

*Concepts in
Biological Oceanography*

AN INTERDISCIPLINARY PRIMER

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Introduction

Biological oceanography is the branch of environmental science whose goal is to predict what kinds of organisms will be found in what abundances where and when within the sea. Its methods are diverse, but its general approach is to identify patterns of organism distribution in space and time, to identify the processes that account for the distributions and their changes, and to quantify those processes. Besides curiosity, sharpened by casual observation at sea, there are many reasons why nonbiologists might wish to understand them. Biota influence the ways that surface waters absorb light and are heated. Organisms interact strongly with optical and acoustical transmission in general. They afford subtle, time-dependent, non-conservative tracers of water movement. Both macroscopic and microscopic organisms change the erodibility of sediments. Biota alter grossly the distributions of marine chemicals. Biological processes determine the pathways, rates of transfer, and ultimate effects of pollutants.

Among specific approaches within biological oceanography, empirical-statistical methods of mapping and correlation have seen heavy use, as they have in other branches of oceanography. Observation, directed explicitly by models or implicitly by previous findings, is a key approach to initial understanding of natural systems in biological oceanography as in all environmental sciences. The idea of "natural experiments" has been borrowed from general ecology—to test one's understanding of cause and effect by finding either cases outside the normal range of variability or unique combinations of driving variables not previously encountered. Does one, for example, understand the controlling processes well enough to predict population responses and community structural changes after a hurricane or a sudden, parasite-caused die-off of a given species? In this sense natural experiments are akin to the special cases sought as strong evidence by astronomers.

On small spatial and temporal scales, controlled experiments have been used both in the laboratory and in the field. In the laboratory, their philosophy is similar to that of physical or chemical experiments done on similar scales, that is, the isolation of one or a few factors to identify clearly cause and effect and to see the quantitative importance of those factors when all others are held constant. Controlled field experiments, on the other hand, are more common in biological oceanography than in most nonbiological, environmental sciences. The approach is to vary one or a few factors in a controlled manner in the field, while allowing all other processes to occur naturally. The issue is whether that one factor remains important in the face of all the other variables left to Mother Nature's control. At the present state of theoretical ecology, usually only the sign and not the magnitude of

an expected effect is predicted a priori. Therefore experimenters generally focus on whether a statistically significant effect can be found and not on whether its magnitude matches some prediction. Because most factors are uncontrolled by the investigator, the answer easily can and often does change from place to place or time to time, making reproducibility and generalizability key issues. Furthermore, although the altered factor is held to be responsible for observed differences, the chain from this cause to the observed effect is not always clear.

Strong potential for semantic difficulty arises from two differing traditions in use of the term *field experiment*. Geophysicists, including astronomers as well as physical, geological, and chemical oceanographers and atmospheric scientists, often apply the term to coordinated sets of observations collected in the field, without any suggestion of environmental modification. The sense is much as in statistics, where the toss of a die is an experiment, the connotation being that the exact result of planned observations cannot be predicted. Biological oceanographers and biologists, on the other hand, usually reserve the term for cases in which one or more variables are manipulated by the investigator. Using manipulations with suitable controls and sufficient replication, one achieves much less ambiguous relation of cause and effect than in the case of the geophysical "experiment." Here I follow ecological practice, reserving the term *experiment* for the narrower, manipulative sense.

Models of diverse kinds help to focus and direct both laboratory and field experiments and all varieties of observations. Analog models are common in biological oceanography. Stirred containers with controlled rates of nutrient input and controlled rates of outflow (called *chemostats*) are often used to produce microorganisms growing at known and constant rates and are sometimes used as analog models of biota-containing water parcels having relatively constant chemical conditions and continuous physical stirring. Biologists also isolate and manipulate to varying degrees small (microcosms) or medium-sized (mesocosms) portions of whole communities. The advantages over study of a natural, open system are ease of manipulation, potential for replication, ability to manipulate inputs of hazardous materials such as radioisotopes and pollutants, and some simplification of either biological or physical processes (e.g., exclusion of large, mobile predators or elimination of physical advection). Although it is tempting to equate the practice of such analog ecological modeling of communities with scale modeling of ship hulls, the rules for modeling of ecological systems are not yet on a firm foundation. For accurate dynamic results with ship hulls, geometry and the body Reynolds number need to be preserved between model and full scale. Reliable dynamic scaling parameters and rules for microcosms and mesocosms remain to be established. Furthermore, although physically small, the isolated segment of the community may still be sufficiently complex to thwart mechanistic understanding of cause and effect within it. At the present phase of understanding of ecological systems in general and of the oceans in particular, it therefore seems wise to avoid chauvinism for any one approach and to play the advantages of each—both in developing ideas about how the system works and even more importantly in testing well-posed, genuinely a priori hypotheses.

To some, biological oceanography is synonymous with marine ecology. Because of their logistical attributes, however, rocky intertidal communities have provided a fertile proving ground for general ecological theories posed and tested by scientists who might call themselves (marine) ecologists, but who would not call themselves oceanographers. Analogously, a geneticist studying fruit flies on account of their convenience in addressing general genetic questions would not be called an entomologist. Because of the difficulties of access and direct observation, open-ocean communities may never be chosen by general ecologists as model systems in which to test general ecological principles, but they will remain frequent targets of biological oceanographic study. A biological oceanographer typically does not pick a particular species, population, community, or ecosystem as a model to explore general ecological principles, but rather as a target of study that is likely to lead to increased understanding of some major class of marine systems. In this sense, biological oceanographers have more limited goals than do marine or general ecologists. Biological oceanographers avidly follow progress in general ecology and use its findings to advance their more specialized studies. In this regard biological oceanographers resemble their oceanographic colleagues; physical oceanographers use the Navier–Stokes equations from general fluid dynamics and keep up to date on theories of turbulence, while chemists use the principles of thermodynamics and keep up to date on theories of adsorption. The trick in each case (biology, physics, chemistry and geology) is to know when and how the general approaches can be applied to solve a particular oceanographic problem.

There is not, nor should there be, any sharp distinction among general ecologists, marine ecologists, and biological oceanographers, but the latter are the most likely to possess several attributes. They typically consider physical, chemical, and geological processes as part of both the problem and the solution in approaching the goal of prediction. They study marine systems out of explicit interest in making predictions for marine systems, whether or not the results are likely to generalize further. They are often willing to bear the discomforts of work at sea, and they prefer the label "oceanographer" to that of "ecologist" or "biologist."

The distinction between biological oceanographers and marine biologists is much clearer. Dating from the period when it was impossible to keep ice at warm, inland locations during summer, many kinds of biologists began migrating annually to marine laboratories to conduct their specialized studies on development of eggs, on nerve structure and function, on physiology of invertebrates, and on countless other attributes and processes shared by marine and terrestrial organisms. Many convenient model systems were found in marine organisms. Collectively, biologists who use components of marine organisms as models often are called marine biologists, although individually they usually prefer more specific labels associated with the goals and not the subjects of their work, such as "developmental biologist" or "neurophysiologist." The way the whole organism interacts with the physical, chemical, and geological processes of the sea is not necessarily of direct interest in their studies. In many cases, variability in biological response imposed by the environment is removed intentionally before precise biological study begins.

