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# 10

## DEEP-SEA COMMUNITY STRUCTURE: THREE PLAYS ON THE BENTHIC PROSCENIUM

## ABSTRACT

From the available literature in spring 1979, we examine the compatibility of data and theories of deep-sea benthic community structure. We begin with a brief review of data, showing that deep-sea infaunal species are small and sparsely distributed, that deposit feeders dominate the deep-sea infauna and frequently are very high in species diversity, that size-frequency distributions of individuals within deep-sea populations generally peak at the larger sizes, and that insufficient data exist to generalize about deep-sea population dynamics. Having thereby set the stage, we explore the respective abilities of theories at the individual, population, and community levels of ecological organization to explain the available observations and, more importantly, to provide predictions that can be tested with available technology in the foreseeable future.

At the individual level, foraging theory holds a great deal of promise for explaining the relative success of feeding guilds and for providing testable predictions. Excluding unusual environments such as hydrothermal vents and regions of high current activity, deep-sea suspension levels apparently do not repay the costs of pumping water. Even passive suspension feeders show adaptations for intercepting enhanced particle fluxes by projecting their feeding appendages into the turbulent portion of the benthic boundary layer. The most extensive predictions, however, can be made for scavengers. Taking into account the diffusion patterns of scent trails away from carrion on the bottom, we would expect crawling scavengers to spend most of their time searching in cross-stream movements. Small, swimming scavengers should be generalists that take what living and non-living food items they encounter. Large, swimming scavengers, on the other hand, should spend more of their time at those greater heights above the bottom where (due to upward and lateral turbulent diffusion of scent trails) they can capture, by virtue of detection ability, the most carrion per unit time, and they should be specialists on carrion. Foraging theory further suggests that motile deposit feeders should move in such a fashion as to minimize recrossing of recently depleted deposits; such minimization has the potential for explaining such seemingly disparate phenomena as the coiled feeding traces of enteropneusta and the herding behavior of urchins. A major impediment to additional applications of foraging theory to the deposit feeders that dominate the deep sea, however, is the inability to identify clearly the resources they utilize. This problem is best attacked in shallow-water communities before a deep-sea answer is attempted.

Theories at the population level are disappointing in their predictive abilities. Stochastic models and  $r$ - $K$  theories, for example, provide conflicting predictions of expected life-history traits, and the meager life-history data as yet obtainable from the deep sea do not promise to provide any definitive tests of these and other models. Shallow-water, terrestrial, and laboratory testing of general population models seems prudent before attempting definitive deep-sea application.

At the community level, Connell and Slatyer's individual-by-individual successional models, especially as formalized through a Markovian approach, deserve further consideration for deep-sea application and manipulative testing. We demonstrate via some simple examples, however, that such applications and tests are premature until predator-prey and competitive relations have been established. The latter, in turn, are not

likely to be discovered until the resources utilized by the ubiquitous deposit feeders are better identified.

On a more optimistic note, at each biological level of organization, the physics of the deep-sea environment is seen to provide potential explanations of phenomena for which other, biological explanations have been sought or used in the past. The physical structure of the deep-sea benthic boundary layer may allow unique foraging tactics among scavengers and certainly does limit viable suspension feeding methods. At the population level, the reduced incidence of physically mediated disturbances capable of causing size-independent mortality may cause size-selective predation to be a relatively more important phenomenon in the deep sea than it is in shallow water. At the community level, in turn, relatively weak bottom currents allow the persistence of biologically generated environmental heterogeneity (e.g., fecal mounds, tubes, burrows) that may facilitate the persistence of higher species diversity than generally is seen in shallow-water communities. Just as biological parameters can influence the survival and persistence of particular species in physically disturbed environments, so can physical parameters influence the relative success of deep-sea species.

The belief that science proceeds from observation to theory is so widely and so firmly held that my denial of it is often met with incredulity. . . . But in fact the belief that we can start with pure observation alone, without anything in the nature of a theory, is absurd; as may be illustrated by the story of the man who dedicated his life to natural science, wrote down everything he could observe, and bequeathed his priceless observations to the Royal Society to be used as inductive evidence. This story should show us that though beetles may profitably be collected, observations may not.

Sir Karl Popper (1965, p. 46)

## INTRODUCTION

Direct observations of biological processes in the deep sea have been rare. The few outstanding exceptions have merited their own chapters in the present volume. Our chapter, by contrast, serves two somewhat divergent purposes. First, it introduces an assortment of data and generalizations on deep-sea community structures as essential background for this and later chapters. The second, more central purpose is to explore an equally wide spectrum of theories which may serve to explain the observed patterns. Recent historians and philosophers of science, while failing to concur on a method for arriving at scientific explanations (see Feyerabend, 1975), do concur that the development of theories takes precedence over the collection of observations both in the recognition of successful research programs from the past (Lakatos, 1970; Kuhn, 1962; Platt, 1964), and in the prescription of how science ought logically to proceed in the future (Popper, 1959).

The extant observations of deep-sea community structure are, for the moment, the only available actors and props, and they inspire the theories which will serve as this season's repertoire. For the sake of brevity, but at the expense of smooth transitions, we will introduce the principal actors and props all at once. All will not be used in each

of our subsequent three plays, and a few specialized extras will be introduced in the individual plays. The decisions we seek are what new actors and props should be hired or obtained and, given the actors who will likely be available, whether a new repertoire of plays should be attempted next season. What new data would be desirable, and what observations would allow rejection of existing theories?

## PATTERNS OBSERVED

The size of our theatrical company is small. Because it takes years to plan and obtain funds for deep-sea expeditions, hours to lower and retrieve a sampler, roughly a month of microscope work per typical sample just to separate the larger animals from sediments too large to sieve away, and months of many taxonomists' time to assign animals from a single locality to species categories, the data are few. Without the ability to observe live, naturally interacting animals, the data are also of few kinds. Much of what we think we know about ecology of deep-sea animals in fact comes from analogy with "similar" shallow-water species—an analogy as dangerous as likening poisonous mushrooms to similar edible species. Despite this paucity of data, but in keeping with our opening quotation, we will treat only enough of the available observations to allow us to delve into the pertinent theory. The data-hungry reader will soon have available a much more detailed review (Rowe, in press).

We will draw repeatedly upon examples from four localities (Table 10-1), each studied via samples taken with the same device, the 0.25-m<sup>2</sup> USNEL spade or box corer described by Hessler and Jumars (1974). It recovers a cube of minimally disturbed mud of about 0.5 m in each dimension, often with animals still swimming in the overlying water (until the temperature rises too high). Quantitative comparisons among regions sampled with different devices are virtually impossible. Hessler and Jumars (1974), for example, show the disparate results obtained in sampling the same locality (CNP) with the box corer versus a towed, fine-meshed (0.5-mm) trawl, the epibenthic sled. No device samples all the deep-sea fauna equally well, and those highly mobile animals (e.g., fishes) living on or just above the bottom (mobile *epifauna* as opposed to *infauna*, the latter living within the sediments) have not yet been sampled quantitatively with any device. It should be remembered, then, that the samples of Table 10-1 include only the *infauna*, together with the less mobile *epifauna*.

TABLE 10-1. Sampling Localities Treated Frequently in the Text<sup>a</sup>

<i>Name</i>	<i>Abbreviation</i>	<i>Depth (m)</i>	<i>North Latitude</i>	<i>West Longitude</i>
Santa Catalina Basin	SCB	1130	39° 58'	118° 22'
San Diego Trough	SDT	1230	32° 28'	117° 30'
Central North Pacific	CNP	5500-5800	28° 29'	155° 23'
Aleutian Trench	AT	7298	50° 58'	171° 38'

<sup>a</sup>For additional data on these localities, see Hessler and Jumars (1974, CNP), Jumars (1976, SCB, SDT), and Jumars and Hessler (1976, AT).

## Body Size and Areal Density of the Fauna

Perhaps the most obvious peculiarity of deep-sea infaunal samples is the small average body size and frailty of individuals. In shallow-water, soft-bottom sampling, the term "meiofauna" is usually employed for animals passing through a 0.50- or 1.00-mm mesh sieve but retained on a roughly 50- $\mu$ m sieve, while the term "macrofauna" applies to animals collected on the 0.50- or 1.00-mm meshes. A 1.00-mm sieve would retrieve virtually no infauna from the CNP site and very few individuals from most other deep-sea localities. Furthermore, unless the samples are handled very delicately, few animals will be retained at all. There is little need of heavy exoskeletons or thick integuments in an environment of weak currents and little sediment motion; excessive agitation during sieving will leave few identifiable remains.

Some taxonomic groups (taxa) of animals in shallow water characteristically are meiofaunal in size—nematode worms and harpacticoid copepods, for example. Adults of other taxa (e.g., bivalves, annelid worms) characteristically are larger than 0.50 or 1.00 mm. Hessler and Jumars (1974) have suggested the terms "meiofaunal taxa" and "macrofaunal taxa" to allow deep-sea recognition of parallel taxonomic groups. At the SCB and SDT sites, a 0.42-mm sieve retains adults of the macrofaunal taxa, while the CNP and AT sites require 0.30-mm meshes. We prefer the taxonomic distinction to one purely of size; it is more reasonable to compare oranges of different sizes than apples with oranges.

One extreme example of deep-sea miniaturization, reminiscent of trends seen in the fauna living in the interstices of near-shore sands (Swedmark, 1964), is the proto-branch bivalve genus *Microgloma*, in which cell size and germ-cell numbers have been so reduced as to produce mature adults less than 1.00 mm long (Sanders and Allen, 1973). While such reduction in size of deep-sea macrofaunal taxa has been discussed at length (Gage, 1978; Thiel, 1975, 1979), its causes remain open to speculation concerning both physiological and ecological mechanisms. Depth alone is not the cause. Of the localities of Table 10-1, the smallest average body size is found at CNP, where food input from the surface is also likely to be lowest. Polloni *et al.* (1979) in fact find little consistent change in macrofaunal body size in the North Atlantic between 400-m and 4000-m depths, although few large individuals are seen below 360 m. They suggest that the greatest reduction in body size may occur between 0 m and 400 m. Although the precise mechanism is unclear, the miniaturization of macrofaunal taxa occurs primarily by species replacements rather than by decreases in average body size within species; Gage (1978), for example, finds no evidence of decreasing body size with depth within three annelid worm species having broad depth ranges (compared at 20 to 150 m versus 1800 to 2875 m). Correlations of depth and distance from shore with sizes of individuals belonging to meiofaunal taxa have not been documented as clearly. However, the ratio (on the basis of numbers of individuals) of members of meiofaunal taxa to members of macrofaunal taxa does appear to increase toward the abyss (Thiel, 1979).

