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Introduction

One objective of benthic ecology is to describe the spatial distribution of living organisms at or near the sediment–water interface, as well as to explain how and why the distribution occurs at that particular location on the seabed. The descriptive part of the job of the benthic ecologist thus becomes a sampling challenge since a depth gradient is involved from the intertidal to the hadal zone – a depth range of 0 to >6000 m (Parsons et al. 1977). Another sampling problem is that of substrate variability, thus hard, e.g. rocks and corals, versus soft substrates, e.g. muds, sands, and gravel, which means that appropriate samplers for each type must be quite different. Because it is considerably more difficult to sample at depth, the bulk of the available sampling results are for the littoral and sublittoral zones down to SCUBA diving depth. Thus, much of our knowledge of the spatial distribution of benthic organisms is heavily biased to these limited depths in the nearshore environment. The benthic animals which we would expect to be present in a grab or core sample of soft sediments in the nearshore region would include micro-, meio-, and macrofauna (Table 1.1). The size ranges shown are arbitrary and based on sampling convenience; thus, if a 0.5- or 0.8-mm mesh was used in sieving, then the lower size limit for macrofauna becomes 500 or 800 μm.

Because of a need to limit the size of this book, we have had to limit its subject matter to marine or estuarine benthic macrofauna and exclude micro- and meiofauna from detailed consideration. This is simply for presentation convenience and it is obvious to us that flow will have many important direct influences on micro- and meiofauna also. Thus, if barnacle cyprids can distinguish between microbial films developed on hard substrates in either low or high shear stress flows (see the section, Hard substrates, Chap. 3), then flow itself must be an important factor in shaping the microbial association which develops there.

Table 1.1. *Arbitrary size divisions of benthic fauna.*

Name	Size range (μm)	Examples
Microfauna	1–100	Some smaller Protozoa
Meiofauna	100–1000	Some Protozoa, e.g. Foraminifera; nematodes; harpacticoid copepods; gastotrichs; isopods; turbullarians; small macrofauna
Macrofauna	>1000	Amphipods, mysids, echinoderms, sponges, brachiopods, corals, hemichordates, echinoderms, molluscs, polychaetes
Megafauna	?	Cannot be adequately sampled with grab or corer, e.g. the mud star *Ctenodiscus crispatus* or benthic fish

Source: Based on Parsons et al. (1977).

The reader should be aware that there is a parallel interest among freshwater biologists (e.g. Hildrew and Giller 1994) in the effect of flow on river or stream benthos. For the same reasons of space limitation, we have not considered this work, except incidentally where research described presents a particularly good example of a pertinent interdisciplinary study.

This book is concerned only with those macrofauna characterized as suspension feeders that live on either soft or hard substrates of the seabed and feed in a particular way, that is by filtering microscopic particulates, or seston, transported to them by ambient flows. Our focus is the interactions which occur between individuals, populations of suspension feeders, or communities and ecosystems containing suspension feeders and the various types of water movement characterized as flow in the last paragraph of this section.

Functionally, benthic macrofauna can be classified as *suspension feeders*, *deposit feeders*, carnivores, omnivores, and algal scrapers (Chap. 7, the section, Benthic limitation by flow). The two major trophic types of macrofauna can be distinguished by their mode of feeding – deposit feeders are limited to soft sediments and ingest sediment which has already been deposited after seawater transport, while suspension feeders feed by capturing *seston*, a mix of microscopic particles which may contain detritus, bacteria, microalgae, small animals, and sediments, suspended in and transported by seawater flows. If the seston is carried by flow directly to the capture surface, the suspension feeder is described as *passive*. If, on the other hand, seawater containing seston is pumped by a ciliary or muscular pump to the capture surface, the suspension feeder is described as *active*. Further classification of passive and active suspension feeders is considered in Chapter 4 (see the section, Background).

Suspension feeders as a group comprise a diverse assortment of taxa drawn from most of the major invertebrate phyla inclusive of corals, hydrozoans, bryozoans, brachiopods, some polychaetes and bivalve molluscs, and a few echinoderms and crustaceans. Taxa which are found on hard substrates, e.g. barnacles, are generally *epifaunal*, living firmly attached to the rock or coral reef surface, and are said to be sessile. A few specialized species are able to burrow into some hard substrates, e.g. the rock-boring bivalve *Petricola pholadiformis*, which is also a suspension feeder. Soft sediment macrofaunal taxa may be either epifaunal and sessile, e.g. tube-living polychaete worms such as many spionids, or *infaunal*, that is to say, able to live and burrow within the sediment matrix, e.g. free-living polychaete burrowers such as *Chaetopterus variopedatus*. Again, both taxa are suspension feeders.