These admitted overgeneralizations do not hold at all across the Atlantic and old with varying fidelity to the west, south, and north of the United States. In Europe the term marine biologist is the much more generally accepted collective term that includes all biologists and oceanographers working on marine organisms. Moreover, there is a resurgence of interest among marine ecologists worldwide in physical features of the environment as modifiers and determinants of biological interactions. The healthy trend, spurred by inspiring popularizations of fluid dynamics (Vogel 1981; Denny 1988) that have brought physical issues to the fore in marine ecology as they long have been in biological oceanography, is toward disappearance of the distinctions between biological oceanographers and marine ecologists. Without an introduction to the historical differences, however, a nonspecialist easily might be confused by the past—and to some extent present—separation of U.S. research traditions in the published literature.

The biological oceanographer (in the provincial, U.S. sense) does not ignore the vast storehouse of marine biological information, but rather draws upon it whenever it can provide useful constraints to aim toward predictive ability. How deep in the ocean do light levels become so low that plants can no longer grow? At what dissolved concentrations is a bacterium unable to sustain an inward flux of a critical nutrient across its outer membranes? What range of salinities can be tolerated by a estuarine species? Physiological answers to such questions may—or may not—sharpen predictive abilities as to where and when a particular species will occur and how abundant it will be. The biological oceanographer must be aware that such physiological constraints exist and must balance them against other factors at other levels of ecological organization as possible explanations for biological oceanographic patterns observed in nature.

Biological oceanographers, as with ecologists in general, tend to focus their efforts at one of four levels of ecological organization (i.e. individuals, populations, communities, or ecosystems). Those studying individuals tend to be the most intimately familiar with physiological and morphological constraints on what an organism can do and where it can live. Such constraints in part account for the success of ecological theories at the level of the individual. With the kinds of models formulated and data collected to date, closure—in the sense of matching numbers of constraints and equations with numbers of unknowns—becomes an increasingly severe problem at the population and community levels. It is arguable whether the situation is substantially improved with added constraints of mass and energy balance at the ecosystem level. For these reasons, and because everyone has an intuition for the constraints on individual organisms, I find it simplest and most satisfying intellectually to introduce biological oceanographic approaches at the level of the individual organism and to work upward in the ecological hierarchy.

Biology is alien to physical scientists in much deeper ways than suggested by the mild semantic problems and methodological differences touched on so far. Integral to each living individual is a "historical, evolving genetic program" (Mayr 1982). Each of those four, carefully chosen words is filled with meanings not found in the same sense in the physical sciences. Because important parts of an organism's capabilities are carried genetically, they depend very directly on the capabilities of

its ancestors. What a billiard ball does when hit depends not a whit on the history of the process that formed it, but the same cannot be said for an organism. Because organisms are evolving, there is no guarantee that a member of one generation will behave identically to a member of the past or the next. Details of the way the genetic code is transmitted constrain what and how much can be changed or carried. The genetic code carries a program analogous to those used in computing, and in some ways the algorithms of evolution are superior to normal computational schemes (i.e., in avoiding being "trapped" by local optima; Brady 1985). Major issues in biology are the degree to which the program is fixed from generation to generation and the degree to which interactions of the program with both the internal environment of organisms (e.g., adjacent cells of multicellular organisms) and the external environment can change the reading and execution of the program.

A consequence of these inescapable features of life is that no two individuals stand an appreciable chance of being precisely alike. Thus, whenever one says something very precise about a group of organisms, it can be true only in a mean sense. Biology did not become a science, however, until attention was focused by Darwin away from mean quantities, which cannot be inherited, and squarely on variations, which can. To understand organisms, one must give up the essentialist idea of one true value and submit to collective, statistical thinking about groups of molecules, cells, or organisms. Essentialism, outside a few fields such as statistical mechanics, would rarely mislead a physicist or chemist even today. It is certain to lead a biologist astray. This simple fact accounts for the frequent necessity of using the calculus of probabilities to describe or analyze biological systems; God most assuredly does play with dice. Snobbishness in favor of simple, deterministic, analytic, closed-form expressions clearly is even more seriously misplaced in biology than it is in statistical mechanics.

The hierarchical, latinized (because it was born when churches were the primary repositories of knowledge and clergymen were fascinated with God-given biological variety) biological classification scheme was developed as an early and pragmatic way of dealing with this diversity. Nonspecialists will most often run into the binomial (or binomen) applied to species, for example, *Spio filicornis*. By convention the formal, latinized name of a species consists of its genus (with the first letter capitalized) and species (all lower case). The operational definition determining whether two individuals belong to the same species is whether they can produce fertile offspring when mated. All other levels in the taxonomic hierarchy are erected much more arbitrarily. Whether a species is assigned to one genus or another is a subjective judgment, and those judgments change as data accrue. Similarly, the successively higher (above genus) levels of classification are also defined subjectively, respectively being the family, order, class, phylum and kingdom to which the species and genus belong. For the species name given, the corresponding names are Family Spionidae, Order Spionida (although not many workers agree on the classification of this species at this level or even that one is necessary), Class Polychaeta, Phylum Annelida, and Kingdom Animalia. Even the number of kingdoms in the complete classification of organisms is debatable, with

a five-kingdom scheme (plants, animals, protozoans, fungi, and bacteria) now being the most popular.

The formal classification scheme is quite useful, but the non-specialist should not be overawed into thinking that the scheme itself imparts deep knowledge. One can gain a deep understanding of organic reactions, for example, with a profound ignorance of chemical nomenclature. I am not arguing in favor of ignorance, but only that much of ecology and biological oceanography is transparent without resort to taxonomic formalism. To understand the fundamental chemical reaction, one must correctly discriminate the interacting chemical species, whether one can name them in accepted fashion or not. Similarly, correct taxonomic discrimination at the species level is absolutely critical to nearly all the approaches taken in this book and in modern ecology. Failure to discriminate species correctly turns reading of a particular historical, evolving genetic program into gibberish and makes a mockery out of tallies of changes in population abundance. Even if one chooses to work at the ecosystem level, correct assignment of individuals to compartments in mass or energy flow models depends on correct identification. The acute need for good taxonomic skills within ecological endeavors makes it lamentable that little provision has been incorporated in the structure of ecological and oceanographic funding for its necessary infrastructure of taxonomists. As a consequence, identifications and species descriptions often are done by amateurs like myself when the press of other commitments permits—sometimes with disastrous results.

Oceanography is the science of the marine environment, much of which itself can be classified as physical, chemical, or geological and studied with the approaches of the physical sciences. The influence of the abiotic marine environment on organisms and the influence of organisms on the abiotic marine environment require, however, some attention to the historical, evolving genetic programs of organisms. Biological oceanography thus must use elements of both physical and biological approaches in seeking its goals.

Some regard oceanography in general and biological oceanography in particular as applied sciences. The apparent reason is that these sciences draw on generalizations from the parent disciplines. Curiously, astronomy, another environmental science that draws on fundamental physics, does not elicit similar opinions. I believe that classification of any of these environmental sciences as applied is a serious error. Specific deductions from physical generalizations, *properly applied and tested in the context of a specific environment*, have added to understanding of fundamental physical principles; the feedback goes in both directions from parent to daughter disciplines. Astronomy, for example, clearly has added to the understanding of fundamental physics in the form of strong tests of relativity theory. Physical oceanography has added to fundamental understanding of fluid motion on a rotating sphere.

Applications of general ecological principles are not purely mechanical deductions; predator-prey interactions in the sea cannot be deduced from the Lotka-Volterra equations, and optimal foraging behavior cannot be deduced from general considerations of costs and benefits independent of an environmental context. The factors that determine predator-prey encounter or foraging costs and benefits (e.g.,

distances over which sensory modes are effective and relative motion imparted by fluid forces) differ radically between terrestrial and aquatic environments. In this sense, general ecological principles are more accurately regarded as formalisms that must be tailored to a given environment rather than generalizations from which specific cases can be deduced without further information. Indeed it would be surprising if ecological principles allowed very many deductions to hold across environments. Such ability to generalize would imply that the environmental context did not alter the results, that is, that ecological predictions could be made accurately without taking the environment into account! I hope to demonstrate repeatedly that abiotic context indeed makes a great deal of difference at all levels of ecological organization.

