The Fertile Fjord

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Plankton in Puget Sound

Richard M. Strickland

With a Foreword by Joel Hedgpeth

PUGET
SOUND
BOOKS

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To my parents, Dick and Margo.
Without their unwavering support,
this book would not have been possible.

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SOUND
BOOKS

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About the Puget Sound Books

This book is one of a series of books that have been commissioned to provide readers with useful information about Puget Sound . . .

About its physical properties—the shape and form of the Sound, the physical and chemical nature of its waters, and the interaction of these waters with the surrounding shorelines.

About the biological aspects of the Sound—the plankton that form the basis of its food chains; the fishes that swim in this inland sea; the region's marine birds and mammals; and the habitats that nourish and protect its wildlife.

About man's uses of the Sound—his harvest of finfish, shellfish, and even seaweed; the transport of people and goods on these crowded waters; and the pursuit of recreation and esthetic fulfillment in this marine setting.

About man and his relationships to this region—the characteristics of the populations which surround Puget Sound; the governance of man's activities and the management of the region's natural resources; and finally, the historical uses of this magnificent resource—Puget Sound.

To produce these books has required more than six years and the dedicated efforts of more than one hundred people. This series was initiated in 1977 through a survey of several hundred potential readers with diverse and wide-ranging interests.

The collective preferences of these individuals became the standards against which the project staff and the editorial board determined the scope of each volume and decided upon the style and kind of presentation appropriate for the series.

In the Spring of 1978, a prospectus outlining these criteria and inviting expressions of interest in writing any one of the volumes was distributed to individuals, institutions, and organizations throughout Western Washington. The responses were gratifying. For each volume no fewer than two and as many as eight outlines were submitted for consideration by the staff and the editorial board. The authors who were subsequently chosen were selected not only for their expertise in a particular field but also for their ability to convey information in the manner requested.

Nevertheless, each book has a distinct flavor—the result of each author's style and demands of the subject being written about. Although each volume is part of a series, there has been little desire on the part of the staff to eliminate the individuality of each volume. Indeed, creative yet responsible expression has been encouraged.

This series would not have been undertaken without the substantial support of the Puget Sound Marine EcoSystems Analysis(MESA) Project within the Office of Oceanography and Marine Services/Ocean Assessment Division of the National Oceanic and Atmospheric Administration. From the start, the representatives of this office have supported the conceptual design of this series, the writing, and the production. Financial support for the project was also received from the Environmental Protection Agency and from the Washington Sea Grant Program. All these agencies have supported the series as part of their continuing efforts to provide information that is useful in assessing existing and potential environmental problems, stresses, and uses of Puget Sound.

Any major undertaking such as this series requires the efforts of a great many people. Only the names of those most closely associated with the Puget Sound Books—the writers, the editors, the illustrators and cartographers, the editorial board, the project's administrators and its sponsors—have been listed here. All these people—and many more—have contributed to this series, which is dedicated to the people who live, work, and play on and beside Puget Sound.

Alyn Duxbury and Patricia Peyton
June 1983

Foreword

In the 1950s, during the first flowering of oceanography after World War II, great public interest and expectation was aroused in the Sunday supplements and more substantial magazines for a future of limitless food from the sea. The vast hordes of plankton were an untapped resource, and certain plankton organisms, especially *Chlorella* would be cultured with ease and economy. As Lionel A. Walford remarked, what was expected "was an entirely new kind of food that can be produced in massive quantities at neglible cost, which somebody will eat, presumably the backward peoples." One Japanese gentleman, lecturing at Scripps Institution of Oceanography, told us that the product of mass culture of *Chlorella* tasted like soy sauce, "but we Japanese like soy sauce."

It was during this excitement that Carl Sauer granted me permission to audit his course in natural resources (Geography 153) provided I took over his pulpit for a week when he was off to Washington. I wish I had had a book like this about the plankton of Puget Sound from which to crib the material and to place on the class reading list. I had only three days to explain the resources of the sea to a group of students who were only beginning to learn that geography, as Carl Sauer saw it, was not an armchair review of the less substantial articles in National Geographic magazine but a solid part of the science of the environment. After my first lecture on the phytoplankton base of the resources of the sea, one of my friends overheard one of the students in the hallway afterwards remarking "I never heard of this business of little one-celled plants without roots. Does this guy know what he's talking about?"