Confusing the issue of size and the definitions of meiofauna and macrofauna still further are the foraminifera [a group of (usually) test-building, acellular Protozoa]. A large majority of shallow-water foraminifera are meiofaunal in size range. In the deep sea, however, they encompass the entire size ranges of other macrofaunal and meiofaunal

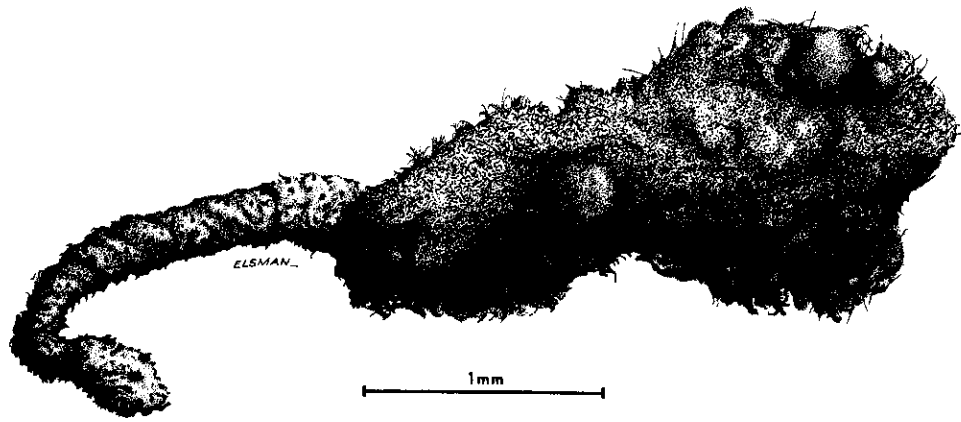


Fig. 10-1. *Baculella hirsuta*, a foraminiferan (suborder Textulariina) from the CNP locality (Table 10-1). It is much larger than individuals of macrofaunal taxa taken there. Its normal posture and ecological role are unknown. With permission, from Tendal and Hessler, 1977, Fig. 9.

taxa (e.g., Fig. 10-1). At the CNP locality, for example, the foraminifera larger than 0.30 mm outnumber the comparably sized metazoans (multicellular animals) by at least an order of magnitude (Bernstein *et al.*, 1978). Similar quantitative comparisons have not been made at the SCB, SDT, and AT sites, but large foraminifera are present in abundance at all these localities. Small animals are the rule among deep-sea infauna,

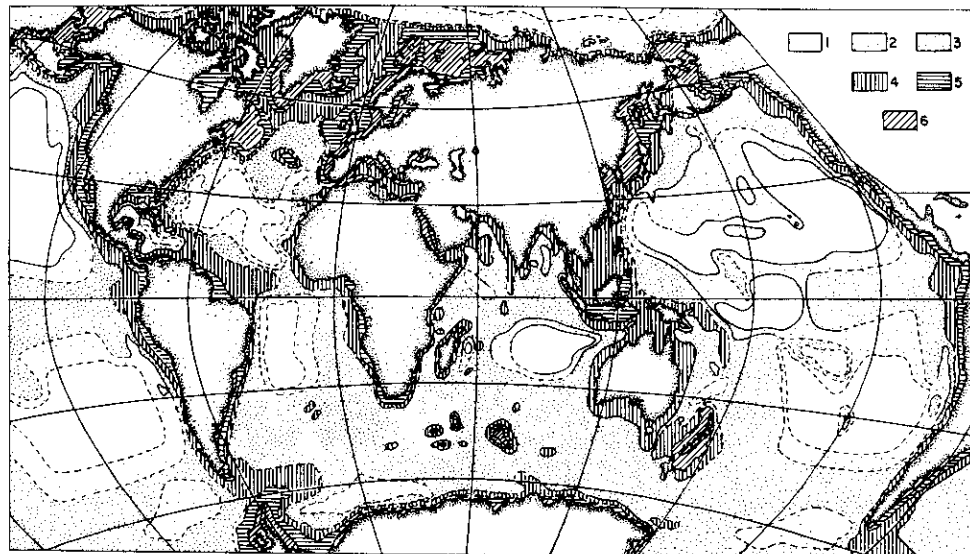


Fig. 10-2. Biomass (wet weight) of infauna from Okean grab samples (Belyayev *et al.*, 1973). Symbols (all in  $g\ m^{-2}$ ): 1, <0.05; 2, 0.05-0.1; 3, 0.1-1.0; 4, 1.0-10.0; 5, 10.0-50.0; 6, 50.0- >1000.0 With permission, from Hessler and Jumars, 1977, Fig. 2.

but foraminifera may well be the exception; a single pseudopod may extend up to 12 cm (Lemche *et al.*, 1976). Size trends among the epifauna, in general, also have not been documented reliably, but demersal (near-bottom dwelling) fishes *increase* in size with depth on the western Atlantic continental slope and rise (Haedrich and Rowe, 1977; Polloni *et al.*, 1979).

Accompanying the reduction of body size in macrofaunal taxa is an even more dramatic decline in standing stock (per unit area) with depth and distance from shore. The very lowest standing stocks in general occur in the food-poor central oceanic regions (Fig. 10-2). The surface waters here have very low rates of input of plant nutrients and consequently low production rates of food, most of which is consumed well before it can sink to the abyss. As a crude generalization, numbers of individuals per unit area decrease roughly exponentially with depth, but the same exponential function will not fit data from all regions (e.g., northwest Atlantic versus Gulf of Mexico, Fig. 10-3), and an exponential function will not fit at all in some regions (e.g., Gulf of Gascogne, Fig. 10-3). Rates and mechanisms (e.g., slumping and turbidity currents over steep topography) of food input to a given depth vary regionally and locally, being especially sensitive to the distance from productive, near-shore waters at which that particular depth is reached. Nor can one assume that deep-sea communities everywhere have equal conversion efficiencies of food into numbers or grams of individuals. In crude analogy with human populations, exceptionally dense assemblages can be expected to occur both where supply is plentiful and where utilization is efficient, or where (for any reason) birth and immigration rates greatly exceed death and emigration rates. In the deep sea, as elsewhere, the temptation to equate standing stocks (Figs. 10-2 and 10-3) with rates of production must scrupulously be avoided.

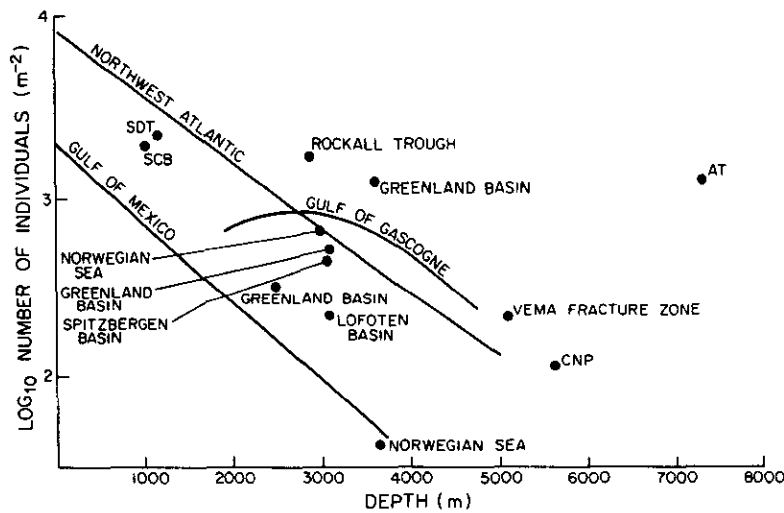


Fig. 10-3. Number of individuals ( $m^{-2}$ ) versus depth for samples from a wide range of geographic localities. Curves summarize numerous data points from the Northwest Atlantic, Gulf of Mexico, and Gulf of Gascogne. Modified, with permission, from Khripounoff *et al.*, 1980, Fig. 6.

TABLE 10-2. Overall Macrofaunal Abundance and Identity of the Most Abundant Macrofaunal Species at the Sampled Localities<sup>a</sup>

Locality:	SCB	SDT	CNP	AT
Total macrofaunal abundance (m <sup>-2</sup> ):	1880	2251	115	1272
Numbers of most abundant species (m <sup>-2</sup> ):	350	142	15	184
Species:	<i>Paraonis gracilis oculata</i>	<i>Tharyx</i> sp.	<i>Chaetozone</i> sp.	<i>Chaetozone</i> sp.
Family:	Paraonidae	Cirratulidae	Cirratulidae	Cirratulidae

<sup>a</sup>All are polychaetes (bristle worms).

### Characteristic Taxonomic Composition and Trophic Structure

What kinds of albeit small and rare animals dominate the deep-sea bottom? Bristle worms (polychaetes) usually constitute half to three quarters of the individuals of macrofaunal taxa and usually contain the most abundant species at any soft-bottom deep-sea location (Table 10-2, Fig. 10-4). At even the grossest taxonomic levels (Table 10-3), however, deep-sea samples are often identifiable to broad depth zones—bathyal, abyssal, and

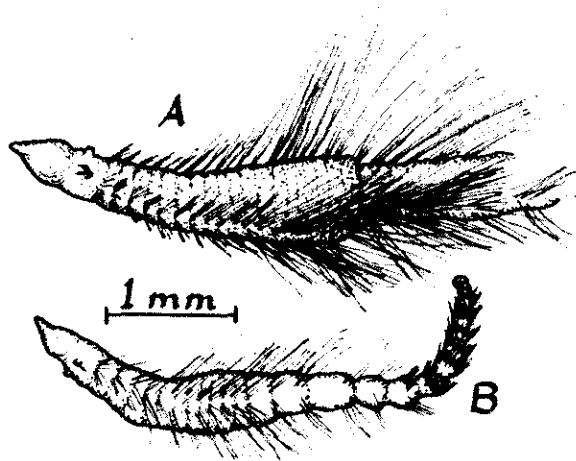


Fig. 10-4. *Chaetozone* sp., the most abundant macrofaunal species found at the AT locality. It is large by CNP standards. The paired feeding palps have been broken off both specimens, but their scars can be seen near the anterior (left) ends of the animals. A specialized construction apparent in the midsection of larger specimens (A), together with the relatively short tail (B) and head sections of some specimens, is suggestive of asexual reproduction.



hadal. Bathyal zones (e.g., SCB, SDT) have high proportions of polychaetes and amphipods; food-poor central oceanic (abyssal) regions (e.g., CNP) have smaller proportions of both polychaetes and amphipods, with correspondingly higher relative abundances of tanaids and isopods; hadal samples (e.g., AT) often have unusually high abundances of taxa which are poorly represented elsewhere (e.g., Aplacophora, Enteropneusta, Echiura). Shallow-water communities, while frequently consisting of fewer phyla, seem to be more highly variable in the proportions of the standing stocks comprised by those phyla (e.g., Friedrich, 1969).