Further readings

- Margulis, L., and K.V. Schwartz. 1987. *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth*, 2nd edition. W.H. Freeman, San Francisco. 416 pp. Easily penetrable, showing the present level of understanding in biological classification schemes—now changing rapidly due to the introduction of molecular biologic techniques for estimating relatedness of species.
- Mann, K.H., and J.R.N. Lazier. 1991. *Dynamics of Marine Ecosystems*. Blackwell Scientific Publications, Boston. 466 pp. Give an alternative view to mine for the small scale and a far more extensive, complementary description of biological-physical interactions at large scales.
- Maynard Smith, J., 1989. *Evolutionary Genetics*. Oxford University Press, Oxford. 325 pp. A fascinating introductory treatment of the modes of transmission of genetic information and their consequences.
- Parsons, T.R., M. Takahashi, and B. Hargrave. 1984. *Biological Oceanographic Processes*, 3rd edition. Pergamon Press, Oxford. 330 pp. This widely used text provides an alternative, data-rich introduction. Chemists find the book to be valuable for providing detail on the chemical compositions of organisms. It is also a useful reference for unfamiliar terms and concepts.
- Sumich, J.L. 1984. *An Introduction to the Biology of Marine Life*, 3rd edition. Wm. C. Brown Publ., Dubuque, Iowa. 386 pp. I strongly recommend that the reader lacking any familiarity with the kinds of organisms found in the sea look through this book or one like it before diving into the next chapters.

References cited

- Brady, R.M. 1985. Optimisation strategies gleaned from biological evolution. *Nature* 317: 804-806. Analogs of mutations, genetic redundancy, recombination, genetic drift and jumping genes show computational utility.
- Denny, M.W. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton Univ. Press, Princeton, NJ. 329 pp. An exploration of observed and potential effects of waves upon bottom-dwelling organisms

of biology and the discipline's historical baggage.

Vogel, S. 1981. *Life in Moving Fluids*. Willard Grant Press, Boston, MA. 352 pp.

The book that more than any other has brought appreciation of the pervasive effects of fluid motion to marine ecology; a masterful and enthusiastic overview of biological effects of fluid motion.

An Introduction to Ecological Principles

The intent of this section is to introduce or review general ecological principles. The reader who is familiar with these principles but not with marine organisms may still wish to skim this section because marine examples are used and because knowledge of these examples is assumed in the remainder of the book. Furthermore, the calculation of encounter rates as a prerequisite to evaluation of interaction strengths is developed in more detail than found in most introductory ecology texts. Chapter 5 on populations is the most traditional. Chapter 7 is an artifice (in the sense of trickery) that is a compromise between two functions, namely an introduction to ecosystems ecology and a transition to the next section.

Individuals and their mass and energy balances

Physiology (biochemical function) and functional morphology (mechanical function) of parts of organisms long have provided basic and reliable predictions to biological oceanography in the form of recognizable, strong constraints. Individuals have limited tolerance ranges of temperature, salinity, and other physical and chemical factors (Fig. 2.1). Thus, it is a truism that populations of organisms will not be found in abundance beyond the tolerance regions of most individuals. Similarly, anatomical limitations often provide sharp boundaries between habitats where organisms will be found and ones where they will not. Only with a technology superior to wax and feathers are humans able to stay aloft; analogously, most burrowing marine organisms are poorly equipped for sustained swimming, although conditions of the water column may be well within their physiological limits. Physiological tolerance and functional morphology go a long distance toward predicting where a particular organism will not occur, but they often give little indication of how well or what the organism will be doing, or whether it will occur at all, within its tolerance limits. One way to learn more is from repeated observation and statistical exploration of correlations with environmental variables. Initially, this approach is a good source of hypotheses, but it usually becomes intellectually unsatisfying and tedious if practiced alone—because so many environmental variables covary that it is difficult or impossible to resolve cause from effect.

Mechanistic models predicting what and how well an organism should do within its tolerance limits both inspire greater enthusiasm and direct observations toward cogent aspects of organism function and behavior. Success with a class of models collectively called foraging theory (Townsend and Hughes 1981; Krebs and McCleery 1984) has been especially rapid and rewarding since its inception in the mid 1960s. This focus on foraging, among all the activities in which organisms engage, is warranted by the amount of time organisms in general, and marine organisms in particular, spend in it. The closest analogy with human endeavor would be with vocation; feeding in the broadest sense is what organisms do for a living. For my introduction to ecology and biological oceanography, therefore I classify organisms by feeding mode rather than taxonomic affinity. Foraging theory already has worked remarkably well for many organisms, and much continues to be learned from observations that fail to fit the simplest formulations (Pyke 1984). Foraging theory works well precisely because it uses the strong constraints of

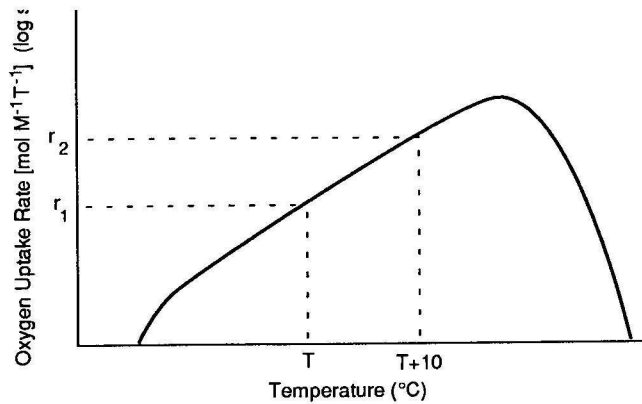


Fig. 2.1 Oxygen uptake (log scale) versus temperature for an individual, cold-blooded organism exposed to short-term (minutes to hours) change in temperature (°C). Results of such experiments often are quoted as $Q_{10} = r_2/r_1$, where r_1 is measured at temperature T and r_2 is measured at $T+10$. Q_{10} values of 2 are typical for respiratory and many other biological rates, just as they are for most chemical reactions. Over longer periods individuals can adapt (shift the curve to the right or left) and populations can evolve (toward comprising individuals with particular curves) to show altered respiration rates and different tolerance ranges, presumably by altering reactant concentrations and reaction pathways. Thus, respiratory rates of individuals can be high at cold temperatures if energy sources are adequate. Individuals also can exploit temperature responses by moving among habitats of differing temperatures.

physics and chemistry and combines them with the strongest constraints on historical, evolving genetic programs.