Flow is the general term that we have used for all the types of water movement which can occur in the marine or estuarine environment. Seawater movements include those caused by the action of winds directly on the sea surface (*wind–wave effects*), by the variable gravitational attraction of both moon and sun on seawater (*tidal currents*), or by density differences between different water masses due either to inequalities of heat exchange across the air–seawater interface or to differences in salinity (Tait 1968).

Asking the right question

Two general types of question apply in biology: *proximate* and *ultimate* (Alcock 1989). The proximate type equates to the "how does it work" questions of Table 1.2 and requires an answer based on a reductionist experimental program of inquiry. By contrast, the ultimate type is a "why" question involving knowledge of evolutionary mechanisms and history of evolutionary trends, often over significant geological periods.

Typical ultimate questions listed in Table 1.2 clearly demonstrate that most cannot be answered by reductionist experimental methods. Thus,

Table 1.2. *Some general questions related to the disciplines listed and referable to suspension feeders or the communities in which they live.*

Discipline	No.	Proximate	Ultimate
Physiology	1	How do suspension feeders filter feed?	Why did active suspension feeders evolve from passive ones (or vice versa)?
	2	How can energy costs of ciliary pumping be estimated?	Why did a ciliary pump evolve?
Ethology	3	How do competent larvae choose substrates suitable for initial colonization?	Why have some sessile suspension feeders evolved a short, and others a long, period of planktonic life?
	4	How do epifaunal suspension feeders become aggregated?	Why do hydrodynamic factors cause epifaunal suspension feeders to aggregate?
	5	How do some bivalve molluscs swim?	What adaptive imperatives resulted in swimming bivalves?
Ecology	6	How does larval retention in an estuary occur?	How do larvae with specific responses to environmental variables, e.g. light, gravity, and flow, evolve?
	7	How do mixed benthic assemblages dominated by suspension feeders occur?	What causes a mixed benthic assemblage dominated by suspension feeders to evolve?
	8	How are materials cycled between pelagic and benthic parts of an ecosystem?	Why do ecosystems evolve over geological time?

for the first physiological ultimate question of Table 1.2, we have no direct knowledge of the ancient environments which may have resulted in the development of an active suspension feeder, nor any idea of the evolution of its ciliary pump since they are soft structures which are not preserved very well in the geological record. Although circumstantial evidence from the geological record may help, e.g. general climatic conditions deduced from stratigraphic deposition or from the morphology and physiology of extant ciliary pumps from "primitive" to "advanced" forms, such deductive methods often do not provide an adequate answer for the ultimate questions. For this reason, we have limited the questions addressed in Chapters 3 to 8 to those that are clearly proximate in nature. In Chapter 9, where possible future benthic biological questions are posed, we include consideration of ultimate ones.

As pointed out by Fenchel (1987), biology as a scientific discipline is organized hierarchically. At the most complex organizational level is the *ecosystem*, by which is meant a community of living organisms, together with the physical and chemical environmental factors present interacting together to form a recognizable ecological unit, e.g. an estuary. Descending the list of hierarchical order, we thus arrive at successively lower levels – ecosystem, community, population, individual, organ, cells, organelles, and molecules (Fenchel 1987). As pointed out by Fenchel, these levels of organization correspond to the specialized subdisciplines of biology: *ecology*, inclusive of ecosystems, communities, or populations; *ethology*, inclusive of social groups and individuals; *physiology*, inclusive of individuals and organs; *cell biology*, inclusive of cells and organelles; and *biochemistry*, inclusive of organic molecules. From this list we have selected the three higher hierarchical levels and thus subdisciplines of biology – ecology, ethology, and physiology – to investigate benthic interactions with flow.

Where the focus of concern is the individual animal as in ethology and physiology, it is easy to appreciate how a reductionist research program could be developed into an experimental study of any suspension feeder. In ecology, where the unit of study ranges from a population to an ecosystem, that is to say, a mussel reef to the whole estuary in which the mussels live, it is much more difficult to see which questions are appropriate. Thus, it becomes necessary to determine exactly what are valid ecological questions. Fenchel (1987) defines ecology as "the study of the principles which govern temporal and spatial patterns of assemblages of organisms." This succinct wording is a good encapsulation but does not quite convey the depth of the subject matter, and a more complete snapshot of ecology, at least in the mid-1980s, can be gleaned from an opinion survey of 645 members of the British Ecological Society (Cherrett 1989). This group was composed of university trained ecologists with mixed backgrounds and employment, who suggested 236 different concepts as fundamentally important in ecology. Considerable overlap in the concepts existed and, using the data provided by Cherrett (1989), we suggest that they can be reduced to the seven shown in Table 1.3.