An ecologically more meaningful comparison between deep-sea and shallow-water community compositions can, however, be made at the level of functional groups or guilds. Root (1975, p. 92) defines a guild as "a group of species that exploit the same class of resources in a similar way." Because there is very little direct evidence concerning

TABLE 10-3. Percentages (by number of individuals) of Macrofaunal Taxa Found in Box Cores (common names in parenthesis)

	<i>SCB</i>	<i>SDT</i>	<i>CNP</i>	<i>AT</i>
<b>Annelid worms:</b>				
Polychaeta (bristle worms)	76.6	75.5	55.1	49.0
Oligochaeta	—	—	2.1	1.4
Hirudinea (leeches)	0.1	—	—	—
<b>Crustaceans:</b>				
Cirripedia (barnacles)	—	<0.1	—	—
Mysidacea (opossum shrimps)	0.1	0.2	—	—
Cumacea (lollipop shrimps)	1.9	1.2	—	—
Tanaidacea	3.8	3.7	18.4	6.1
Amphipoda (sand fleas)	5.9	4.2	—	1.4
Isopoda	3.9	2.9	6.0	0.7
<b>Mollusks:</b>				
Gastropoda (snails)	0.4	1.0	0.4	0.7
Aplacophora	0.4	0.5	0.4	10.5
Bivalvia (clams)	1.5	3.1	7.1	11.5
Scaphopoda (tusk shells)	1.2	0.3	2.5	—
<b>Other groups:</b>				
Porifera (sponges)	<0.1	—	1.1	—
Cnidaria	0.1	0.1	1.4	—
Nemertinea (proboscis worms)	0.6	1.6	—	—
Pycnogonida (sea spiders)	—	—	—	0.3
Pogonophora	—	0.3	—	—
Sipuncula (peanut worms)	0.4	0.5	0.4	0.3
Echiura (gutter worms)	—	—	0.4	3.0
Priapulida	—	<0.1	—	0.7
Bryozoa (moss animals)	0.1	1.4	2.0	6.4
Brachiopoda (lamp shells)	—	—	0.7	—
Enteropneusta (acorn worms)	0.4	0.2	—	8.1
Ophiuroidea (brittle stars)	2.5	2.6	0.7	—
Holothuroidea (sea cucumbers)	0.1	0.5	0.4	—
Pterobranchia	<0.1	—	—	—
Asciacea (sea squirts)	<0.1	0.3	1.1	—

patterns of day-to-day resource utilization by deep-sea species (as noted, with cautions, in the introduction), deep-sea guilds are usually erected by analogy with better-known shallow-water relatives, in conjunction with examination of morphology and gut contents of deep-sea specimens. Very rarely, however, have investigators devised such classifications for all the taxa from a particular set of samples. In the following discussion, then, we often will be forced to jump from taxon to taxon in illustrating supposed generalizations.

One trend has nonetheless become clear across a wide spectrum of taxa: Suspension feeders show a marked decrease in abundance with increasing depth and distance from shore. No more than 7% (by numbers of individuals) of the total CNP macrofaunal taxa potentially are suspension feeders (Hessler and Jumars, 1974). A dramatic corroboration of the dearth of suspension feeders in the deep sea is the shift among guilds within major taxa as depth increases. Most deep-sea bivalves, for example, are deposit feeders (protobranchs) or even carnivores (septibranchs), while a much greater proportion of shallow-water bivalves are suspension feeders. Perhaps even more surprising is the tendency for deep-sea sea squirts (ascidians) to evolve carnivorous or deposit-feeding habits (Monniot and Monniot, 1978). Only in regions of anomalously high rates of food-supplying water flow (Lonsdale, 1977) or of high *in situ* chemoautotrophic (bacterial) production (Rau and Hedges, 1979), such as at the newly discovered hydrothermal vents near oceanic spreading centers (Ballard, 1977), are suspension feeders prevalent in the deep sea.

As they are in the classical Eltonian pyramid, carnivores too are relatively rare among animals captured in cores. Among the polychaetes, for example, we estimate (using the guilds defined by Fauchald and Jumars, 1979, together with our own observations) the following proportions (by numbers of individuals) of carnivores: SCB, 2%; SDT, 13%; CNP, 12%; AT, 7%. Operationally, however, carnivores are difficult to distinguish from scavengers and omnivores; gut contents do not reveal whether food is taken alive. As pointed out above, the larger, more mobile members of the latter guilds have not yet been sampled quantitatively. Highly mobile scavengers are nonetheless known to be present at all deep-sea depths and to respond quickly (hours or less) and in large numbers to bait (animal flesh) lowered to the deep-sea floor (Isaacs and Schwartzlose, 1975). Scavenging amphipods (family Lysianassidae), in contrast to the general disappearance of other amphipod guilds at greater deep-sea depths, are attracted to bait at any oceanic depth. While fishes are quick to respond to bait at bathyal and abyssal localities, and fishes are known to occur at hadal depths, scavenging fishes appear to be missing from many trenches (Hessler *et al.*, 1978). The less motile (crawling as opposed to swimming) scavengers, such as brittle stars (ophiuroids) and quill worms [curious polychaetes which drag their tubes along with them (family Onuphidae)], by contrast, disappear more gradually with increasing depth and distance from shore and have not been observed to respond to bait at the CNP locality (Dayton and Hessler, 1972). One question left unanswered by these otherwise highly informative studies of species responding to bait, however, is what the animals do when bait is not present. Do they wait, or search for comparable windfalls, or do they hunt live prey?

Surprisingly, herbivores (or, more precisely, animals feeding on recognizable plant

remains) are not wholly absent from the deep sea. The fauna colonizing wood has been the most thoroughly studied (Turner, 1977), but there are deep-sea species that seem to utilize more ephemeral plant structures such as sea grass blades (Jumars, 1976). Because of the proximity of most trenches to land, such vegetable matter and these sorts of vegetarians have been recorded relatively frequently there (Wolff, 1976).

The majority (usually 80% or more by numbers in macrofaunal taxa) of animals captured in deep-sea cores are deposit feeders, ingesting sediments and the smaller, less motile organisms they contain. Thus, while we tentatively call these animals deposit feeders, their exact trophic positions and impacts depend on the degrees to which they are incidental carnivores (Anderson, 1976; Dayton and Hessler, 1972; Feller *et al.*, 1979). Deposit feeders, then, are the animals to which the earlier remarks about size and areal density largely pertain. This guild, in turn, is divided between surface deposit feeders and species which feed on sediments below the sediment-water interface. In many deep-sea areas, deposit-feeding polychaetes, for example, are divided approximately equally (by numbers) between surface and subsurface deposit feeders (Fig. 10-5).

### Species Diversity

Perhaps more surprising than the above patterns, as judged by the wealth of speculation it has produced, is the finding of high species diversity in the deep sea. We will forego reviewing the initial and now well-known documentation of this finding (Hessler and Sanders, 1967) and will instead make a few pertinent points by again relying on the

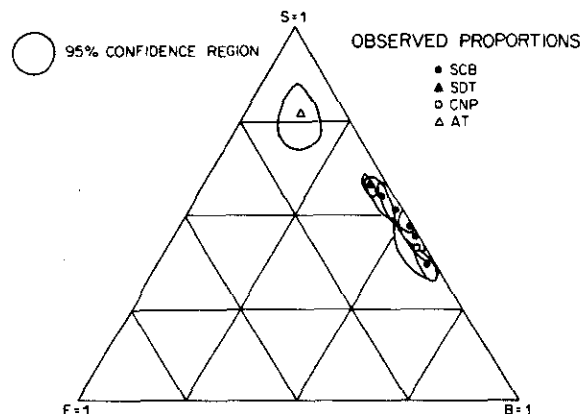


Fig. 10-5. Relative proportions (by numbers of individuals) of suspension feeding (F), surface deposit feeding (S), and subsurface deposit feeding (B) polychaetes found at the localities of Table 10-1. In all but the Aleutian Trench, surface and subsurface deposit feeders share dominance approximately equally. Modified, with permission, from Jumars and Hessler, 1976.

internally consistent set of data from the North Pacific. The curves of Fig. 10-6 were generated from this data set via the Hurlbert (1971) rarefaction procedure. This statistically rigorous method uses data from field samples to provide unbiased (Smith and Grassle, 1977) estimates of the number of species that would most likely be seen in field samples of smaller size (fewer individuals). It provides an objective means of comparing species diversity in samples of varying sizes. A high slope near the origin in the curves produced by this method indicates great evenness (equitable distribution of individuals among species), while a high asymptote represents a substantial species richness (total number of species in the community).

Several facts are apparent from the figure. First, there is high variability in deep-sea species diversity from one basin to another; while species diversity is high in some deep-sea regions, it is not uniformly so. Second, high species diversity standardized to numbers of individuals does not necessarily imply that the number of species per unit area will

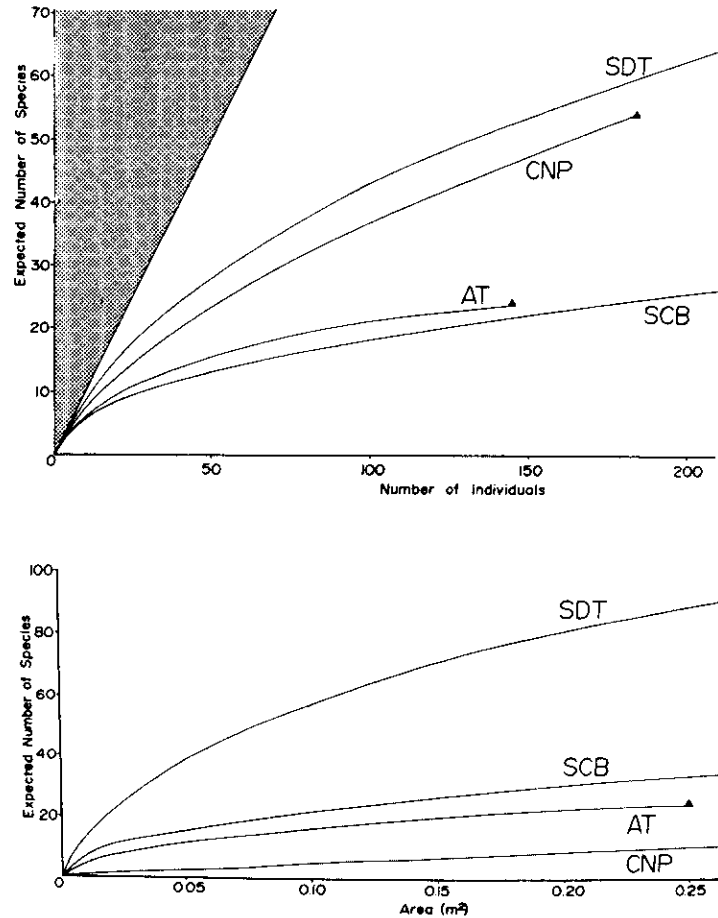


Fig. 10-6. Polychaete numerical and areal diversity at the localities of Table 10-1. Triangles: total number of species and individuals collected; stippling: region cannot be occupied. With permission, from Jumars and Hessler, 1976, Fig. 2.

be correspondingly high. Third, and not as obvious to those working in more accessible environments, is the fact that no one has fully enumerated the total species richness of any deep-sea macrofaunal community; none of the curves of Fig. 10-6, for example, closely approaches the asymptote where additional sampling would cease to provide additional species. Few authors have been foolish enough to estimate what such a total might be, but one guess (Jumars, 1975) is 177 to 212 polychaete species for the SDT, versus the 146 species (among 2125 individuals) actually sampled. The polychaetes comprise roughly half the macrofaunal species sampled there, so that one might expect the total macrofaunal community of the SDT to contain roughly  $4 \times 10^2$  species.

It is not difficult to appreciate the intrinsic problem of obtaining basic ecological information such as microhabitat preferences, food resources, motilities, predator-prey relations, or generation times to accompany a species list of this length, even without the logistical problems of deep-sea sampling and observation. Consequently, the usual sorts of correlations between species diversity and habitat diversity, trophic position, or dietary specialization have been fragmentary. Two of these fragments are nonetheless germane to the theories we will discuss. First, high species diversity has not been demonstrated in all the deep-sea guilds. Most of the species of Fig. 10-6 are deposit feeders. Diversity in deep-sea scavengers (e.g., Shulenberg and Barnard, 1976), predators (e.g., Fig. 2 in Rex, 1976), and suspension feeders is rather low by contrast. Second, the greater part of deep-sea diversity is found among the more sedentary, infaunal species (Jumars, 1975, 1976). Successful explanations of high deep-sea diversity thus must hold for the small, relatively sedentary, largely infaunal deposit feeders that comprise the majority of this diversity.