Growth of an individual is determined by mass and energy balances. Acquisition and digestion of energy-containing foods or of specific nutrients to serve as building blocks for additional body tissues often limit the rate of growth. Fortunately, one need not keep track of all nutrients because at any one time availability of one kind of food will be rate limiting. Usually, either available calories for fueling the metabolic machinery or labile nitrogen sources for building proteins seem to be the bottlenecks in the marine realm. Furthermore, the formalism of the balance (Fig. 2.2) is the same whether one tracks calories or mass. Although some of the terms in this balance are biological, the mass- or energy-balance approach is familiar to any chemist or physicist. The strong biological constraint that such feeding budgets provide is through a division of terms into costs and benefits. Those individuals that make the greatest net profits after paying the necessary metabolic costs of living will have the greatest mass and energy (per unit of time) available to put into body growth and reproduction, giving the potential to leave the greatest number of progeny with related genetic programs. This idea of net reproductive advantage integrated over the reproductive lifespan of the individual

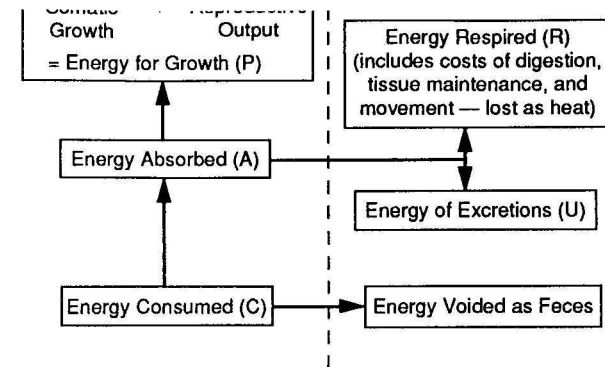


Fig. 2.2 Flowchart of energy through an individual. (Alternatively, mass could be followed in a similar fashion.) P is the focus of optimal foraging theory, and items to the right of the dashed line are considered to be losses. The flowchart is deceptively simple, as there are numerous important feedbacks. For example, varying the costs expended on digestion or movement (R) clearly can alter energy consumed (C) and absorbed (A).

is what ecologists call *fitness*. The term has its roots in the “survival of the fittest” and should not conjure images of jogging or weight lifting; a sloth can be quite fit in this sense if it maintains a high net rate of gain by having a moderate acquisition rate coupled with an exceptionally low expenditure rate.

The premise of optimal foraging theory is that natural selection continually acts to leave higher proportions of those foragers with the highest net rates of gain of mass or energy. The formalism of the optimal foraging approach consists of (1) choosing a currency, (2) designing or selecting appropriate cost-benefit functions in that currency, and (3) solving for the behavior *within the organism's repertoire* that comes closest to the optimum. An organism of a given mass $[M]$ or energy content $[M L^2 T^{-2}]$ requires a given rate of mass $[M T^{-1}]$ or energy $[M L^2 T^{-3}]$ supply to maintain it and an even greater rate of gain to grow or reproduce. The correspondence of the best strategy to the greatest power $[M L^2 T^{-3}]$ is no accident. Thus, the natural currency of optimal foraging for most problems is rate of gain and neither absolute gain nor efficiency of utilization. The genetic program that provides the highest rate of gain—not the program that is most efficient in energy use—produces surviving copies of itself at the greatest rate. The natural time scale for optimization arguments, therefore, is the reproductive lifespan, but if foraging at one time does not alter optimality of later behavior, then optimal behavior becomes independent of time scale.

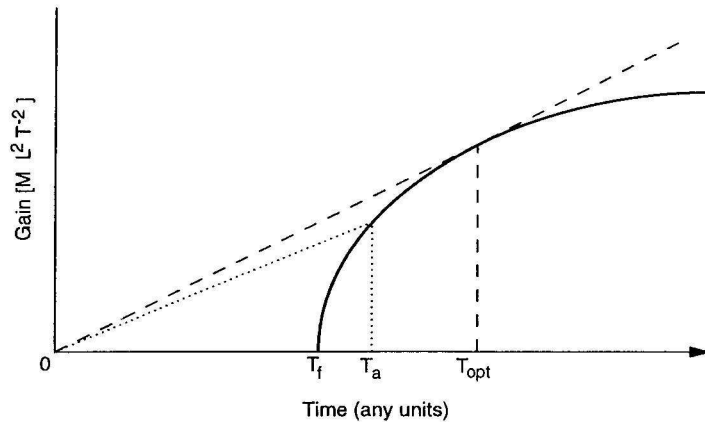


Fig. 2.3 Gain of energy versus time searching for and foraging within a patch of food. The interval from 0 to T_f is the mean time searching for and foraging within a patch. The curve that originates from the point $(T_f, 0)$ is the average rate of gain once a patch has been found. The optimal time to remain in a patch (T_{opt} , dashed line) before beginning the search for the next one is found by drawing the tangent through the origin to the patch-gain curve. This tangent and any other line through the origin and the curve represent average rates of gain (over the search and after the patch is encountered) for the line-indicated patch-leaving time. Note that any alternative patch-leaving time (e.g., T_a , dotted line) has a lower slope (average rate of gain) for the line connecting its position on the curve to the origin.

Where to forage

Among the first (and still useful) predictions of optimal foraging theory is where to forage among the patches of a heterogeneous environment. The arguments are most simply evoked graphically (Fig. 2.3), assuming that energy expenditure while searching is the same as while feeding. Otherwise, corrections are required, and the graphical approach becomes cumbersome. A mobile predator stopping in a patch of food experiences diminishing returns (numbers, mass or energy content) of prey per unit of time as it feeds within that patch. The exact shape of the curve is of no consequence for the following arguments, as long as it is convex upward (returns are diminishing as the predator depletes a patch). Given a predictable average time of search to find a food-containing patch upon leaving the present one, the graphical approach allows easy solution for the time to stay in a patch that provides the greatest net rate of energy gain—averaged over both the time spent in the patch and the mean (expected) search time.

This simple model can be extended easily to predict how long the predator should stay when it enters a patch whose food value or prey content is greater or lesser than that of the average patch. Given that the predator has some sort of memory or sensor adjustable to detect the instantaneous rate of gain when the

of gain under the optimal policy for average patches and travel times (tangent through the origin to the average curve of energy return). If the instantaneous rate of gain for a predator in the patch falls below that under the (average) optimal policy, it should leave because it can expect to increase its rate of gain by doing so. This statement is an approximate formulation of the so-called *marginal value* theorem. Its consequences are that an animal will forage longer in a richer patch and shorter in a poorer one, tending to reduce variability in quality of patches toward the regional average.

These predictions and more sophisticated ones have been well tested. Although lack of fit to predictions has been observed for some animals under some conditions, it has led to more specific and accurate modeling (e.g., incorporating more detail of the particular species' search pattern and sensory capabilities) rather than to overthrow of the approach. Explanatory power now extends in fact to phenomena like "curiosity." If an organism has the integrative capability to track the conditions of several patches, then it can expect to reap a greater rate of gain in the long run by exploring patches and knowing which ones will become productive in the future rather than by simply following the threshold rule for leaving individual patches.

What to eat

Diet choice is more easily treated via equations than via graphs, and the formulation rapidly leads to what initially is a counterintuitive result. Assuming again that energetic costs are constant [T^{-1}] and independent of activity, and now assuming that searching for and handling food items are separate activities (i.e., that they cannot be done simultaneously), define the following variables:

λ_i = encounter rate with the i th prey type [number T^{-1}];

T_s = search time [T];

E_i = energy per item of the i th type [$M L^2 T^{-2}$];

h_i = handling time for an item of the i th type [T];

E = total energy gained searching and handling [$M L^2 T^{-2}$];

T = total time spent searching and handling [T].

