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**T. Kiørboe: A Mechanistic Approach to Plankton Ecology**

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## *Chapter One*

### INTRODUCTION

#### 1.1 BIOLOGICAL OCEANOGRAPHY—MARINE BIOLOGY—OCEAN ECOLOGY

**I** LIKE SPORTS FISHING. I used to have a small boat from which I fished for herring, cod, and trout in the Øresund. Angling there can be quite productive, in particular if you learn where to go. At certain spots there are more cod than at others, for whatever reason. Once such spots were found, we used to find them again from land or sea marks. For example, 200 m north of a particular green buoy very often there would be cod. Eventually I knew so many “hot spots” that, whenever I went fishing, I would catch some cod. And eventually this lost its excitement. I sold the boat and started fishing for trout from the coast. Here the approach is not blind. You can see both the fish and its environment. You learn to know where to find the fish using relevant cues—that is, not a green buoy but a certain type of vegetation or structure of the seafloor. You learn to think as a trout; you develop intuition. When you visit new beaches, and if you are good enough, you can “read” the coast, and you can find fish. You can extrapolate the insights gained at one site to new, unknown locations.

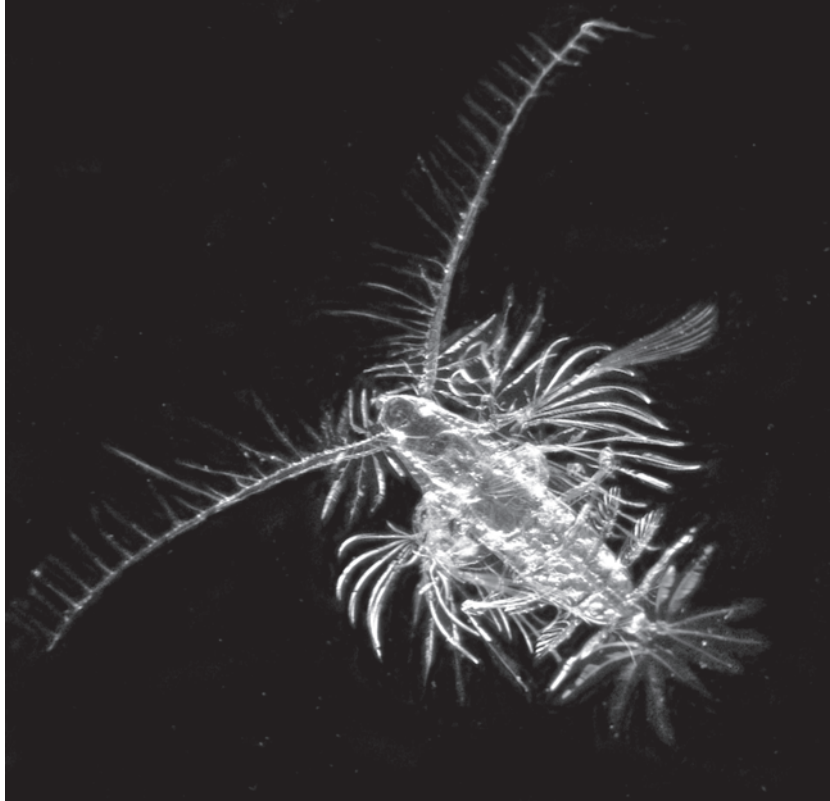
Much of our knowledge of the biology of the oceans is derived from “blind” sampling. We use instruments to measure bulk properties of the environment, such as salinity and temperature, and we use bottle or net samples to extract knowledge about the organisms living in the ocean. This kind of approach has contributed important knowledge but has also influenced the way we view marine life. It leads us to focus on abundances, production rates, and distribution patterns. Such a perspective is very relevant in the context of the ocean as a resource for fisheries. It is also helpful in developing an understanding of biogeochemical issues such as ocean carbon fluxes. But on its own, this approach is insufficient, even for those purposes. The kind of intuition that we develop about marine life is, of course, influenced by the way we observe it, and because the ocean is inaccessible to us, and most planktonic organisms are microscopic, our intuition is rudimentary compared, for example, to the intuitive understanding we have about (macroscopic) terrestrial life. Our understanding of the biology of planktonic organisms is still based mainly on examinations of (dead)