#### Size-Frequency Distribution and Population Dynamics

Among the other ecologically relevant parameters which can be measured or estimated from preserved samples are size-frequency distributions. Implicit in their estimation is the possession of a random sample of individuals with respect to body size. No piece of deep-sea sampling gear is ideal from this standpoint. Discrete samplers such as grabs and corers recover individuals which lived in close proximity to each other and may be of similar size [e.g., the maps of *Polyopthalmus* sp. (Polychaeta, Opheliidae) abundance and size in Jumars, 1978, Figs. 3 and 4]. Towed samplers such as dredges and trawls, on the other hand, have winnowing problems which are likely to eliminate selectively the smaller individuals.

Sampling problems aside, size-frequency distributions produced for deep-sea species typically have one of two forms. They may be bimodal or unimodal, but small individuals are almost invariably infrequent. While larger individuals will, on the average, be older, one must avoid the temptations to equate size increments with time increments. Figure 10-7 illustrates the difference and leads naturally to the question of population dynamics.

In many shallow-water environments, population growth and death rates may be followed by sampling a cohort, or group of organisms born at the same time, as they grow in size and dwindle in numbers. Such cohorts are tracked as moving (over time) peaks in size-frequency distributions. Most deep-sea size-frequency distributions produced for the same population over a number of seasons have, however, been monotonously

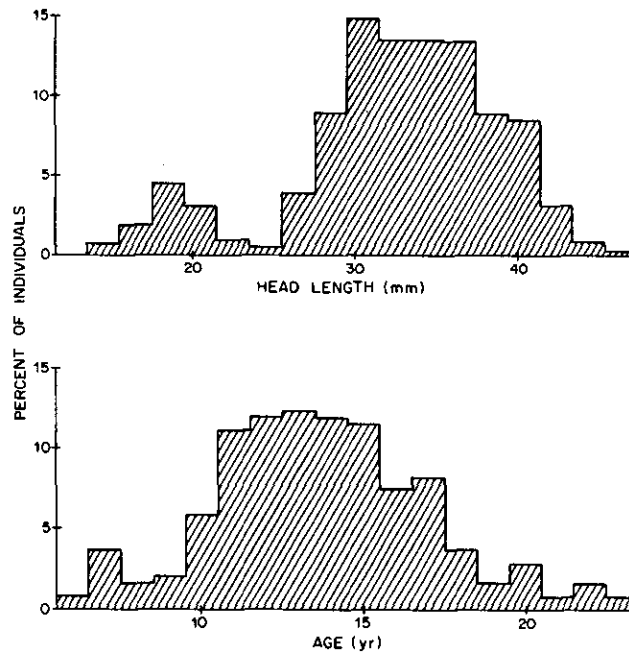


Fig. 10-7. Size-frequency and age-frequency plots for *Nezumia sclerorhynchus*, a rattail fish found in the eastern Mediterranean Sea at bathyal (300 m to over 3000 m) depths. Based on data of Rannou, 1976.

similar, without apparent cohorts. Many deep-sea populations apparently reproduce year round, producing no large, synchronized cohorts (Rokop, 1974) and closing that convenient avenue to population dynamics information.

The other major way of gaining a knowledge of population dynamics is to estimate the ages of individuals. In shallow-water species, laboratory rearing often provides the necessary estimates of age (versus growth stage or size); similar methods have been unavailable to deep-sea biologists. Alternative aging techniques have been applied to deep-sea populations in only a few cases. One example is given in Fig. 10-7 and relies on the existence of annual growth rings in the otoliths of the fish. Turekian *et al.* (1975), by contrast, used an isotopic ( $^{228}\text{Ra}$  content of the shell) chronology to establish that the generation time of *Tindaria callistiformis* (a deposit-feeding, protobranch bivalve) is about 50 y, and its life span about 100 y. Unfortunately, the (95%) confidence intervals around these estimates are quite wide, being  $\pm 76$  y for the latter estimate. Temptations to infer slow individual and population growth rates as special characteristics of the deep sea should further be tempered by long life spans documented for offshore, shallow-water species (e.g., Jones *et al.*, 1978), and by the more recent finding of Turekian *et al.*, (1979) which shows much more rapid growth rates in a (suspension-feeding) deep-sea bivalve from the Galapagos Rise. While fecundities of many deep-sea species do appear to be low, with few, relatively large ova being present at any one time (e.g., Sanders and Allen,

1973), the (unknown) frequencies of spawning must be compounded over the entire year for continuously reproducing species (Rokop, 1974) to allow comparison of reproductive rates with seasonally reproducing, shallow-water populations.

A third means of gaining information on population dynamics, namely on potential for reproduction and immigration, has been applied to opportunistic species. In these experiments, new resources (space, food) are provided and colonization is monitored. By placing wooden objects on the deep-sea floor at known times, Turner (1973) has established that some members of the genus *Xylophaga* (wood-boring bivalves) can have generation times as short as three months. In analogous experiments with azoic muds, Grassle (1978) demonstrated that *Nucula cancelleta*, a deposit-feeding, proto-branch bivalve, and *Polycarpa delta*, an ascidian, may reach maturity within two years. Seki *et al.* (1974) similarly showed that bacterial populations can grow rapidly in the deep sea, given the proper combination of bacterial inoculum and growth medium. While such demonstrations show how quickly deep-sea species *can* colonize and reproduce, the degree to which they reflect natural rates depends critically upon the degree to which they mimic naturally occurring conditions.

## PROCESSES IMPLICATED

We present three plays. They explain the behaviors of the actors in very disparate ways. The first play suggests that the characters can best be understood as individuals, the second is a study of clans, and the third submits that the players are controlled by more varied interactions among groups of characters.

By treating, successively, the individual, population, and community levels of organization, we seek by example to show that processes operating at all these levels exert control over community structure. The lengths of the respective treatments have been set by the availability of compatible data and theories and do not reflect our relative degrees of faith in explanations at the respective levels. While we will cite a large number of past theoretical studies of the problems, we are not attempting a balanced review. The latter can be found elsewhere (Gage, 1978; Rowe, in press).

### Individuals

To gain insight into the lifestyles of the individuals that comprise deep-sea communities, we will explore applications of the theory of optimal foraging. The development of optimal foraging theory has recently been summarized by Pyke *et al.* (1977). We will review a few of its basic tenets before we attempt deep-sea applications and will introduce additional complexities only as needed. The simplest and most frequently applied models assume that evolution has constrained the individual to maximize its net rate of energy gain. According to this model, the animal should engage in that foraging activity,

and at that rate, which produces the optimal balance between the rate of energy gain and the rate of energy loss (Fig. 10-8).

We do not mean to imply that individual behaviors and species' ultimate capacities for survival are governed entirely by their net rates of energy gain. Just because the rate of food supply to the deep-sea benthos is relatively low does not mean that most individuals or populations there are food limited, as we shall discuss below. The surprising degree of success of optimal foraging theory as applied to a wide variety of environments (Pyke *et al.*, 1977), however, suggests that other constraints do not carry most animals far from their energetic optima. Guild by guild, then, we shall examine the ability of foraging theory to explain the behaviors and relative successes of deep-sea species.

Suspension feeders come in two not entirely distinct varieties: active and passive. Active suspension feeders use their own energy to pump water, while passive suspension feeders rely on externally produced flows, often accentuated by their morphologies or orientations (e.g., Vogel, 1978), to carry food through or onto their food-catching devices. To a first approximation, active filterers are independent of external flow speeds and directions, being influenced only by the concentration of suspended food particles. Passive filterers, on the other hand, depend on external flow velocity and often on flow direction (e.g., sea fans) as well as on suspended load. Active suspension feeders succeed only where particle concentrations repay the costs of pumping; passive suspension feeders succeed only where particle concentrations are high enough and flow conditions are predictable and fast enough to allow use of their particular passive collectors (Fig. 10-9). Suspended particle concentrations in general decrease with depth in the deep sea, but flow conditions become more predictable. Because the energetic costs of pumping water

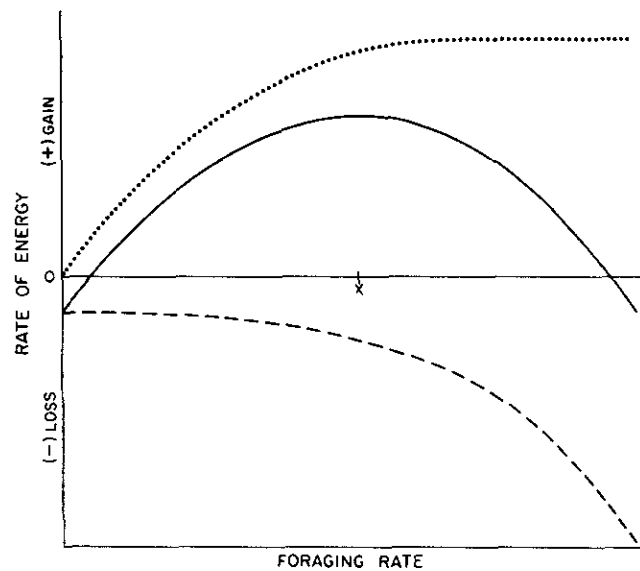


Fig. 10-8. Gross rates of energy gain (dotted curve) and loss (dashed curve) of a hypothetical individual as a function of foraging rate. An optimal forager should forage at the rate (x) which maximizes its net rate of energy gain (solid curve).



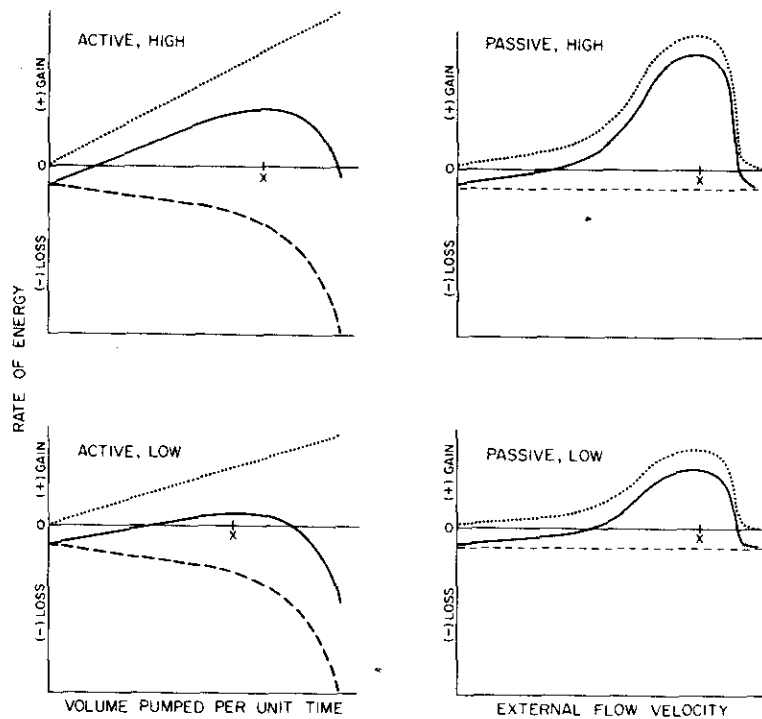


Fig. 10-9. Hypothetical optimization curves for both active and passive suspension feeders at high and low concentrations of suspended food. Symbols as in Fig. 10-8.

stay relatively constant with depth, active suspension feeders disappear as suspended loads dwindle (Jørgenson, 1966). The large suspension feeders that are most obvious in deep-sea photographs (e.g., Heezen and Hollister, 1971) all appear to be passive and to utilize the structure of the benthic boundary layer effectively.