Things have changed since then, even at Berkeley. We do know enough, I think, to realize that plankton is part of a system, not a harvestable end in itself. The world of the plankton and its intricate internal relationships is not a subject for a brief overview if we are concerned with man's present and future reliance upon the resources of the sea. The National Sea Grant College Program is a response to the need for understanding the resources of the sea and how to utilize them in the future. This book on the plankton of Puget Sound meets that need admirably, and, along with the handbook of marine birds and mammals and future volumes on biology and oceanography (in conjunction with those on history and economics of Puget Sound) will be a most significant contribution of the Washington Sea Grant Program to the people of the region it serves. It should be the envy of, and set the example for, other Sea Grant programs in the nation. Knowledge acquired and stored away in data banks or presented in scattered brochures is not really knowledge. Like the tree that falls in distant Siberia, it makes no sound when there is no one to hear it.

Joel W. Hedgpeth

Preface

Great literature, until the last century or so, glorified only great adventurers and nobility. It ignored the masses of common people that make society function. So it is still with popular studies of the sea—the noble whales and sharks get more attention than the multitudes of tiny organisms that they simultaneously rule and depend upon. This book attempts to redress that imbalance, at least for Puget Sound. The Sound is a bountiful body of water due to a unique coincidence of physical and biological properties, at the center of which is the invisible, anonymous proletariat of the plankton.

This book is intended as a capsule review for scientists and nonscientists with an interest in natural history of plankton and its relationship to the pelagic food web in Puget Sound. It is not intended as a field guide to plankton, several of which already exist; instead, it is a synthesis of ecological knowledge that bridges some conceptual gaps in existing data. Paradoxically, although there is much more information about plankton than reasonably could be presented here, there are also disturbing voids in our knowledge that can be filled only by further research. If readers are left with unanswered questions and an appetite for more information, the book will have achieved its goal of capturing interest in this fascinating but often overlooked subject.