If foraging were completely nonselective, then energy collected after T_s seconds of searching would be (restricting for simplicity the items to two kinds):

$$E = T_s (\lambda_1 E_1 + \lambda_2 E_2) \quad (2.1)$$

and would require

$$T = T_s + T_s (\lambda_1 h_1 + \lambda_2 h_2). \quad (2.2)$$

Energy gain per unit of time thus becomes

Suppose now that $E_1/h_1 > E_2/h_2$, that is, an item of type 1 has the higher energy content per unit of time spent in handling. Then only type 1 should be eaten if the energy return by doing so is greater than the energy return of taking both:

$$\frac{\lambda_1 E_1}{1 + \lambda_1 h_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + (\lambda_1 h_1 + \lambda_2 h_2)} \quad (2.4)$$

Algebraically, this inequality simplifies to

$$\frac{1}{\lambda_1} < \frac{E_1}{E_2} h_2 - h_1 \quad (2.5)$$

Then, the abundance of the poorer item makes no difference in whether the better item should be taken. This result generalizes readily to greater numbers of food types, in which case there will be a threshold value of E_i/h_i below which items of the i th type should be ignored. It can also be seen that the diet should expand to include poorer items as the abundance of better ones decreases.

These simple predictions have met with a surprising degree of success in experimental tests and with an informative level of failure. A poor item is taken when predator assessment of food quality takes so long or rejection otherwise is so expensive in energy or mass lost during the decision that a greater rate of gain is attained by simply including the poor item in the diet. This specific example is one of the first-discovered special cases of the so-called *principle of lost opportunity* (Stephens and Krebs 1986), from which spring many of the initially counterintuitive predictions of foraging theory. Alternatively, in some cases recognition is simply beyond the sensory capabilities of the predator (Pyke 1984).

An even simpler version of this model (MacArthur 1972) again assumes a constant rate of energy expenditure, irrespective of the activity in which the forager is engaged (i.e., that time can be equated to energy utilization rate through a simple constant), and also assumes a constant food value per unit of mass of food successfully captured—irrespective of prey species. It would be easy to factor differences of energy expenditure among types of activities and of differences in weight-specific [M^{-1}] food value among prey types into such a model, but doing so would defeat the purpose of providing a better intuition than usually can be gained from first exposure to the diet-choice model presented. First, divide activity into search time (S) and pursuit (including prey handling) time (P). A particular item i should be eaten when encountered only if $P_i < \bar{P} + \bar{S}$, where the overbar represents the mean over prey items, and all terms in the inequality are taken to be per gram of prey successfully ingested. If $P_i > \bar{P} + \bar{S}$ it is better to pass up the item because by

the examples provided by MacArthur (1972). At one end of the spectrum is an animal that spends much more time searching than pursuing (i.e., for which $\bar{S} \gg \bar{P}$). Because \bar{S} overwhelms \bar{P} , any item once found should be taken: $P_i < \bar{P} + \bar{S}$. Foliage-gleaning birds that take small, stationary insects from plant surfaces would seem to fit well in this category. Other foragers find food items to be so abundant that they are always within sensory range; it can be argued that a lion on a game-rich plain falls in the latter category. Here $\bar{P} \gg \bar{S}$, and the forager should pursue only items that take little time to pursue, capture, and ingest (i.e., for which $P_i < \bar{P}$). Thus, the searcher should be a generalist, while the pursuer should be a specialist.

How fast to eat and digest

Once a food item is ingested, how long should it be held for digestion? The simplest prediction is again graphic (Sibly 1981). Costs of a basal level of metabolism are again taken as constant (per unit of time). To those basal costs are added (lumped for present purposes) costs of digestion, assimilation, and synthesis of new tissues (Fig. 2.4). Optimal retention time is found analogously to the graphic solution for patch utilization (see Fig. 2.3). The animal should digest a given food item only as long as it could not expect a greater rate of gain by passing it through and ingesting the next one. Food items from which rapid gain continues longer than for items of average quality should be held longer than these typical items. To meet or exceed fixed metabolic costs as average food quality decreases, an animal may have to carry more gut contents at any one time to provide that given rate of net gain from digestive products.

These more recent predictions of foraging theory have not yet been tested thoroughly, but evidence of some strong constraints has emerged. Geese provide perhaps the most striking example, probably because of the strong energetic constraints on takeoff weight for flight (Sibly 1981). Their gut lengths (and gut volumes) increase by as much as 30% in a month when food quality drops (winter in the wild). Penry and Jumars (1987), focusing particularly on deposit feeders and ruminants, placed digestive considerations in a general theoretic scheme and showed how optimal gut operating procedures change with food quality, digestive reaction kinetics, and gut structure. Dade and colleagues (1990) extended this quantitative treatment to include absorption of digestive products and thereby produced an explicit solution for the curves shown qualitatively in Fig. 2.4. Their predictions also remain to be tested. One of the surprising generalizations beginning to emerge from this sort of study is that the mechanical and chemical costs of moving food through the gut and digesting it are trivial in comparison with the costs of chemical synthesis of new flesh from that food (e.g. Bohrer and Lampert 1988; Taghon 1988).

How big to grow

An example of the unexpectedly far-reaching predictive power of foraging theory is an especially creative application by Sebens (1987). He worked with sea anemones

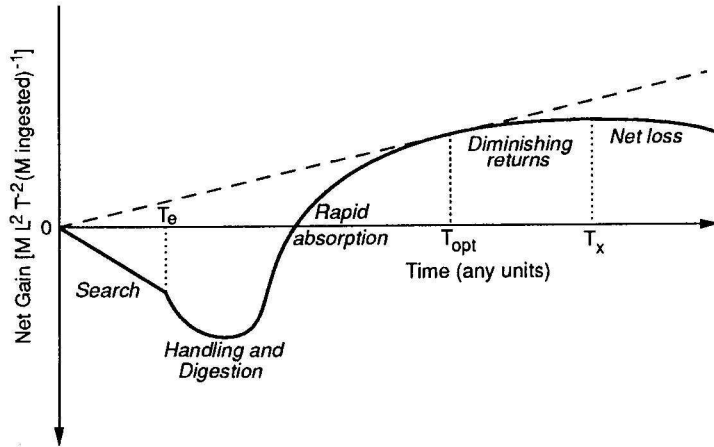


Fig. 2.4 Net gain of energy per unit of mass of food ingested versus time (modified from Sibly 1981). The interval from 0 to T_e is the mean time after egestion of one item of food until the next is encountered. (For continuous feeding, more complex models are needed because search, handling, and digestion costs become simultaneous rather than sequential.) Similarly to Fig. 2.3, a straight line from the origin through the curve at any point represents the average rate of gain that would be obtained from the gut retention time indicated by the curve. Note that it is in the animal's best interests to maximize the rate of energetic gain [$M L^2 T^{-3}$] (holding time T_{opt}) rather than maximizing net gain [$M L^2 T^{-2}$] (holding time T_x). The two correspond closely only when T_e is long.

that display what biologists call indeterminate growth. Adult size is not fixed, but rather varies from environment to environment. Sebens devised and tested cost-benefit functions that predicted what the optimal body size should be. Metabolic costs in most organisms (including humans) do not scale linearly with body mass, but instead scale with mass to some exponent between two-thirds and three-fourths (or roughly with some characteristic length squared or with body surface area). Where M is body mass and k and c are both dimensionless constants (the latter falling in the range suggested), metabolic costs are of the form kM^c . Sebens found that food intake was of the same form, but with different numerical values for the two coefficients, causing the cost and benefit curves to cross (Fig. 2.5). The benefit function was found to vary considerably with food abundance and type from one environment to another, moving the optimal size with it. Again it is worth stressing that there is no teleological or goal-directed behavior implied. Individuals varied. Those that grew to optimal size left more progeny than those that grew to other sizes.