Friction with the bottom causes physical mixing of deep-sea bottom water from ten to several hundred meters above the bottom, depending on the velocity of these bottom water masses and on bottom topography (e.g., Armi, 1978). This mixing maintains a higher suspended load near the bottom than is found in the clearer, overlying water. The near-bottom, slightly cloudier (or "nepheloid") layer typically contains 50 to 100  $\mu\text{g l}^{-1}$  of solids, a very low suspended load by shallow-water standards. The friction, however, keeps water in the thin layer immediately over the bottom (the viscous layer of Table 10-4) moving very slowly and regularly, rather like molasses (in June). Many of the passive deep-sea suspension feeders are large (such as the passively feeding groups of sea squirts; Monniot, 1979), or have long stalks (such as the glass sponges, e.g., Rice *et al.*, 1979, Pl. 5), extending them into water moving fast enough to induce flow through their feeding structures and to bring by numerous particles (per unit time) for potential capture. The younger stages of such passive filterers are often found on objects such as manganese nodules or bits of wood which protrude through and disrupt the viscous sublayer, thereby providing a means of escaping the slowest flows during ontogeny.

TABLE 10-4. Typical Structure and Nomenclature of the (unstratified) Deep-Sea Benthic Boundary Layer<sup>a</sup>

Layer Name	Distance Above Bottom (m)		Characteristics
	Lower Boundary	Upper Boundary	
Viscous sublayer	0	10 <sup>-2</sup>	Slowest, viscous flow
Logarithmic layer	10 <sup>-2</sup>	10 <sup>0</sup> to 10 <sup>1</sup>	Turbulent flow; velocity rapidly increasing with height above the bed (to 10 <sup>1</sup> cm sec <sup>-1</sup> ); most rapid mixing.
Bottom mixed layer	None usually given	10 <sup>1</sup> to 10 <sup>2</sup>	Weakly turbulent flow; mixing of suspended and dissolved constituents.

<sup>a</sup>For further details, see Wimbush (1976) and Armi (1978).

Close scrutiny of this application of foraging theory, however, leaves at least two problems unsolved. The resources utilized in the field by suspension feeders in general and by deep-sea suspension feeders in particular have not been identified clearly. This problem is not particularly severe with respect to application of the theory so long as food (now speaking only of material actually digested and absorbed) quality stays constant and its quantity remains strictly proportional to total suspended load. Secondly, if there are a few suspension feeders in the deep sea, why are they not more abundant? It is virtually inconceivable that the few existing suspension feeders could cause any appreciable decrease in the suspended resource. Either these suspension feeders select microhabitats with enhanced particle fluxes (i.e., all the good spots for larval settlement have been taken) or their abundance is controlled by factors other than foraging success (e.g., predation).

Resource identification at first seems no problem for the abundant scavengers attracted to meat bait in the deep sea. They are clearly generalists in terms of the variety of baits to which they will respond; in one experiment at 1200-m depth in the San Diego Trough<sup>1</sup> the ever-present lysianassid amphipods responded to dead fish, raw egg, and bologna with roughly equal avidity. Our observations on *Eogammarus confervicolus*, an intertidal and shallow subtidal gammarid amphipod in Puget Sound, however, suggest some caution in concluding from observations of bait that deep-sea, scavenging amphipods rely solely on such windfalls from the plankton and nekton (drifting and swimming organisms of the water column). *E. confervicolus* is attracted in large numbers to baits at least as varied as dead opossum and filamentous algae. Immunological techniques (Feller *et al.*, 1979), our visual field observations, and our laboratory experiments (unpublished), however, reveal that this species also feeds on a wide variety of smaller in-

<sup>1</sup>Jumars and Hessler, unpublished.

fauna and that many of these items are taken alive. Wolcott (1978) showed, analogously, that the beach-dwelling ghost crab *Ocypode quadrata*, which is generally regarded as a scavenger, obtains most of its food through active predation. Without similar observations on deep-sea scavengers, we cannot know what proportions of their diets come from the sinking of planktonic and nektonic remains versus dead or easily captured infauna and epifauna. Available information on deep-sea demersal (near-bottom living) fishes, however, suggests that even closely related species can differ markedly in the degree to which they depend on benthic versus nektonic and planktonic foods (e.g., Percy and Ambler, 1974), but strict specialization has not been seen.

One can argue on the basis of foraging theory that when additional experiments and observations become feasible for deep-sea scavenging amphipods that they will be found to be generalists as well, i.e., that their diets will be found to include easily captured, living fauna. The simplest optimal foraging model that leads to this conclusion is neatly outlined by MacArthur (1972). He divides foraging into four phases: deciding where to search; searching, looking out for palatable items; deciding whether to pursue a located food item; and pursuing (and possibly capturing and eating) the item. The animal should search where the expected yield is maximal; we will return to this consideration later. With respect to the third phase, "an animal should elect to pursue an item if and only if, during the time the pursuit would take, it could not expect both to locate and to catch a better item." The division of time (=energy) between search and pursuit in order to maximize energy intake is now easy to make and depends in a general way on the overall abundance of food. When food is abundant, such that food items of several kinds can be located at any time (are always in "sight"), and if more energy must consequently be spent in pursuit than in search, the animal should elect only those food items whose ease of capture and caloric content provide the greatest net gains, making it a specialist. If food is scarce, on the other hand, and most energy must be spent in searching, no easily caught and ingested food item, once located, should be passed over. The latter situation seems more likely for epibenthic scavengers in the deep sea (naturally occurring carrion rarely having been photographed or found in samples), arguing that they should be generalists.

The argument is complicated somewhat by the probably enhanced detection abilities of deep-sea predators via any one of a number of sensory modes. Deep-sea diffusion rates are relatively low, especially in the viscous sublayer, making chemical gradients more persistent in the deep sea than elsewhere. Background acoustic noise is low, making weak acoustic signals relatively easy to detect. Turbulence levels are low by comparison with shallow-water benthic boundaries, making the sorts of high-frequency pressure waves generated by prey (e.g., Ockelmann and Vahl, 1970) easier to detect. Even some visual cues may be easier to detect in the deep sea than in sunlit, near-surface waters; there is no background "noise" to hide even weak bioluminescence. While such enhanced sensory possibilities may allow more prey items to be detected in a given period than would otherwise be possible, the prey may also more easily detect and evade their predators. We will avoid such potential co-evolutionary interactions by restricting further discussion to carrion feeders. For the sake of brevity, and to tie our discussion to the preceding material, we will discuss only the chemosensory mode. We do

not deny that any of the other modes may be important (e.g., Hawkins and Rasmussen, 1978; Reid and Reid, 1974).

As implied in the mention of the first phase of foraging (above), optimal foraging theory suggests not only what should be eaten, but also what foraging pathways should be useful in finding and harvesting food. Hydrodynamics of the benthic boundary layer dictate divergent strategies for two kinds of searchers capable of detecting "prey" at a distance. Because a chemical stimulus in the viscous sublayer will move much more rapidly downstream than cross-stream, animals restricted to the bed (e.g., brittle stars or quill worms) should spend most of their search time traveling perpendicular to the flow. Once a prey item is detected, such benthic scavengers should proceed upstream (oriented movement with respect to flow being called "rheotaxis"), turning only when they fail to detect the chemical stimulus. Time-lapse photographs of scavenging ophiuroid movement in response to bait should demonstrate such behavior. Scavengers capable of swimming or hovering off the bed (and out of the viscous layer) might adopt quite a different strategy, more akin to that used by mosquitoes for long-distance host location (e.g., Kennedy, 1939). Just as the passive suspension feeder can use the energy of the external flow to avoid energy expenditure in pumping, the hovering scavenger can use turbulent mixing within the bottom mixed layer to bring the chemical signal from a food parcel sitting on the bottom. The fact that this chemical plume is widened and extended vertically by turbulent mixing downstream of its point source (much the way the smoke from a smokestack broadens in both vertical and horizontal extent downwind) means that the scavenger (or mosquito) need not be directly downstream of (or at the same vertical elevation as) its respective food item in order to detect it. The optimal forager should hover if the improved detection ability provided by turbulent diffusion provides otherwise undetected food in excess of the additional energetic costs of hovering and pursuing the food item from the chosen hovering height. Such hovering costs can be reduced and amortized by using buoyancy mechanisms such as fat bodies or gas bladders.

What should this hovering height be? We assume that a piece of carrion emanates a chemical signal proportional in strength to its size. We further assume that a threshold concentration for detection exists below which the carrion cannot be sensed. Above this threshold concentration, we assume that the stimulus elicits a pursuit response which might be as simple as positive rheotaxis (moving upstream) in conjunction with a positive geotaxis (swimming downward), with more frequent turning when the signal is lost. Similar mechanisms, as alluded to above, have been demonstrated in insects (Shorey, 1977). Note that we do not invoke a chemical gradient as a necessary prerequisite of this location mechanism; such gradients are unlikely in the presence of turbulent mixing. Given the threshold concentration for response, however, larger pieces of carrion can be detected at greater distances from the seabed and at greater distances from the source of the stimulus. The optimal hovering height can then be deduced by analogy with the optimal foraging height in visually searching buzzards or with optimal perching height in kingfishers (MacArthur, 1972, pp. 67-68; refined and extended by Orians and Pearson, 1979). Just as a kingfisher should perch at the height from which "the greatest number of grams of fish per day can be captured," so should the scavenger hover. This height will depend upon, among other parameters, the effective vertical diffusion rates of the

chemical stimulus and the size-frequency distribution of carrion. If competition for carrion is prevalent, then swimming speed of the scavenger (Hessler and Jumars, 1974) and its ability to sequester food once it has arrived would also be important. Whereas catches of scavengers above the bottom have been interpreted as being due to attraction of scavengers off the bed (e.g., Smith *et al.*, 1979), we suggest instead that these scavengers may spend most of their time hovering well above the bed. We would predict that larger scavengers, which could more effectively sequester large food parcels, would hover higher above the bottom and that larger pieces of bait would attract animals from higher in the water column. Animals hovering higher above the bed must, however, spend more time and energy pursuing a detected item than do scavengers hovering lower in the water column. Hence, based on the four-phase foraging model presented above, we would predict that scavengers further from the bed would be more specialized and less likely to prey incidentally on easily captured benthic individuals.