Table 1.3. *Important concepts in ecology derived from a survey conducted by the British Ecological Society.*

No.	Description	Examples
1	Spatial	Studies involving the ecosystem, community, and niche
2	Temporal	Studies involving succession, climax, and diversity
3	Energy flow process study	Energy flow, materials cycling, and food webs
4	Biological interactions	Competition, density dependence, and predator–prey studies
5	Limiting factors	Physical limitations in ecology at various hierarchical levels
6	Evolution	Life history strategies, adaptations, and co-evolution
7	Ecosystem management	Conservation, ecosystem fragility, and maximum sustainable yield

Source: Cherrett (1989).

In this book we have excluded the long-term, temporal perspective in line with our resolve to exclude ultimate questions (number 6, Table 1.3), and because succession, climax, and diversity concepts (number 2, Table 1.3) have not been studied in relation to flow. This means that our attention is given entirely to numbers 1, 3, 4, and 5, but omitting 7, in Table 1.3. This is not as ruthless as it may sound since there is only a small amount of work published on evolutionary aspects of benthic biology. In any case, we return briefly to pertinent questions concerning numbers 6 and 7 (Table 1.3) in Chapter 9.

Benthic biology is a relatively young scientific discipline. Its quantitative study dates from the work of the Danish investigator Petersen (1911), who studied those factors which regulate benthic macrofaunal density and biomass in order to predict the productivity of benthic feeding and commercially important groundfish. It is only since the early 1970s that the focus of benthic biological research has moved from observation to inferential experimentation, with a more rigorous effort at field or laboratory experimentation. This may help explain why benthic biology has so few widely applicable predictive models to offer the newcomer to this field.

Table 1.4. *Major types of scientific method.*

Type	Description
Observation	*Simple*: involves direct experience, e.g. looking down a microscope. Includes descriptive taxonomy, natural history observations. *Complex*: sampling or measurement which may involve bias, e.g. benthic grab sampling involving different sieve mesh sizes in sorting the animals.
Theory/model	*Reductionist*: a way of looking at a subfield of benthic biology which can be represented verbally or by a simple conceptual model, e.g. the benthic limitation by flow theory (see Chap. 8). *Holistic*: as above, except that because of complexity or the nature of the model, formal mathematical representation is required, e.g. an ecosystem simulation of a bivalve reef based on energy flow.
Inferential experimentation	Laboratory or field experimental tests of formulated null, H_0, and alternate, H_1, hypotheses.
Criticism	Logical refutation of any conclusions or constructs derived from any of the types of scientific method described here.

Scientific methods

Science is concerned with the creation and communication of knowledge. Concerning the first of these, scientific knowledge is created by one of the four major methods shown in Table 1.4.

Observation, in both the field and laboratory, is fundamentally important to the scientific enterprise. During this process, realistic questions and, hence, theories, models, or hypotheses are formulated. Such formulations are possible constructs determined by logical reasoning concerning the relations of benthic animals to the observed external world.

As pointed out by Peters (1991), there is no consensus on how words like theory, model, and hypothesis are used, and he recommends using them synonymously. In our account, we define *hypothesis* as a working explanation of observations proposed in such a way that an experimental test can choose between two contrasting constructs – null and alternate. The hypothesis may apply fully, or only partially, to the theory or model constructs which are conceived to be at a higher hierarchical level. The

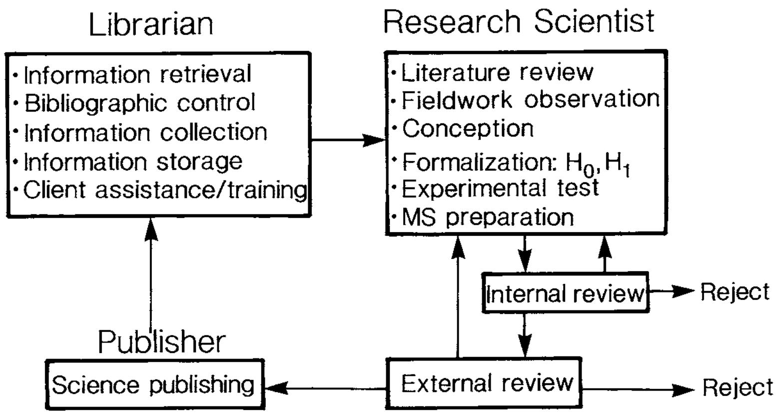

Figure 1.1 Outline of the process used in science to conceive, experimentally test, disseminate, and store information.

alternative and null hypotheses are tested by inferential experimentation with the desired outcome that one or other of the constructs can be discarded as a result of the test. As pointed out by Sprintall (1990), care must be taken to distinguish between post facto and experimental research. The former concerns field studies where independent and dependent variables are not assigned before the work begins and, hence, causation or rejection cannot be established. In experimental research, the independent and dependent variables are established before the work begins and, if the results warrant, can lead logically to the rejection or establishment of cause. If a theory or model can be represented by a simple conceptual model, we refer to it as a reductionist model, in contrast to a complex model, which requires mathematical formalism to express it and which is referred to as an holistic model.