This problem is solved as easily by equations as it is graphically. Let kM^c be the rate of metabolic gain and let jM^b be the rate of metabolic loss. Take rate of energy gain, G , [$M L^2 T^{-3}$] to be given by

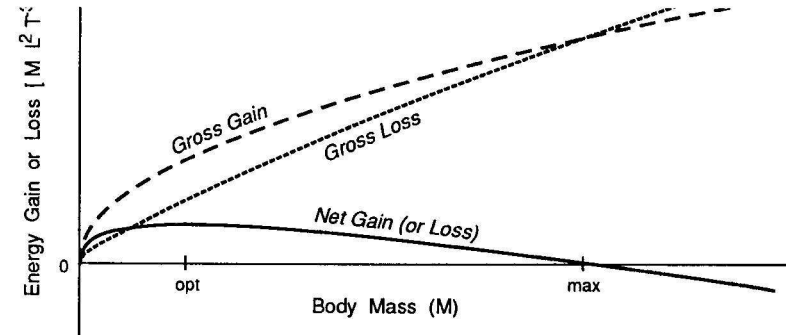


Fig. 2.5 Rate of energy gain and loss versus body mass. At the optimal (*opt*) body mass, the net rate of gain is greatest. Above the maximal (*max*) steady-state body mass, loss exceeds gain. Rather than using its maximal rate of gain to grow further and hence lose this rate of gain, an animal of the optimal size should thus shunt its gain into reproductive products.

$$G = kM^c - jM^b. \quad (2.6)$$

Then take the derivative of G with respect to body mass:

$$\frac{dG}{dM} = kcM^{c-1} - jM^{b-1}. \quad (2.7)$$

Setting it equal to zero and solving for the optimal mass yields

$$M_{opt} = \left(\frac{jb}{kc}\right)^{\frac{1}{c-b}}. \quad (2.8)$$

If the optimum is peaked, there will be strong selection for that body size, whether or not the organism shows indeterminate growth.

Nonforaging constraints

Detractors from the optimal-foraging approach are quick to point out that it is silly to think that foraging and digestion are the only activities important to organisms. This criticism has some validity but misses several key points. First, gains from optimal foraging should aid in other critical activities. Therefore, the need to engage in these other activities should accentuate, rather than detract from, selective pressure to attain foraging optima. A valid aspect of the criticism is that the

energy gain over the short haul may not necessarily correlate with survival to reproductive age. Thus, there is growing evidence that frequently feeding individuals among prey populations are at greater risk to predation, shifting the feeding-rate optimum as a function of predation risk. It is clearly possible, however, to add this predation constraint to foraging theory (Gilliam and Fraser 1987). Game theory (Maynard Smith 1982) further allows the development of optimality models when rewards to an individual are affected by activities of other individuals of the same or different species, but I have avoided this level of complexity for the moment.

An invalid criticism of foraging theory is that optima may not be achievable. Any optimality argument for organisms must start with the possibilities actually open to individuals within a species. That is, selection should operate to leave (and cannot itself create) that heritable behavior or structure that—among the variability seen in the species—works best in a fitness sense. To advocates of, as well as detractors from, optimality arguments it is nonsensical to predict an unachievable result. It is precisely this limitation in real organisms' approaches to optimality that again lends focus to the historical, evolving genetic program and thereby distinguishes a hypothesis-testing field of ecology that uses optimality arguments to make predictions from the dreamy realm of pure theory that might apply to no organism of the past, present, or future.

Further readings

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- MacArthur, R.H. 1972. *Geographical Ecology*. Harper and Row, New York. pp. 61–64. A clear introduction to diet choice from one of the co-originators of optimal foraging theory
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge. 224 pp. Clearly explains the concept of an “unbeatable” or evolutionarily stable strategy (ESS); introduces a theoretical approach that is extremely versatile in applying constraints imposed by the presence of other individuals to optimality approaches; a stochastic, discrete-variable approach that many physical scientists find so alien as to be distracting; only for the latter reason is it excluded from the body of the chapter.
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- Stephens, D.W. and J.R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ. 247 pp. An excellent summary of the state of the art that goes well beyond the models included here.
- Taghon, G.L. 1988. The benefits and costs of deposit feeding in the polychaete *Abarenicola pacifica*. *Limnology and Oceanography* 33: 1166–1175. Finds the mechanical costs of deposit feeding trivial in comparison to the energetic costs of synthesizing new tissues.

Physical oceanography

Physical oceanography classically is divided into three gross scale categories. The largest involves general circulation—the structure and dynamics of the earth's major current systems. Mesoscale oceanography considers structures of approximately the local Rossby radius of deformation in horizontal scale, typically a few tens of kilometers. Small-scale physical oceanography picks up the study of water movements generally at the scale of 10 m and less. The classic view is of an energy cascade from currents driven by winds at the large scale, to mesoscale features and in turn to small-scale turbulent and viscous dissipation. Modern physical oceanographic approaches fit less well into these pigeonholes and recognize that, although energy generally moves toward smaller scales, it does not always do so. Especially active arenas for study at present are exchanges of energy in both directions across the traditional scale separations, together with the mechanisms accounting for such exchanges. Thus, for example, seasonal thermocline evolution has become of interest to physical oceanographers studying general circulation.

Advection and both turbulent and molecular diffusion are widely recognized as primary forcing variables by biological oceanographers. Until recently it has appeared safe, on the other hand, for physical oceanographers to ignore biological variables in terms of any proximate causes of physical oceanographic events. Fouling (see Chapter 16) and other biological effects on physical measurement devices have provided minor exceptions in terms of *apparent* events. With increased application of optical and acoustic technology to oceanography, however, the importance to physical oceanographers of understanding biological effects is growing. For example, acoustic Doppler methods depend on the assumption that the backscattering particles (mostly zooplankton) have no mean motion vector different from that of the water, and utility of features used in remotely sensed color images to estimate advective velocities (as from cloud tracking in the atmosphere) degrades not only with physical mixing but also with biological modification of the features. Furthermore, and perhaps providing the greatest impetus for physical oceanographers to study biota, several recent analyses demonstrate that it is unsafe to disregard effects of phytoplankton and biogenic particles in heat transfer to (and because of depth distribution of the input) heat loss from the upper ocean.

There are some major impediments, however, partly due to scale differences, toward increased dialogue between physical oceanographers and biologists. Biological oceanographic curricula have gone a long way toward reducing the physical naiveté of biological oceanographers and thus toward reducing a primary impediment. More subtle, however, is the fact that organisms are particles, and physical oceanographers usually get scant training in the physics of two-phase

flows. This lack does not impede physical oceanographic understanding except in dense suspensions where buoyancy and viscosity effects emerge from the suspended load, but it means that physical oceanographers may be able to tell biological oceanographers rather little about the motion of particles that are not both very small and neutrally buoyant. Biological oceanographers, on the other hand, often desire a description of particle motions in the absence of behavior (but including effects of gravity, fluid shear, motion-produced pressure differences across particles and skin friction)—as a simple null hypothesis against which to evaluate whether behavior is important in determining the trajectories of organisms. They can be slow to realize that most physical oceanographers will be unable to frame this null hypothesis for them and that most physical oceanographic models that they might run for themselves cannot readily accommodate differential particle and water motions. Further, and again with justification, many physical oceanographers are untrained in the low Reynolds number regimes of most direct influence on marine biota or in boundary layer flows of a scale within which molecular viscosity plays an important role and geostrophy safely can be ignored. Thus the biological oceanographer may need to read a great deal or find a suitable intermediary in the form of a sediment dynamicist to make use of physical oceanographic information. With growing payoffs of two-way information exchange between physical and biological oceanographers, however, there is hope that these desires and impediments will be better realized and perhaps removed.