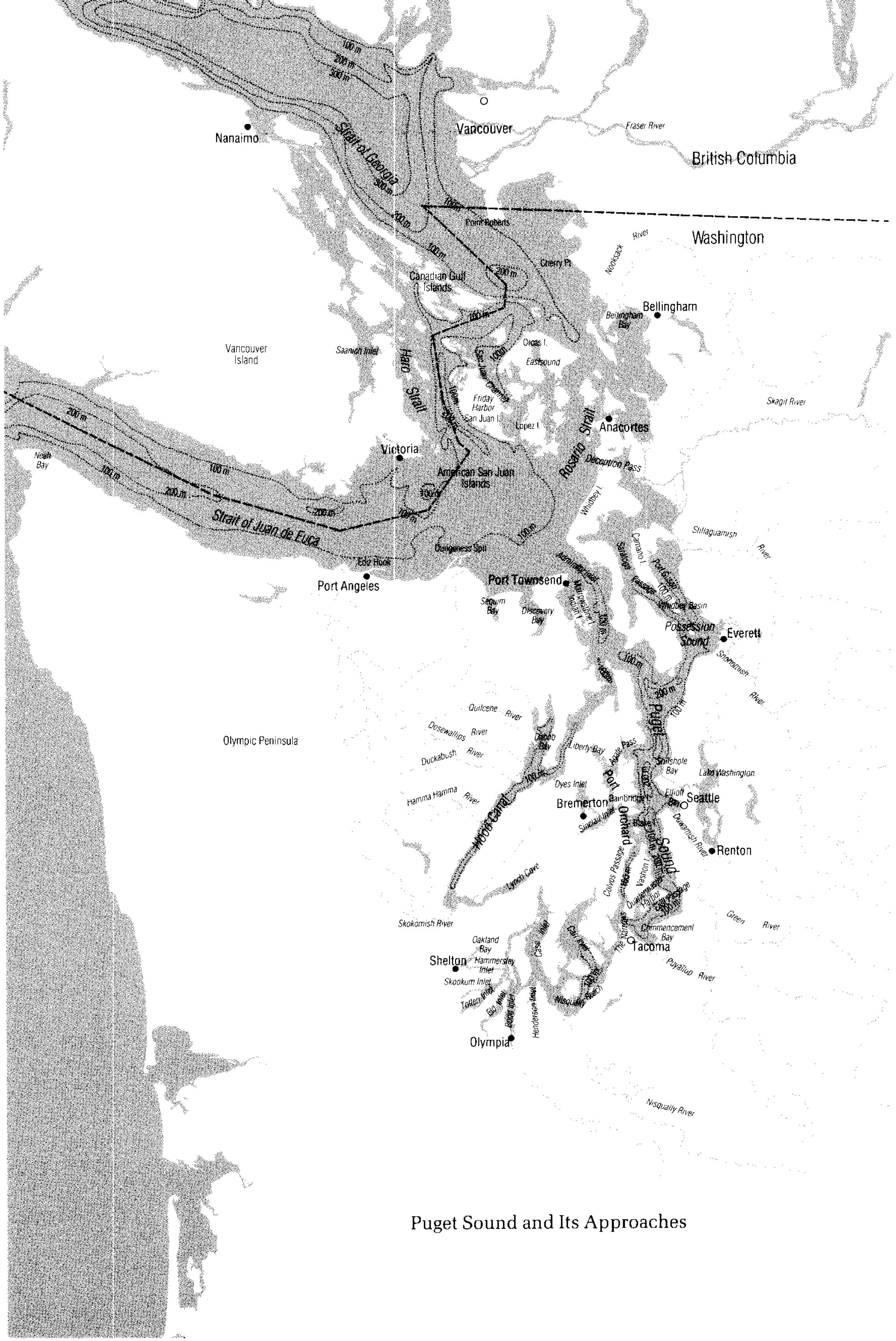
Richard Strickland
June 1983

Acknowledgments

This book represents the enormous efforts of many people besides myself, especially Washington Sea Grant staff members Andrea Jarvela, Cathy Lauenstein, Patricia Peyton, Alyn Duxbury, Kirk Johnson, Diana Jensen, and Laura Mason. Valuable contributions came from the careful reviews of Karl Banse, Mark Ohman, Louisa Nishitani, and Eugene Collias of the University of Washington, Kurt Fresh of the Washington Department of Fisheries, and Puget Sound Books Editorial Board members Michael Waldichuk and Elizabeth Twiss. George C. Anderson of the University of Washington helped obtain the contract and offered encouragement at the outset, as did Alexander J. Chester (now of Beaufort, North Carolina) and Kathleen J. Smith, M.D., (now of Durham, Pennsylvania). The title was graciously provided by Cynthia Marks of the University of Washington.

Many people generously discussed the text and helped develop illustrations: Kenneth Adkins, Keith Benson, Kendra Daly, T. Saunders English, Noel McGary, Kathy Newell, Mark Ohman, James Postel, Jeanette Yen, and the staff of the Fisheries-Oceanography Library of the University of Washington; Kevin Bailey, Edward Baker, Robert Burns, David Damkaer, Richard Feely, Howard Harris, and Marilyn Lamb of the National Oceanic and Atmospheric Administration; Dale Anderson, Michael Bertman, Robert Dexter, and Elizabeth Quinlan with whom I worked at the URS Company, Seattle; Steve and Jan Smyth of Smyth Associates Inc., Kirkland; and Buzz Shaw of the Seattle Aquarium. Some electromicrographs appear courtesy of Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle. Some unpublished data appear courtesy of Municipality of Metropolitan Seattle (METRO).

A special thanks to Denise Krouse and to all my friends in Seattle for their moral support.



Puget Sound and Its Approaches

Plankton

Sometimes, at night, each one
has a lightning bug in it.
That's how you see them,
invisible
under and around the boat.
I drop a pail over the side

think how for herring
they are three meals,
phosphorescence
in the flesh of bass
and the deep blueness of whales.

They live their lives unseen,
not just gray mobs without faces
but like calm steady workers
in some underground plot
to keep the world alive.