Criticism, either from one's self, using accumulated experience, or from others and formally expressed as in a written review, informally as during a workshop, and as part of the peer review process before primary publication (Fig. 1.1), is important to the well-being of the scientific knowledge database. It is during the critical process that judgements of hypotheses are made.

An outline of the process used to conceive, test, and store scientific information is shown in Fig. 1.1. Peters (1991) has characterized hypothetico-deductive science as an alternation between creation and criticism. For the research scientist, it is in the private or synthetic phase of the process shown in Fig. 1.1 (first three items in the box) where the individual creates a new theory and/or new hypothesis referable to an already established theory. Exactly what is involved in the synthetic phase of science has proved difficult to define (Peters 1991). The creative process involves keen observation and intuition, an ability to juxtapose two apparently unrelated ideas, or use of accepted theories from related disciplines. It is the latter process which is the main approach used in this book with benthic biology as the recipient of theory from the well established discipline of hydrodynamics.

It is frequently necessary to use multiple hypotheses to solve a scientific question, e.g. in determining the precise mechanism of filtration in suspension feeders (Chap. 5), and this approach is championed by Platt (1964) and Chamberlin (1965). Quinn and Dunham (1983) drew attention to the difficulty of applying Baconian experimental tests to pairs of mutually exclusive hypotheses in many ecological questions where multiple alternative hypotheses represent the usual situation. As an example, we site the growth or production of a suspension feeder population. Here, the null hypothesis might be that flow does not affect suspension feeder growth, but is swamped by multiple alternative environmental factors, e.g. seston concentration, seston quality, temperature, or growth-limiting flow at high velocity. According to Simberloff (1983), multiple alternative hypotheses should be met by increased ingenuity from researchers in framing unambiguous hypotheses capable of dealing with multiple alternatives and the potential interactions between them.

Scientific communication

Concerning the communication of science results mentioned earlier, the active participants in science tend to form into natural groups which are referred to as an "invisible college" because of shared research interests and problems. Communication is the most important function of the invisible college and various ways have been tried to optimize it. These include personal communication (often electronic), workshops, symposia, published periodicals, and books.

In regard to periodicals, there are four distinct types: *science magazines*, which provide interpretive articles for a multidisciplinary audience, but not original research articles (e.g. *New Scientist, Scientific American*); *technology transfer periodicals*, whose purpose is to transfer science to a commercially active field such as aquaculture (e.g. *World Aquaculture*) but which does not usually carry original research; a few *multidisciplinary journals*, notably *Science* and *Nature*, which contain original abbreviated research articles thought to be of wide general interest and from all fields of science, including physics, chemistry, biology, geology and medicine; and single discipline or *primary journals*, which contain original research articles from a specific area of research or subdiscipline and therefore are targeted to a specialized audience. As a result of recent advances in electronic publishing and the widespread use by research scientists of personal computers, the future possibility of online journals is real (Maddox 1992). Nevertheless, in 1997, the printed word remains the pre-eminent means of communication for the aquatic sciences.

The creation and communication of scientific knowledge in printed multidisciplinary or primary journals involve three different types of professional (Fig. 1.1). The research scientist creates scientific knowledge and describes the work in research articles or evaluates the work of other research scientists in review articles. The publisher prepares copy for the journal consisting of a series of research articles and is responsible for preparing a sufficient number of copies for wide dissemination among the extended invisible college. Wide dissemination of printed copy is less important today because of the availability of online electronic abstracting services with which, and by using key words, relevant articles can be obtained. The librarian assists the research scientist by facilitating access to published sources by collecting, storing, and retrieving articles involving bibliographic control inclusive of indexing, abstracting, and classification.

Newcomers to the interdisciplinary field of hydrodynamics/benthic biology may need assistance in finding reliable literature sources which explain the physics of flow. Some of the sources which we have found helpful may be of interest. There are two excellent introductions to hydrodynamics for biologists: Vogel (1981), *Life in Moving Fluids: The Physical Biology of Flow*, recently revised and expanded in a second edition (Vogel 1994); and Denny (1993), *Air and Water: The Biology and Physics of Life's Media*. Both provide an introduction to the fundamental principles of hydrodynamics and many applications of interest in benthic biology. Denny (1988) has also provided a similar introduction and also an account of flow phenomena on the wave-swept shore. These books interpret the solid body of accepted hydrodynamic theory developed by mathematicians, physicists, and engineers over a period of more than 150 years. For the more mathematically adept, there are many introductory texts in fluid dynamics which might be consulted. We have found Daugherty et al. (1985), *Fluid Mechanics with Engineering Appli-*