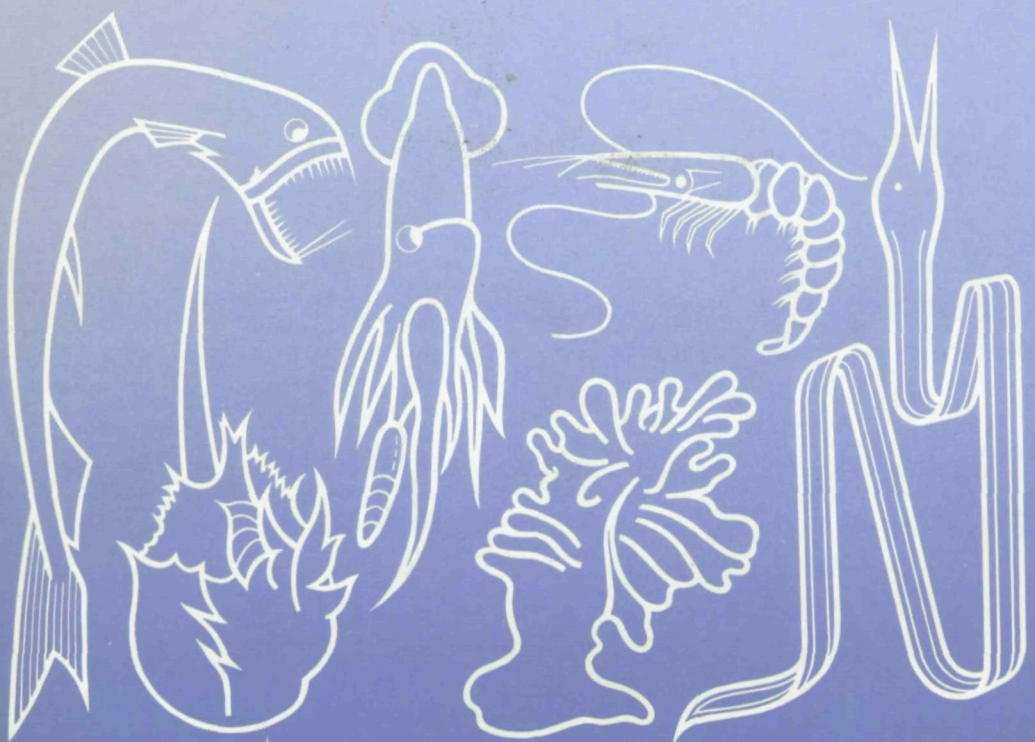

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