Geographic variation in the structure of the benthic boundary layer would also be expected to influence foraging strategies of hovering scavengers. Increased turbulence intensity could decrease optimal foraging height above the bed by decreasing the height above the bed at which threshold concentrations for detection would be reached and might increase the locomotory costs of hovering. Decreased turbulent mixing, on the other hand, might decrease the advantage of higher hovering in a rather different way. If upward diffusion were very slow, carrion could be detected and consumed by lower-hovering or epibenthic scavengers before it could be detected higher in the water column. Thus, it is tempting to speculate that the apparent absence of fishes and other large (presumably hovering) scavengers in trenches (Hessler *et al.*, 1978) is due to the weak currents thought to prevail there (Bishop and Hollister, 1974).

Geotaxis and rheotaxis toward upstream prey, however, is not the only conceivable pursuit strategy that could be used by a hovering scavenger. Hamner and Hamner (1977) have documented that neritic zooplankton can detect sinking carrion by following the scent trail left during settling through the water column. Despite the relatively low eddy diffusion rates in the deep sea, we do not feel that the flux of large particles arriving in the deep sea is sufficient to give a hovering scavenger a reasonable probability of detecting such an item during its fall. Even in the deep sea, a vertical scent trail would dissipate in a matter of minutes. Carrion on the bed, by contrast, would emanate a chemical plume for hours or even days, depending on its size and rate of consumption.

We can find fewer explicit predictions to apply to deep-sea deposit feeders than we have generated for scavengers for several intertwined reasons, the majority of which apply to shallow water as well as to the deep sea. First, foraging theory for deposit feeders is in its infancy (Levinton and Lopez, 1977; Taghon *et al.*, 1978). Second is the recurrent problem of identifying the resources used and the resource axes on which particle selection might occur (Self and Jumars, 1978). Third, infaunal deposit feeders are difficult to observe directly, even in shallow water. Consequently the applications we propose are even more tentative than those for suspension feeders and scavengers. Sessility in deposit feeders is feasible only if the morphologically available (e.g., via tentacles) foraging area provides resources at a sufficient rate to meet metabolic demands (Jumars and Fauchald, 1977), either by microbial renewal *in situ* (Levinton, 1972; Levinton and Lopez, 1977),

or by advection. The prevalence of motility among the deposit feeders of food-poor deep-sea regions (Fig. 10-10) suggests that the requisite renewal rates are not met there in general.

Assuming that the resource (e.g., microbial coatings on sediment grains) is renewed slowly, what sorts of foraging strategies should be successful? Foraging theory suggests that the animals should move in such a fashion as to minimize ingestion of deposits from recently depleted foraging sites. One way of accomplishing this goal is to produce fecal pellets that either by virtue of location (e.g., vertical stratum in the sediments) or of physical-chemical characteristics (e.g., size) are unlikely to be ingested. Another, not necessarily mutually exclusive, method available to motile deposit feeders is to avoid returning to recently foraged areas. We know of foraging pathway evidence for only two deep-sea feeders, enteropneusts and herd-forming urchins. [See Kitchell (1979), however, for a stimulating discussion of fossil and deep-sea foraging trails irrespective of their producers.] Enteropneusts [acorn worms] appear to avoid crossing their feeding trails (e.g., Fig. 4 in Thiel, 1979). They may, however, turn more tightly in response to encountering food-rich deposits (e.g., Risk and Tunnicliffe, 1978), which may account for the interspersion of relatively straight tracks and tightly coiled ones. Herds of the urchin *Phormosoma placenta* on the continental slope, as described by Grassle *et al.* (1975), may form and move as an alternative solution to the recrossing problem (as Grassle *et al.* imply). Cody (1971, 1974) studied finch flocks in the Mohave Desert and hypothesized that they were "return time regulators," minimizing the variance of the time intervals between successive visits to a foraged area and adjusting the mean return time to a given area to match the rate of resource renewal in that area. The precise predictions of the flock turning frequency in Cody's model are heavily dependent upon the size of the habitat and the turning behavior of the flock at the boundary of the habitat (Pyke, 1978; Pyke *et al.*, 1977). We cannot even hazard a guess for either of these crucial parameters for *Phormosoma* and so are unable to make predictions in terms of precise turning frequency. In the absence of any boundary, there is nothing in the

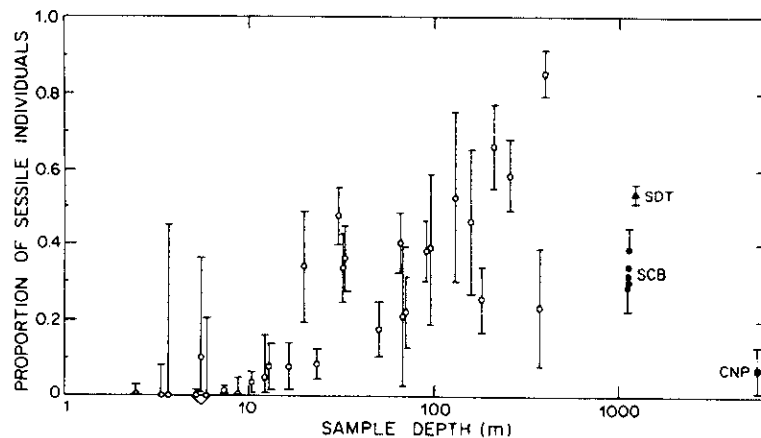


Fig. 10-10. The proportion of sessile polychaete species as a function of depth offshore from southern California. Bars indicate 95% confidence intervals. Modified, with permission, from Jumars and Fauchald, 1977, Fig. 7.

theory of optimal foraging pathways that would preclude the herd traveling in a straight line. If there is a boundary which necessitates *Phormosoma* returning to previously foraged areas, the pattern of turning and the rate of return to a given area should be coupled with the resource renewal rate. Herd size should also be proportional to the degree of resource limitation. With no resource limitation, herds should not form, while herds should increase in size with increasing resource limitation. We realize that there are a considerable number of explanations, other than optimal foraging, that could be invoked to explain the herding behavior of *Phormosoma*, including avoidance of predation and reproductive aggregation. We have opted for the present explanation to complete our survey of applications of foraging theory to the entire spectrum of major deep-sea guilds and to offer some predictions which might be testable in the deep sea.

## Populations

At the population level, there is a particularly wide variety of often conflicting theories from which to choose (Stearns, 1976). We will avoid the more elaborate treatments of age-specific reproductive behaviors in order to avoid a gross mismatch in detail between theory and available deep-sea observations. We will again utilize an optimization approach, but rather than maximizing net rate of energy gain by an individual, we will maximize either population growth rate or the probability of long-term persistence of a population.

Despite the controversy surrounding its application (e.g., Stearns, 1977), we will first introduce the concept of “*r*” versus “*K*” selection. These terms derive from the usual symbology in the (Verhulst-Pearl) logistic equation (Wilson and Bossert, 1971) (Fig. 10-11), which has been reasonably successful in describing the growth rates of many

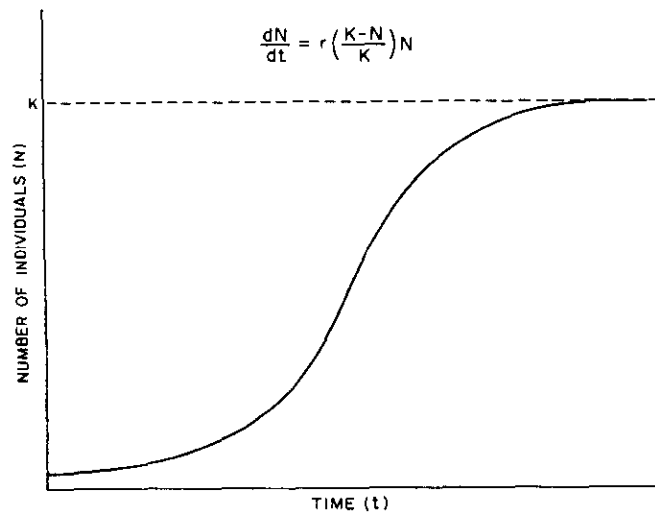


Fig. 10-11. Graph of the logistic equation, which is the basis of *r-K* selection theory. *K* is the carrying capacity, while *r* is a measure of the potential rate of population growth.

laboratory and field populations. Populations which are disturbed so frequently that they rarely approach their carrying capacities (population levels supportable by the available resources) ensure their persistence by investing much of their energies into reproduction, (i.e., into maximizing  $r$ ). A particularly lucid mathematical treatment of the critical frequency of disturbance is given by Southwood *et al.* (1974), but we will avoid such details, again due to the lack of applicable deep-sea data. The most effective methods for achieving high population growth rates have been recognized for some time (Table 10-5).

Optimal means for ensuring persistence of populations which frequently approach their respective environments' carrying capacities, on the other hand, are not agreed upon with comparable unanimity (Stearns, 1977). While agreement as to the specific life history tactics which achieve this end most effectively is lacking, it is clear that, if the carrying capacity stays constant, ( $K$ ) selection will favor the population that keeps its abundance as high and as constant as possible from generation to generation (Table 10-6). Part of the problem in defining optimal life-history tactics of such a "K strategist" is that both intraspecific and interspecific competition are likely to occur as populations approach their carrying capacities, and similar population behaviors may not be optimal under both sorts of competition: The component problems of zero population growth are complex and may have competing solutions.

While it would thus be difficult to decide whether species are  $K$  selected, it may be easier to assess whether or not they are  $r$  selected. Grassle and Sanders (1973) undertook this sort of analysis for deep-sea benthos (a term including all organisms that live in the benthic environment) and concluded that deep-sea species in general have smaller clutch sizes than do comparable shallow-water species, even when corrected for the relative sizes of the animals. They pointed out, however, that the time markers needed to assess any of the other population growth enhancing methods of Table 10-5 are generally lacking. In addition, it is becoming ever clearer that there are some deep-sea environments that are more ephemeral or variable than others, e.g.: logs utilized by boring bivalves and their associates (Turner, 1977); hydrothermal vents utilized by suspension feeders and their associates (Ballard, 1977); catastrophic, avalanche-like ("turbidite") deposits which decimate local populations but whose organic contents subsequently can be mined by deeper burrowers (Griggs *et al.*, 1969); regions of at least occasionally erosive flow velocities (Gage, 1977; Greenwalt and Gordon, 1978); and areas of fluctuating oxygen concentration (e.g., some of the bathyal basins discussed by Emery, 1960). Hence, the

TABLE 10-5. Life-History Tactics Enhancing Population Growth Rate ( $r$ ), Listed in Generally Decreasing Order of Effectiveness (the first is by far the most effective)<sup>a</sup>

- 
1. Decrease age at first reproduction.
  2. Increase number of individuals per clutch.
  3. Increase number of clutches born per unit time.
  4. Increase reproductive lifespan.
  5. Reduce prereproductive mortality rate.
  6. Reduce mortality rate of reproductive stages.
- 

<sup>a</sup>After Cole, 1954.



TABLE 10-6. Example of *K* Selection<sup>a</sup>

Popu- lation	Initial Size (no.)	Calculation of Reproductive Success Over Time Interval		
		Time 0 to Time 1	Time 1 to Time 2	Time 2 to Time 3
A	1000	$1.1 \times 1000 = 1100$	$1.0 \times 1100 = 1100$	$0.9 \times 1100 = 990$
B	1000	$1.5 \times 1000 = 1500$	$1.0 \times 1500 = 1500$	$0.5 \times 1500 = 750$

<sup>a</sup>Note that although both populations on the average leave one individual for each individual starting a time interval, the population with less variation in reproductive success (Population A) leaves more progeny in the long run.

ability to make sweeping generalizations for the entire deep-sea fauna should not be expected.