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individuals, field samples, and incubation experiments, and even our sampling may be severely biased toward those organisms that are not destroyed by our harsh sampling methods. Similarly, experimental observations are limited to those organisms that we can collect live and keep and cultivate in the laboratory. One may argue that these limitations have biased our understanding of the ecology of the plankton and thus constrained our comprehension of the function of pelagic food webs (Smetacek and Pollehne 1986).

The ocean is structured on all spatial scales, but sampling averages over volumes, and this has led us to focus our attention on the potential importance of certain scales over others. In particular, sampling averages over volumes that exceed the ambit of individual plankters by orders of magnitude. Thus, we may relate organism distributions to distributions of salinity and temperature, for example, without knowing whether these are the cues to which the organisms respond. From sampling we can enumerate phytoplankton, zooplankters, and other particles, but we do not know how they are distributed relative to one another at a scale that is relevant to the organisms. We do not know whether the particles in a sample were originally aggregated as marine snow because such aggregates disintegrate to component particles when sampled by traditional means. In a water sample, we can also measure the concentrations of various solutes (dissolved organics, oxygen, nutrient salts), which may lead us to think that the solutes were homogeneously distributed in the sample before it was collected; they rarely are. And we may incubate water samples with radiotracers to get estimates of production rates of bacteria and phytoplankton. The implicit assumption is that such rates are representative of the corresponding rates in situ. But are they? These numbers, concentrations, and rates that are measured at scales that exceed the daily ambit of the individual organisms by orders of magnitude are insufficient to provide an understanding of how the organisms function in their environment. Visualization and observations as well as considerations at the level of the individual plankter are keys to establishing a mechanistic understanding of how the organisms function and interact and, hence, how the system of which they are part works (e.g., Azam and Long 2001).

Ecosystems consist of populations, which in turn consist of individuals that interact with one another and with the environment. Biological interactions in the ocean are not between populations or between trophic levels, as many box-model representations of pelagic food webs might lead us to think. Trophic levels and populations are abstractions, and interactions occur at the level of the individual. “Blind” sampling of bulk properties may result in observed distributional patterns, for example, that cannot be



**Fig. 1.1.** *Haloptilus plumosa*. The beauty of the plankton is a main motivation for studying it. The copepod in the picture has extensive setation on all appendages that together forms a large basket. While feeding, a feeding current keeps the animal stationary in the water, ventral side up. Sinking particles and particles drawn in by the feeding current are collected by the large basket. Courtesy of Russ Hopcroft.

understood and explained from such an approach on its own. The picture must be complemented by approaches that consider the individual in its immediate environment and that provide a mechanistic understanding of the functioning of individuals and of components of the larger systems. This allows us to build models and to extrapolate observations beyond the system in which the observations were made.

Traditionally, scientists who go on cruises and examine distribution patterns of both biota and environmental properties using sampling are considered biological oceanographers, and those who explore the functioning of individuals, for example by conducting laboratory experiments

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with organisms, are considered marine biologists. We need to combine the two approaches to understand the ecology of the oceans. This book considers the functional ecology of planktonic organisms but with a view on how organism biology shapes the ecology of the oceans. In fact, as we proceed, and particularly by the end, we shall try to integrate our understanding of individual-level processes to predict properties of planktonic populations and of pelagic food webs.