Effects of biota on ocean physics and uses of biota in physical oceanography

Marine biota have scant direct effect on momentum at the scales of general circulation and eddies. They have, however, a broad range of indirect effects on atmospheric and oceanic heat budgets. Part of the impetus to know more precisely the magnitude of primary production and its fate in the ocean is that the biological pathways of carbon after its fixation into organic matter to a large extent determine whether the fixed carbon will be remineralized in surface ocean waters or transported into the deep sea. Recent results show (Watson et al. 1991) that biological uptake can drive air-sea CO₂ transfer on the scale of phytoplankton patches (see Chapter 8). Of order 1% of primary production typically is trapped in the geological record, but carbon contained in organic matter that reaches the deep sea and is oxidized before burial—a highly variable fraction but closer to 10% of primary production—effectively is isolated from the atmosphere for roughly 10³ yr. The particulate pathway toward the seabed (see Chapter 14) represents a potential short circuit over what would be expected from downward mixing of water and bottom water formation. Virtually all the other radiatively active gasses, such as CH₄, H₂, and CO also are both products of and further reactants in biological processes. Phytoplankton in addition are major sources of atmospheric sulfides of importance in climate and weather as well as in acid rain (Andreae and Raemdonck 1983).

On a smaller scale and in a more direct manner phytoplankton can directly affect the vertical distribution of heating and thus the evolution of diurnal and

seasonal thermoclines. Through this modulation of heating and its effects on circulation, they can also further affect the physical transport of dissolved CO_2 . As per the example of stacked razor blades (see Chapter 12) a nepheloid (turbid) layer that results in light trapping by scattering will entail localized heating when the photons are absorbed (Stavn 1982, 1987). Thus, subsurface chlorophyll maxima can increase local heating by up to $0.003^\circ\text{C} \cdot \text{d}^{-1} \cdot \text{m}^{-1}$ at the top of the chlorophyll maximum (Lewis et al. 1983). Calculations suggest (Zaneveld et al. 1981) that the presence of a phytoplankton bloom on one side of a front can increase relative heating rate on that side by up to $0.1^\circ\text{C} \cdot \text{d}^{-1}$ in the open ocean. There is evidence of such cross-frontal differences in the mismatches between ocean color (chlorophyll *a* concentration) and sea-surface temperature seen in remote-sensing studies (Abbott and Zion 1985). On a much broader oceanic scale there is now reason to believe for temperate oceans (Simonot et al. 1988) that sea surface temperature in the spring will be predicted inaccurately without taking the presence of phytoplankton blooms into account. Predictions of seasonal variation in sea surface temperature have been calculated to err by as much as 3°C if turbidity (in the open ocean due largely to phytoplankton) is not taken into account (Woods and Barkmann 1986). Within the Arabian Sea, similar calculations based on remotely sensed ocean color and calculated heating rates suggest biological contributions to heating of as much as $3.6^\circ\text{C} \cdot \text{mo}^{-1}$ (Sathyendranath et al. 1991).

The depth distribution of heat inputs has a major influence on the total heat energy stored in the water column. Heat introduced at the surface during daytime heating can be lost from the water by reradiation, evaporation, and conduction at night. Heat emplaced below the diurnal mixed layer, however is retained longer. Although for a 20-m mixed layer Lewis et al. (1990) calculated that subsurface (vs. surface) heating can account for annual reduction in upper mixed-layer temperature of $5\text{--}10^\circ\text{K}$ (vs. those modeled assuming heat transfer only into the surficial layer), a more subtle consequence is that on average more heat energy is stored [L^{-2}] in the water than would be the case if incoming light were converted to heat only in the uppermost layer. This effect is most apparent in small lakes, which show wide ranges of turbidities and mixed-layer depths. Lakes with less light penetration have shallower mixed layers (stabilized by thermal reduction of surficial fluid density) and store less heat than clearer lakes (Mazumder et al. 1990). Organism control on the depth distribution of radiative inputs of light energy to the ocean thus can have strong indirect effects on subsequent heat loss.

Biota also can affect, via production or consumption of organic films on the surface of the ocean, momentum transfer from winds to surface waters. These films can cause surface-tension changes (Van Vleet and Williams 1983) that alter capillary waves and hence alter the strain rate or efficiency of energy transfer achieved from a given wind stress. Such effects may be important in interpreting scatterometer measurements. Direct and indirect effects on gas transfer also can be expected (Goldman et al. 1988). Furthermore, these films and slicks may have more subtle effects on the character of other remote sensing signals. The origins, residence times and fates of the hydrophobic materials that constitute these films are

1986). There now also is evidence that organisms can measurably alter fluid viscosity (Carlson et al. 1987) and the suggestion from water obtained from plankton cultures that these changes can be locally important (Jenkinson 1986).

Just as biota can alter momentum inputs at the surface (and, by viscosity changes, potentially alter momentum transfer further down), they can alter momentum extraction at the seabed. Small-scale (1 m or less) roughness over most of the seafloor is biologically produced, or its production is at least biologically mediated (e.g., manganese nodules). Assumption of a constant bottom drag coefficient in circulation models can be in error by a factor of two (e.g., Nowell et al. 1981). In seasonal, coastal environments where bottom roughness-producing populations vary dramatically in abundances and activity levels, time-dependent changes in bottom drag coefficients should not be a major surprise. Even in the deep sea, biogenic roughness changes can be surprisingly rapid. In a region of episodic mesoscale smoothing of the seabed at 4800 m depth by erosion and redeposition events in benthic "storms," for example, biota restore prestorm roughness levels in only 10 d (Wheatcroft et al. 1989). Such roughness effects of biota should be expected to dominate bottom friction, however, only where the bottom is relatively flat and drag is not dominated by larger, abiotic topographical roughness. Beds of large, anchored kelps, however, can exert substantial effects not only on nearshore mean flow in the presence of irregular, rocky topography, but also on propagation of internal and surface waves (Jackson and Winant 1983; Jackson 1984).

At small scales comparable to their body dimensions, biota can exert direct effects on momentum. At the low density [N L^{-3}] of swimming biota in the sea, however, it is unreasonable under most conditions to expect a major contribution from them to kinetic energy budgets (e.g., Yen et al. 1991). Nonetheless it is important to recognize that pulses of turbulent energy observed during measurement series may be due to biota (e.g., Farmer et al. 1987).

Although direct and immediate effects of biota on physical oceanographic processes are quite limited, the same cannot be said of the potential for extracting physical information from biota. Conservative tracers are the stock in trade of physical oceanographers, and transient chemical tracers of specified kinetics have produced valuable insights in recent years, particularly with respect to such phenomena as downwelling, thermocline evolution, and formation of deep and intermediate waters. Key to fuller utilization of biota as tracers of water movement is better understanding of their (birth and death) kinetics and of their movements relative to the water masses that they inhabit. Over some time scale any particular biotic component can be considered conservative and perhaps passive (in terms of following streamlines), whereas over others it cannot. Just as cloud velocities are sometimes used to estimate wind speed, phytoplankton patch tracking in remote-sensing images can give estimates of mean current velocity between images (e.g., Abbott and Zion 1985). In oligotrophic oceans, chlorophyll *a* concentrations estimated from ocean color images often covary strongly (and inversely) with temperature because low temperatures are indicative of upward movement of nutrient-rich waters. Ocean color, because the backscattered signal emanates from the top few meters or tens of meters, can provide an indirect indication of

temperature that is less sensitive than are infrared emissions to peculiarities over the upper millimeters of the ocean. Biota characteristic of particular water masses have sometimes been used as indicators of time variation in current systems, and biota attached to flotsam and jetsam have been used to reconstruct paths of floating debris.