In attempting to apply *r-K* selection models, we thus again run headlong into two poorly answered questions which arise in each of our three theoretical sections, namely, "What are the resources utilized by each of the deep-sea guilds, and what sorts of disturbances (if any) depress deep-sea populations below their respective carrying capacities?" Levinton (1972) has presented some cogent arguments that deposit feeders will, by virtue of being buffered from environmental variability by the sediments, experience less environmental variability than will suspension feeders. How stable the resource supply for scavengers might be is unknown; it depends on the rate of carrion production (or arrival) within areas of the size in which individuals forage. The succeeding discussion, then, will be restricted implicitly to deposit feeders, the group for which small clutch size and relatively low abundance of juveniles hold most surely (Grassle and Sanders, 1973), and to the physically stable regimes typical of the abyss.

Grassle and Sanders (1973), in response to Dayton and Hessler's (1972) suggestion that predation regulates population size of the smaller deep-sea species, cite the aforementioned small clutch size of and the preponderance of larger (older) life stages as evidence that neither predation nor any other sort of disturbance is likely to exert a strong effect on life-history traits in the deep sea. We suggest, alternatively, that this size-frequency distribution can arise precisely because of the sort of size-selective predation that Dayton and Hessler (1972) hypothesize. Briefly, Dayton and Hessler suggest that the deep-sea benthos is comprised largely of generalist "croppers," animals that will eat any food item small enough to ingest. Deposit feeders dominate the benthos, and there is little reason to think that they would (or could) reject larvae and small juveniles from the items they select for ingestion (Isaacs, 1976; Self and Jumars, 1978).

We begin, in development of an alternative to *K* selection for explaining the albeit meager data on deep-sea life-history traits, at the same deep-sea environmental feature that provides a springboard for Dayton and Hessler (1972) as well as for Grassle and Sanders (1973)—the extreme physical constancy of the deep-sea milieu. We find no compelling reasons (and certainly no data) to suggest that predation is more intense, in an absolute sense, in the deep sea than elsewhere among benthic environments. Temperature, salinity, and oxygen stresses capable of killing adults as well as juveniles are all but absent, however, making predation *relatively* more important as a mortality source. Particularly

because deposit feeders are generally selective of smaller particles (Taghon *et al.*, 1978), we concur with Dayton and Hessler (1972) that small forms are exposed to more intense and more diverse predators (more mouths accommodating them) than are larger ones. Hence, larvae and juveniles of deep-sea species will be subjected to higher mortality rates, and likely also to more variable mortality rates, than will adults. To reiterate, the essential difference between shallow water and deep sea is that the relatively more frequent and severe environmental variations (capable of eliminating both adults and juveniles indiscriminately) in shallow water mitigate the predation-produced disparity between adult and juvenile mortalities.

The simplest model we can find that will evoke this behavior is that of Charnov and Shaffer (1973), as lucidly summarized by Schaffer and Gadgil (1975). We use the symbols (slightly modified) from the latter reference as follows (all per unit generation time):

- $\lambda$  = the rate at which a population multiplies
- $B$  = the number of larvae produced
- $c$  = the probability that a larva survives to reproduce
- $p$  = the probability that an adult survives (through one generation time)

For a population in which the adult dies upon shedding gametes (denoted by the subscript "s," for semelparity or one reproductive event per adult), then  $\lambda_s = cB_s$ . For a closely related species (i.e., one having no difference in  $c$ ) surviving beyond first reproduction (subscript "i" for iteroparity or repeated reproduction), the reproductive rate is  $\lambda_i = cB_i + p$ . What condition, then, is necessary for  $\lambda_i > \lambda_s$ ? It is  $B_s < B_i + p/c$ . By our previous arguments,  $p/c$  is higher in the deep sea than in shallow water, making multiple reproductions (iteroparity) and relatively higher abundances of adults more likely in the deep sea.

If the greater diversity of predators to which juveniles are susceptible or some other biogenous variability (Jumars, 1975, 1976) makes juvenile mortality also more variable than adult mortality, then the relative fitness of the iteroparous form is increased further. Let  $\bar{\lambda}$  = the mean (per generation time) rate of multiplication, and let the probability of larval survival be  $c(1 + q)$  in "good" times and  $c(1 - q)$  in "bad" (where  $1 > q > 0$ ). Then

$$\begin{aligned}\bar{\lambda}_s^2 &= (1 + q) cB_s (1 - q) cB_s \\ &= (1 - q^2) c^2 B_s^2\end{aligned}$$

and

$$\begin{aligned}\bar{\lambda}_i^2 &= [(1 + q) cB_s + p] [(1 - q) cB_s + p] \\ &= (cB_i + p)^2 - q^2 c^2 B_i^2\end{aligned}$$

Then for  $\bar{\lambda}_i$  to exceed  $\bar{\lambda}_s$ , it follows that

$$B_s^2 < B_i^2 + \frac{2cpB_i + p^2}{c^2(1 - q)^2}$$

Hence, the larger variability ( $q$ ) in survival of larvae, the more likely it is that this inequality will hold, and the iteroparous population will be favored.

Besides favoring iteroparity and consequently greater standing stocks of adults, more intense and more variable predation on larvae and juveniles will favor evolution of fewer, larger progeny (Schaffer and Gadgil, 1975) and will favor rapid growth past the predation-susceptible sizes (Connell, 1975; Lynch, 1977). Unfortunately, in terms of providing an unequivocal test of whether predation is an important cause of the evolution of low fecundity, with few large progeny per clutch in deep-sea species, the theory of  $K$  selection (Gadgil and Solbrig, 1972) and other considerations of increased competitive demands on young stages (e.g., Harper *et al.*, 1970; Schaffer and Gadgil, 1975) suggest that these same life-history tactics will result from the evolutionary pressures of competition.

Whatever its ultimate and proximate causes, the existence of few large larvae, often without any obviously free-swimming stages, in deep-sea species (i.e., in the majority of deposit feeders of physically stable regions) suggests a limited requirement for long-distance dispersal. Suitable habitat for deposit feeders is more or less continuous and easily accessible, physically caused disasters are rare, and the environment may be as variable on small scales (10 cm) as on large scales (km) (Jumars, 1976, 1978). Both long-term and short-term selective forces for high dispersal ability (summarized by Strathmann, 1974) thus appear to be lacking. Exceptions to this generalization are again to be expected in the more ephemeral and unstable deep-sea habitats.

## Communities

So much theory has been written about deep-sea community structure—and with so little consensus—that we would be remiss to omit at least a brief review before entertaining the theory we regard as the best contender for providing new insights. Most of this past discussion has centered on species diversity, and so will ours. The application of theories to the empirical finding of high deep-sea diversity has been a meandering process and has treated phenomena on both evolutionary (Slobodkin and Sanders, 1969) and ecological time scales (Dayton and Hessler, 1972). We will limit our attention primarily to what we interpret to be the focus of recent discussions of factors potentially maintaining (rather than producing) high deep-sea diversity, (i.e., to ecological rather than evolutionary time scales). Initially we will address three questions: Are diverse deep-sea assemblages resource limited? If so, how is the resource partitioned? If not, how is resource limitation for these diverse assemblages prevented?

Early theoretical treatments (i.e., Sanders, 1968, 1969; Slobodkin and Sanders, 1969) assumed that competition is a strong structuring force in communities inhabiting stable environments and hence that resources are indeed limiting these deep-sea populations. Various resource partitioning mechanisms were invoked (Slobodkin and Sanders, 1969, p. 86): "We might expect stenotopy, complex behavior of rather specific and stereotyped kinds, and the possibility of specialization to specific foods, hiding places, hunting methods, and environmental periodicities—in short, to the details of the most significant parts of its environment." Dayton and Hessler (1972) challenged the assumption of resource limitation. They suggested that if resource partitioning occurred, it

would be unlikely to occur on the basis of habitat (space) or time "because of the high physical homogeneity, both temporally and spatially, of the deep-sea environment" (*op. cit.*, pp. 199-200). Hence, they reasoned that measures of food-type specialization would provide a test of whether food resources were indeed limiting for most deep-sea populations—that the documentation of catholic taste would support the view that most deep-sea populations are limited by predation, whereas the finding of specialized diets would support the alternative position.

Grassle and Sanders (1973) rebutted the idea that most deep-sea populations are predator controlled, mainly by citing life-history data. They suggested that (p. 644), "In a community that is intensively cropped (or suffers a sustained mortality from any source), the population of prey species will be composed preponderantly of younger stages." We have discussed alternative interpretations of the general rarity of smaller life stages above. Size-frequency histograms cannot refute unequivocally the limitation of populations by predation.

Grassle and Sanders (1973) suggested, however, that food-type specialization is not the only likely resource partitioning mechanism. As they proposed, subsequent study (reviewed by Jumars and Eckman, in press) has revealed a great deal of spatial inhomogeneity and has implicated local successional series (Richerson *et al.*, 1970) in structuring the benthic community. Jumars (1975, 1976) has argued that a large part of the environmental heterogeneity is biogenous and that the deep-sea environment is unusual in permitting relatively fragile, small-scale structures (e.g., animal tubes and burrows) to persist without physical homogenization. Thistle (1979) tested this hypothesis and found that at least part of the diversity of harpacticoid copepods in one deep-sea community may be attributed to microhabitats provided by other animals. The existence of environmental heterogeneity vitiates the proposed critical tests of Dayton and Hessler (1972). If food is limiting, one would expect habitat specialization and not food-type specialization or resource partitioning by time of feeding (Schoener, 1974); an animal can obtain more food by feeding in a habitat or microhabitat which is not depleted by its competitors. In fact, population limitation by predation would probably permit more food-type specialization among the limited populations by leaving more resources and more kinds of resources available—exactly the reverse of Dayton and Hessler's predictions.

To demonstrate the complexity of the above issues alone, we have, however, omitted one critical question from our list: Whichever mechanism prevents competitive exclusion, how is a higher diversity maintained in the deep sea than in shallow water? We can envisage four possibilities: (1) Resources are more finely partitioned due to refined biological interactions (Slobodkin and Sanders, 1969) in the deep sea; (2) predators are somehow more effective at controlling populations in the deep sea (implicit in Dayton and Hessler, 1972); (3) some combination of these two explanations holds; or (4) neither predators nor competitors are appreciably different in shallow water versus deep sea, but the unique deep-sea environment somehow affects the interactions to maintain high species diversity.

We have already suggested that if finer resource partitioning occurs in the deep sea than elsewhere, it is probably accomplished on the basis of (micro)habitats. The arguments for increased efficacy of predation in the deep sea are homologous with our previous reasoning with respect to the increased importance of size-selective predation.

If predator populations are more rarely or never decimated by physical disturbances, predation becomes a relatively more important source of mortality, and prey become less likely to escape predator control and thereby to risk competitive exclusion (Dayton and Hessler, 1972; Connell, 1975). In support of such reasoning, Dayton and Hessler (1972) and Menge and Sutherland (1976) show that deep-sea species of lower trophic levels are more diverse, and Rex (1977) provides indirect evidence (via their weak patterns of zonation) that infaunal deposit feeders are kept below population levels at which strong competition occurs.