The motivation to try to understand the ecology of planktonic organisms is twofold. The first driving force has to do with a simple interest in natural history. It is fascinating to watch the behavior of live plankters under the microscope or—better—free-swimming plankters by video; they have different but often beautiful forms and colors, and even closely related species may behave very differently, which makes identifying live plankton much easier than identifying dead ones. My own love for the plankton was elicited by one photograph in particular, of a very beautiful echinoderm larva, published in a popular book by Gunnar Thorson, and by the beauty of plankton in general (fig. 1.1). This fascination led me to a desire to understand why and how a plankter does what it does and how it solves various problems, among them, finding food in a dilute environment. The second reason for examining the adaptations and behavior of plankters is our interest in understanding overall properties of pelagic systems and how the pelagic system relates to the larger-scale issues of fisheries' yield, CO<sub>2</sub> balance, global climate, and others. Understanding the mechanistic of individual behaviors and interactions may allow us to predict rates and to scale rates to sizes, which, in turn, may help us understand the (size) structure and function of pelagic systems and to predict effects of environmental changes and human impacts.

### 1.2 THE ENCOUNTER PROBLEM

Life is all about encounters. In the ocean, for example, phytoplankton cells need to encounter molecules of nutrient salts and inorganic carbon; bacteria need to encounter organic molecules; viruses need to encounter their hosts; predators need to encounter their prey; and males need to encounter females (or vice versa). There is no life without encounters, and the pace of life is intimately related to the rate at which encounters happen. Other important processes in the ocean, such as the formation of marine snow aggregates, likewise depend on encounters, here encounters between the component particles. We are therefore interested in encounter rates. And we are interested in understanding the mechanisms that govern encounters. What are the constraints, and what are the implications of these constraints?

All organisms, including plankters, have three main tasks in life, namely to eat, to reproduce, and to avoid being eaten, all related to encounters or avoiding encounters. The behavior, morphology, and ecology of planktonic organisms must to a large extent represent adaptations to undertake these missions, and the diversity of form, function, and behavior that we can observe among plankters must be the result of different ways of solving the problems in the environment in which they live. The pelagic environment seen from the point of view of a small plankter is very different from the environment experienced by humans, and our intuition is often insufficient to allow us to understand the behavioral adaptations of planktonic organisms. Thus, although ornithologists to a large extent may be able to understand the behavior of their study organisms by using common sense, copepodologists rarely can, to rephrase the title of a classical ecology paper (Hutchinson 1951). For example, at the scale of planktonic organisms, the medium is viscous, and inertial forces therefore are insignificant, which makes moving an entirely different undertaking than what we as humans are used to or have seen other terrestrial animals do; the density of water is orders of magnitude higher than the density of air, which makes floatation easier and currents more important; for the smallest pelagic organisms (bacteria), thermally driven Brownian motion makes steering impossible; and most plankton use senses different from, and less far-reaching than, vision to perceive the environment. In addition, the pelagic environment is three-dimensional, whereas humans mainly move in only two dimensions. This implies, among other things, that average distances between a planktonic organism and its target may be very large, maybe thousands of body lengths. Because of the often nonintuitive nature of the immediate environment of small pelagic organisms, we need to appeal to fluid dynamic considerations in order to achieve a mechanistic understanding of the small-scale interactions between plankters and their environment.

In pursuing the encounter problem we can write a very general equation that describes encounter rates

$$E = \beta C_1 C_2 \quad (1.1a)$$

where  $E$  is the number of encounters happening per unit time and volume between particle types 1 and 2,  $C_1$  and  $C_2$  are the concentrations of these particles, and  $\beta$  is the *encounter rate kernel* ( $L^3T^{-1}$ ) (see table 1.1 for definition of symbols used). Often we are interested in looking at the per capita rate, that is, the rate at which one particle of type 1 encounters a particle of type 2:

$$e = E/C_1 = \beta C_2 \quad (1.1b)$$

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TABLE 1.1  
Definitions of Symbols Used