These applications to date, however, make comparatively little use of the potential temporal information that might be read from the historical, evolving genetic programs of organisms. New molecular methods of interrogating genetic structures and of interrogating whether specific gene functions have been "turned on" certainly will provide an unprecedented capability to read biological information on water masses (e.g., Lee and Fuhrman 1991). Because species vary dramatically (Granata and Horne 1985) in their dispersion characteristics (in the physical sense of the word "dispersion"), the potential information on water movement from inverse analysis is substantial. Physiological and population biological changes each have characteristic time scales that can yield information on the history of a water mass. Organisms "record" to varying extents and for varying periods, the thermal, nutrient, light, and even shear histories of their environments. Light adaptation in individual phytoplankters should reflect their recent light exposure on a time scale of minutes to hours (e.g., Denman and Marra 1986; Lande and Lewis 1989), and thus assaying the state of light adaptation can give an indication of the extent of vertical mixing (Fig. 13.1), even in a water column that shows no salinity or temperature structure.

To date the mean state of individuals has been assayed, with some estimates of vertical mixing resulting (Falkowski 1983), but a much more powerful approach is on the horizon. Flow cytometry (see Chapters 9 and 12) can resolve the states of light adaptation of single cells and thus permits analysis of the distribution of light adaptedness for comparison with what would be expected under various mixing models (e.g., Platt and Gallegos 1980; Lande and Lewis 1989). A slightly more exotic use of biota would be of bioluminescent dinoflagellates to indicate shear and even shear history. Bioluminescent emissions are stimulated by threshold shear levels across the dinoflagellate body, and the first flash of a given night is by far the brightest, with exponential decay in intensity from the second flash onward (see Chapter 12). Thus, in theory, a phytoplankton population could be interrogated to yield instantaneous shear estimates (by imaging of bioluminescent output at a given time) or recent shear history of a water mass (by measuring stimulative bioluminescence of a sample of dinoflagellates).

On a time scale of days to weeks, in an upwelling regime it is in principle possible to estimate from the apparent successional state of its contained community the time since a water parcel was upwelled. It may similarly be possible to estimate the time since formation of eddies from an inverse analysis of their contained biota. The precision that can be attained with such procedures, including refinement of organism trajectories via modeling of their swimming behaviors (e.g., Kamykowski et al. 1988), remains to be explored. When better chemical structural resolution of the bioenergetic molecules constituting dissolved organic carbon is achieved, a wide

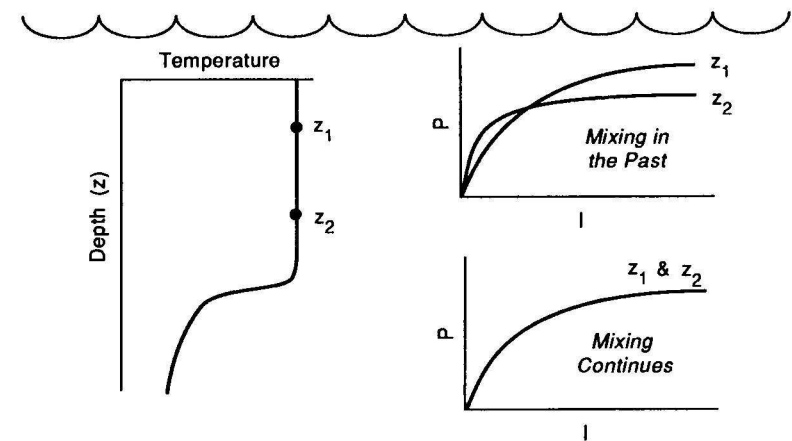


Fig. 13.1 Potential utility of measuring light adaptation in determining whether an isothermal water column continues to undergo vertical mixing. If rapid mixing continues, deeper phytoplankton within the mixed layer cannot show adaptation to lower light levels than do shallower phytoplankton. P is the net rate of photosynthesis per unit of chlorophyll a concentration or (preferably) per cell, whereas I is light intensity applied to the sample in short-term incubations. See also Figures 4.14 and 4.15.

range of transient tracers with diverse kinetics will become available. Bacterial activities almost certainly will be major determinants of their disappearance rates.

Effects of oceanic physics on biota

Much of this book concerns physically driven responses of biota. At the most fundamental level, plankton versus nekton are defined on the basis of insignificant versus significant swimming ability relative to mean horizontal current speeds. Various mechanisms have evolved that use vertical shear to maintain Eulerian position or to follow a particular Eulerian path during development (see Chapter 11). The plankton-versus-nekton classification is a crude one, much like the classification of turbulent versus laminar flows, and the beginnings of a more informative quantification are emerging. Swimming speeds range from 0 through the 30 to 50 $\mu\text{m s}^{-1}$ characteristic of motile bacteria to the 30 m s^{-1} seen in tunas and mammals. As information on advective velocities and swimming speeds accrues, it becomes possible to consider, for example, whether protozoans can hold position during convective overturn under nighttime cooling of the mixed layer or whether copepods can hold position in a Langmuir circulation. The traditional scaling of mean horizontal current speed against organism swimming speed will be resolved into a more informative quantification of time-varying vertical and horizontal advective velocities versus swimming velocities.

Beyond these nondimensionalizations (which could be termed Plankton or Nekton numbers) on the basis of water and particle velocities, biological

oceanographers have a growing interest in particle-particle separation distances in a Lagrangian framework. To what extent do the subtly different swimming behaviors of plankton keep them together with neighbors having the same swimming habits or force them to encounter new neighbors? Does a particular pattern of vertical migration cause net change in long-term average encounter frequency with predators or prey over what would be achieved by being purely passive? These problems are not easy ones because they entail scales from that of the individual to the mesoscale, with organism behaviors superimposed on Lagrangian, time-varying paths of fluid parcels.

Biologists are sure to benefit from the new focus by coastal physical oceanographers on cross-shelf exchanges and model boundary conditions at shelf-edge fronts, at estuarine fronts, and between the shelf and near-shore zones. Prominent biological issues here are transport and return of larvae of benthic forms and expatriation of plankton (see Chapter 11).

Progress is now being made and anticipated in examining how turbulent water motions affect encounter rates among predators and prey. It is known from both theory and experiment that turbulence increases shear-produced encounter rate among suspended particles (see Chapter 14) and these results have been extended to predators and prey that follow streamlines (see Chapter 3). From the biological perspective, turbulence can shift effective prey abundance (encounter rate) from unprofitable to profitable levels (Sundby and Fossum 1990) without any change in mean prey density [$N L^{-3}$]. Previous models of prey encounter by biota have dealt primarily with laminar flows (Rubenstein and Koehl 1977). Turbulence also affects the abilities of predators and prey to detect each other, whether fluid dynamic motion is detected directly (e.g., Kalmijn 1988) or chemosensing is used (e.g., Costello et al. 1990). Even more realistic models and measurements of predator-prey encounter will incorporate animal behavior, passive settling (due to specific gravity differences between organisms and the fluid), and shear across animals, as they influence particle trajectories and encounters. These modifications cannot help but improve upon Lotka-Volterra descriptions of population change (see Chapter 6)—which implicitly assume a constant coefficient relating encounter rate with predator and prey abundances.

More generally it is now known from long time series of fish catches and zooplankton populations that power spectra of marine population abundances over time generally are red (show increasing variance as the record is extended). There is good reason to believe that physical changes drive population changes, and that variation summarized in red physical spectra drives population fluctuations. A remaining challenge is to untangle the causal linkages, many of which are sure to be nonlinear.

Additional readings

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