Huston (1979), in  $r$  and  $K$  terms, gives a more mechanistic explanation of deep-sea predator efficacy. He points out, assuming an abundant supply of species with an assortment of life histories, that dynamic equilibrium maintaining relatively high species diversity will be produced by a particular balance between population growth rates and (density-independent) disturbance rates. What would be special about deep-sea predator-prey relationships would be this balance between predation rate and prey population growth rate. If population growth rates of prey are slow, then the highest species diversity can be maintained by a relatively modest predation rate. Where growth rates are higher, as suggested for hydrothermal vents by Turekian *et al.*'s (1979) data on clam ages, a higher disturbance rate would be necessary to maximize species diversity via Huston's (1979) dynamic equilibrium process.

For lack of an appropriate theory, we will not discuss the possibility that both predation and resource specialization in concert are effective in promoting high deep-sea diversity. We will, however, discuss how physical habitat differences may make both predation and competition less effective at eliminating deep-sea species. This discussion is in the spirit of the "neutral model" of Caswell (1976). While in our chronological development of deep-sea diversity theory we have left the question until last, it should probably be asked first, i.e.: Can one develop a reasonable model explaining higher species diversity in the deep sea versus shallow water without invoking any differences either in the processes of resource partitioning via competition or in predation? The need for discrediting a neutral model that could account for this phenomenon—without invoking special biology—can be likened to the need for rejecting the null hypothesis in statistical hypothesis testing. Why invoke the special when the ordinary will do?

There is reason to suspect (Jumars and Eckman, in press) that the deep seabed may exhibit more environmental heterogeneity on small scales than do shallow, soft substrata. Increased environmental heterogeneity is perhaps the single most universally accepted correlate of higher species diversity. As Menge and Sutherland (1976) discuss in the context of marine benthos, such environmental heterogeneity buffers against competitive exclusion by making resource partitioning on the basis of habitat more likely and buffers against overexploitation by predators by providing structural (habitat) refuges for prey. If the deep sea is indeed a more heterogeneous environment than the physically homogenized shallow seabed, then there is good reason to expect both predation and competition to be less effective at eliminating species.

Osman and Whitlatch (1978) formalize such a patch model for species diversity. They also deal with processes over evolutionary time, but we will consider only their discussion of relatively short-term dynamics. Their model suggests that deep-sea species diversity will depend heavily on four parameters, i.e., areal extent of the community in question, patch sizes within it, disturbance (patch-clearance) rates, and animal motilities

(dispersal rates among patches). The dearth of estimates for any of these parameters is sobering, but Jumars (1976) has argued on the basis of spatial sampling that the typical deep-sea "patch" may, for lack of physical disturbance, be close in size to that of the individuals which comprise the community; the relevant patch size or extent of a given microhabitat in the deep sea may be the area occupied or influenced by a single individual.

Connell and Slatyer (1977) recently have presented a model of succession that is uniquely suited to this spatial scale. They conceptualize succession as an individual-by-individual replacement process; given that a spot is occupied by species *X*, there is a finite probability that at the next time of observation it will be occupied by species *Y*. Their family of models subsumes the various possibilities discussed above and again points toward the kinds of data that desperately are needed for the deep sea. We find Markov representation a convenient means of formalizing their models, as can be illustrated with the classical ("facilitative" in Connell and Slatyer's terms; meaning that early colonists make the environment more suitable for later colonists and less suitable for themselves) picture of succession (Fig. 10-12).

We will not introduce the Markov approach in detail; little would be added to the conceptual content. The best such introductions we know of are the classic text by Kemeny and Snell (1960) and the considerably shorter but quite intriguing version by Roberts (1976, Chap. 5). A selection of past applications of Markov models to succession can be found in Horn (1975, 1976), Maynard Smith (1974, Chap. 6), and Kauppi *et al.*, (1978). Knowing the short-term ("transition") probabilities that one species will be replaced by another or that the space occupied by the individual will be vacated, one can easily (via elementary matrix algebra) calculate the long-term (dynamic) equilibrium composition of the community, as well as numerous other ecologically interesting parameters (e.g., the mean time between successive occupations of a spot by a given species).

To show what may be a more realistic Markov model of succession in the deep sea, we present Fig. 10-13, which bears a vague resemblance to Dayton and Hessler's (1972) "cropper" model. A location occupied by species *A* can be invaded and taken over by any other species because all the others can eat *A*. *B* can be eaten only by *C* and *D*, and *C* can be eaten only by *D*. *D* is the largest, and *A*, the smallest of the species. Con-

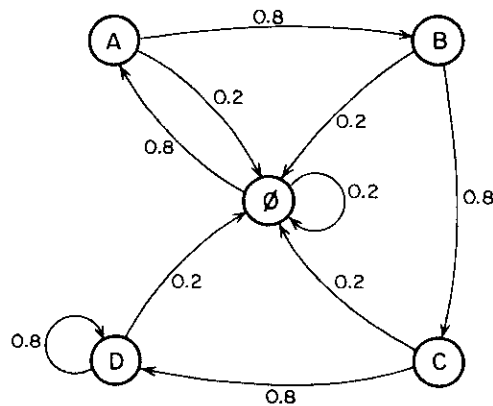


Fig. 10-12. Diagram of Markovian transition probabilities representing the classical (though suspect) picture of succession, wherein species *D* succeeds *C* succeeds *B* succeeds *A* unless some disturbance clears the space occupied by any of these individuals ( $P = 0.2$  in this example), leading to an empty space ( $\emptyset$ ) and restarting the succession. See also Table 10-7.

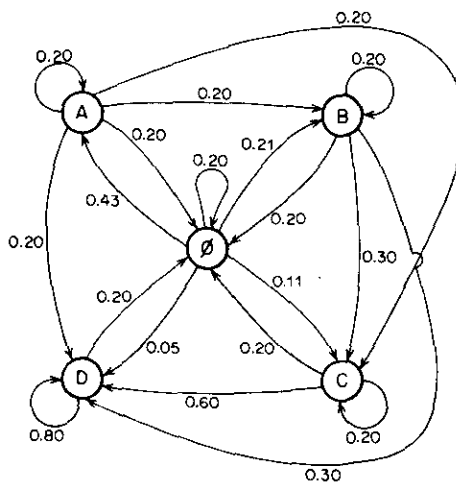


Fig. 10-13. Diagram of Markovian transition probabilities for a hypothetical community wherein species *A* is the best colonist ( $P = 0.43$ ) of cleared space ( $\emptyset$ ), and *D* is the worst ( $P = 0.05$ ). Species *A*, however, is also the most easily displaced, while no other species can displace *D*. See also text and Table 10-7.

sequently (viz., Fenchel, 1974), we make *A* the best colonist of unoccupied territory and *D*, the worst.

The importance of knowing the details of such transition probabilities is then illustrated by comparing the hypothetical communities of Figs. 10-12 and 10-13 under varying disturbance rates. While the communities are similar in equilibrium composition when the probability that any space will be cleared is 0.20, increasing the disturbance rate (transition probability to the vacant state) has decidedly different effects on the communities (Table 10-7); the change in the community of Fig. 10-12 is far more severe. Eliminating disturbance entirely, however, has exactly the same effect on the equilibrium compositions of both communities (Table 10-7).

We could present a wide variety of alternative Markov models to correspond with the various views of deep-sea community organization presented above, but the present examples (Figs. 10-12 and 10-13, Table 10-7) suffice to illustrate several salient facts. Neither these transition probabilities nor the biological processes determining them

TABLE 10-7. Equilibrium Composition of the Two Communities Depicted in Figs. 10-12 and 10-13 as the Probability of Disturbance Is Altered (and all other transition probabilities are changed proportionately)<sup>a</sup>

Community of Fig.	Probability of Disturbance	Relative Abundance of Species			
		A	B	C	D
10-12	0.00	0.0	0.0	0.0	1.0
10-12	0.20	1.6	1.3	1.0	4.0
10-12	0.80	80.0	16.0	3.0	1.0
10-13	0.00	0.0	0.0	0.0	1.0
10-13	0.20	1.3	1.0	1.0	6.6
10-13	0.80	3.1	1.7	1.1	1.0

<sup>a</sup>The 0.20 probability level of disturbance is illustrated in the figures.

(e.g., competitive or predator-prey networks, other kinds of disturbances causing mortality, and the spatial extents and frequencies of such biotic and abiotic disturbances) are well known for any deep-sea community, and without them the results of manipulative experiments (e.g., caging to exclude certain predator-induced disturbances) will be difficult to interpret (cf. Table 10-7, and Paine, 1979).

## CONCLUSIONS AND FUTURE DIRECTIONS

In our opinion, the first play is the best, and the second is the worst. Optimal foraging theory appears to have the power for generating a large number of predictions which can be tested in the foreseeable future. The most detailed predictions are now possible for scavengers. The weakest predictions concern deposit feeders; more detailed information on their food resources and their foraging methods and on the way these characteristics vary among species is certainly required for more definitive applications of the theory. Such information, however, is also lacking for shallow-water animals in the same guild, and it would seem foolish for purely logistical reasons to attempt a deep-sea answer first.

In the case of optimal life-history tactics, both adequate theory and adequate data are lacking. As Stearns (1976, 1977) points out in his reviews, there is no generally accepted theory to explain life-history tactics. Tests of the  $r$ - $K$  models in accessible environments continue to be ambiguous; part of the results supports the theory, while other parts refute it, though the refutations have not been strong enough to discredit the approach entirely. Easily manipulated systems, i.e., populations outside the deep sea, should be used to test the multiplicity of models (Stearns, 1977). With the theoretical understanding of deep-sea populations blocked by the plethora of competing theories, the dearth of time (age) markers in deep-sea populations all but closes the door to an alternative, empirical approach.

At the community level, Connell and Slatyer's (1977) individual-by-individual successional models, especially as formalized through a Markovian approach, deserve further consideration for deep-sea application and manipulative testing. Such applications and tests are unlikely to be possible, however, without a knowledge of predator-prey and competitive relations. The latter, in turn, are not likely to be discovered until the resources utilized by the ubiquitous deep-sea deposit feeders are better identified. Again, the deep sea seems to be a poor place to try out new methods for determining these ecological unknowns, when they are nearly as poorly understood for shallow-water deposit feeders (e.g., Feller *et al.*, 1979; Self and Jumars, 1978).

At each biological level of organization, however, the physics of the deep-sea environment is seen to provide potential explanations of phenomena for which other, biological explanations have been used or sought. The physical structure of the deep-sea benthic boundary layer may allow unique foraging tactics among scavengers and certainly does limit viable suspension feeding methods. At the population level, the reduced incidence of physically mediated disturbances capable of causing size-independent mortality may cause size-selective predation to be a relatively more important phenomenon in the deep sea than it is in shallow water. At the community level, in turn, relatively



weak bottom currents allow the persistence of biologically generated environmental heterogeneity (e.g., fecal mounds, tubes, burrows) which may facilitate the persistence of higher species diversity than generally is seen in shallow-water communities. Just as biology can influence the survival and persistence of particular species in physically disturbed environments (e.g., Menge and Sutherland, 1976), so can physics influence the survival of deep-sea species.

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