<i>Symbol</i>	<i>Definition</i>	<i>Dimensions</i>
$a$	Radius	L
$ \mathbf{a} $	Acceleration	$LT^{-2}$
$C$	Concentration	$ML^{-3}$ or $L^{-3}$
$d$	Separation distance	L
$D$	Diffusion coefficient	$L^2T^{-1}$
$E$	Encounter rate	$L^{-3}T^{-1}$
$e$	Specific encounter rate	$T^{-1}$
$f$	Production rate of fertile eggs	$T^{-1}$
$I$	Light intensity	$L^{-2}T^{-1}$
$J$	Flux	$MT^{-1}L^{-2}$
$k$	Specific light attenuation coefficient	$L^2$
$K$	Boltzmann's constant	$ML^{-2}T^{-1} \text{ } ^\circ K^{-1}$
$l_x$	Survivorship at age $x$	—
$L$	Plume length	L
$m_x$	Fecundity at age $x$	$T^{-1}$
$M$	Carrying capacity	$L^{-3}$
$Pe$	Péclet number	—
$Q$	Flow (of molecules or particles)	$MT^{-1}$
$r$	Radial distance	L
$R$	Reaction distance	L
$R_0$	Net reproductive rate	—
$Re$	Reynolds number	—
$S$	Signal strength	$LT^{-1}$
$Sh$	Sherwood number	—
$t$	Time	T
$T$	Generation time	T
$U, u$	Speed	$LT^{-1}$
$x, y, z$	Distance along $x$ -, $y$ , or $z$ -axis	L
$\alpha$	Stickiness	—
$\beta$	Encounter rate kernel	$L^3T^{-1}$
$\gamma$	Shear rate	$T^{-1}$
$\delta$	Step length	L
$\Delta$	Deformation rate	$T^{-1}$
$\varepsilon$	Turbulent dissipation rate	$L^2T^{-3}$
$\zeta$	Egg-hatching time	T
$\eta$	Kolmogorov length scale	L
$\iota$	Handling time	T
$\kappa$	Maturation age	T
$\lambda$	Detachment rate	$T^{-1}$
$\varsigma$	Dynamic viscosity	$ML^{-1}T^{-1}$
$\mu$	Specific growth rate	$T^{-1}$
$\nu$	Kinematic viscosity	$L^2T^{-1}$

TABLE 1.1 (continued)

<i>Symbol</i>	<i>Definition</i>	<i>Dimensions</i>
$\rho$	Density	$\text{ML}^{-3}$
$\sigma$	Mortality	$\text{T}^{-1}$
$\tau$	Run duration	T
$\Phi$	Volume fraction	—
$\omega$	Vorticity	$\text{T}^{-1}$

The dimensions are L for length, T for time, M for mass, and °K for degree Kelvin.

For example, if particle 1 is a suspension-feeding ciliate and  $C_2$  the concentration of its phytoplankton prey, then  $\beta$  is the ciliate's clearance rate, and  $e$  its ingestion rate (assuming that all encountered particles are ingested). The clearance rate is the equivalent volume of water from which the ciliate removes all prey particles per unit time. In many suspension-feeding ciliates, the clearance rate can be interpreted directly as a filtration rate; that is, the rate at which water is passed through a filtering structure that retains suspended particles. As a different but similar example: if particle 1 is a fish larva looking for food, and particle 2 its microzooplankton prey, then  $\beta$  is the volume of water that the larvae can search for prey items per unit time; if all encountered prey are consumed, then  $e$  is the ingestion rate of the fish larva. We may also see the process from the point of view of the prey, in which case  $\beta C_1$  is the mortality rate of the phytoplankton or microzooplankton prey population through ciliate grazing or fish larval feeding. As a final example: if  $C_1$  is the concentration of bacteria, and  $C_2$  the concentration of organic molecules on which the bacteria feed, then  $e$  is the assimilation rate; it is more difficult to give a physical interpretation of  $\beta$  in this case. However, it is, like a clearance rate, the imaginary volume of water from which the bacterium removes all molecules per unit time. In fact, any encounter problem that I can think of can be cast in terms of the general equation (eq. 1), but obviously the interpretation or meaning of the terms may be very different.

The processes or mechanisms responsible for encounters are contained in the encounter-rate kernel. Obviously, from the examples above, these mechanisms are diverse. Intuitively, encounter rates depend on two factors: the motility of the encountering "particles" and the ambient fluid motion that may enhance encounter rates. Motility encompasses here the diffusivity of molecules, the swimming of organisms, and the sinking of particles. In regard to planktonic organisms, ambient fluid motion essentially means turbulence because planktonic organisms (contrary to benthic ones) are embedded in the general flow. From this consideration, one can see that there may be different components

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entering into the encounter-rate kernel depending on the specific problem under consideration.

The encounter problem—and equation 1—will be the primary issue throughout most of this book and of chapters 2–5 in particular. We shall examine the encounter problem for a number of fundamental processes in the plankton (e.g., feeding, mating, coagulation). And for each of the processes considered, we shall try to write simple models for  $\beta$ , as far as possible based on first principles. My presentation is case driven, but wherever possible or necessary, I will make excursions to more general explanations.

### 1.3 THIS BOOK

The purpose of this book is twofold. First and foremost, I want to explore the ecology of plankton organisms at the level of the individual by examining how they are adapted to the viscous, three-dimensional, and dilute (in terms of food) environment in which they live. My goal is to provide a mechanistic understanding of the functioning of individual plankters, both in terms of the interactions between the organisms and their immediate environment and in terms of the interactions between individuals. These are the topics of chapters 2–6. Second, I want to use the insights into individual-level processes to examine population- and ecosystem-level processes and patterns. Biological processes in the plankton occur at the level of the individual, and biological interactions in the ocean are between individuals rather than between populations or trophic levels; the latter are abstractions. Although the structure and function of pelagic food webs cannot be derived solely from a mechanistic understanding of the functioning of the individuals, important properties of distribution, population, and community patterns, and of the turnover of matter and energy in the plankton can be predicted from individual-level processes. This extension is the topic of chapters 7 (population processes) and 8 (pelagic food webs). The intention of these two final chapters is to illustrate the usefulness of combining oceanographic and biologic approaches to examine ocean ecology rather than to provide a complete description of pelagic ecosystems. Overall, throughout this book, emphasis will be on telling a coherent rather than a comprehensive story, and there are therefore many aspects of plankton ecology that are not covered here.

The intended audience of this book is motivated graduate and post-graduate students as well as researchers interested in plankton ecology. Most of the text has been developed for and used as teaching material for such groups. Knowledge of basic concepts of biological oceanography

and plankton ecology is assumed. Many biologists are afraid of hard sciences, such as physics and mathematics. However, to understand the adaptations and ecology of small pelagic organisms, we need to draw on simple fluid dynamics and diffusion theory. Use of mathematics is, if not unavoidable, then at least extremely useful in describing and communicating such issues. We shall keep it as simple as possible, and high school level performance in calculus is sufficient to be able to follow the arguments, if not always all details in the less important and trivial derivations. This is not only for pedagogic reasons—I am not a mathematician myself and, hence, am largely restricted to high school level math. Often I shall refrain from formal proofs but rather copy solutions from books and papers where such proofs have been derived. Emphasis is on understanding the causal relations and the idea of the argument rather than the formal proofs.

There are several books that treat the same general topic of small-scale biological/physical interactions as this one and provide both a much broader and deeper level of insight. I have myself been much inspired by Denny (1993), Vogel (1994), and Berg (1993), and the last two must be considered classics. All three books are written at a level that biology students will be able to read. Okubo (1980) is another classic but somewhat more difficult to read. None of these books refers particularly to plankton, and the present volume is an attempt to apply the principles described in the above books to plankton ecology. I will make particular reference to Denny (1993), and there will be some overlap between his book and this one. Finally, chapter 2 of Mann and Lazier (1991) provides an easy and helpful introduction to several of the topics covered here.

I will give many examples, and much of this account will in fact be driven by examples from which I shall try to generalize. I must confess that the choice of examples is very biased toward my own research and that of my students and close colleagues. This is not because these examples are the best but mainly because these are the examples through which I myself developed my understanding of planktonic organisms and pelagic food webs.