I stare into the pail
where thousands drift.
When the sky is dark enough
I'll row the dinghy out and lift
oarsful of their dripping light.
I won't miss the sun on the other side
because it is here,
brushed angel wings
when I dive and float
flapping my arms.

Later, I'll towel them from my skin,
taste salmon,
oysters,
some of the little light.

Joan Swift

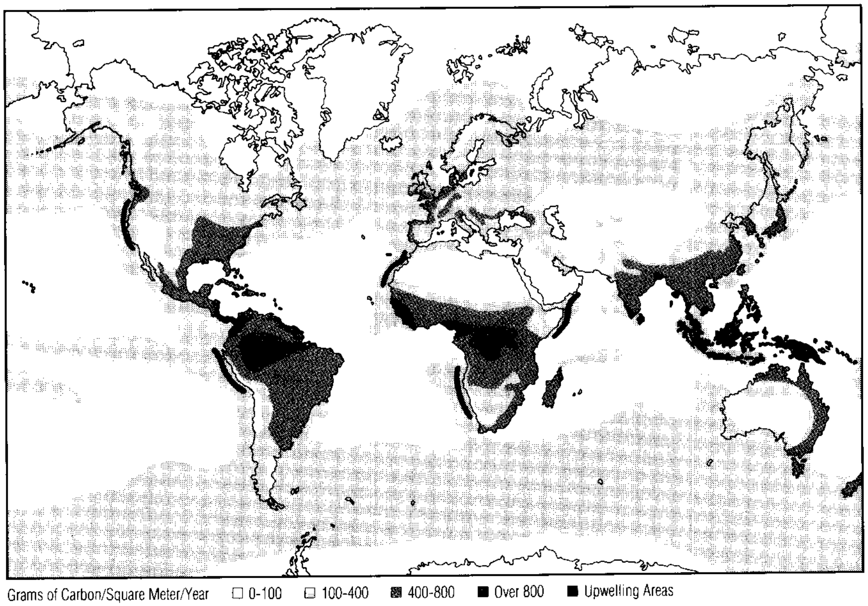


Figure 1.1 Global distribution of plant productivity, based on average annual production of plant matter per unit area. The most productive regions are marshes, reefs, and tropical forests. The open oceans are as unproductive as terrestrial deserts. Coastal waters, on the other hand, are where planktonic plants are most productive and support 99 percent of the world's commercial fish catch. Half of that catch comes from areas where plankton growth is stimulated by upwelling of water, as also occurs in Puget Sound. (After Rand McNally, 1977)

CHAPTER ONE

Plankton Primer

> The role of the infinitely small in nature is infinitely great.
> Louis Pasteur

The most important animals in Puget Sound, as in the ocean at large, are neither the most obvious nor the most beloved. They are not the whales, nor the salmon, nor the clams, crabs, or octopi. Neither are seaweeds the most important plants in the Sound. Floating freely with the tides and currents, little known and nearly invisible, are the tiny plants and animals of the plankton. What these organisms lack in size and glamour, they compensate for in importance to all marine life.

The larger, better known, and seemingly more important marine organisms are barely significant to the living yield of the sea as a whole, and their absence, though regrettable, would not threaten the grander web of life on earth. Steinbeck said:

> The disappearance of plankton, although the components are microscopic, would probably in a short time eliminate every living thing in the sea and change the whole of man's life, if it did not through a seismic disturbance of balance eliminate all life on the globe.

We have since learned that terrestrial life could continue without the plankton, and that some exotic animals subsist only on hot chemicals belching from the sea bottom, independent of other marine life. Yet despite these discoveries, plankton still is to the ocean what grasses and flowers, insects and rodents are to the land. Fishes fatten on swarms of diminutive animals grazing in pastures of microalgae, all suspended in a four-dimensional fluid world. Indeed, a diet of planktonic krill sustains the largest creature ever to live, the blue whale.

Plankton dominates the biological budget of the sea. Of all the marine plant and animal tissue produced beyond the immediate fringes of the shoreline and the bottom, more than 90 percent is plankton. This is particularly true in Puget Sound, where the rate of plant production ranks among the highest in saltwater environments, rivaling that of terrestrial forests and farms (Figure 1.1 and 1.2). Furthermore, the yield to humans of fish and shellfish is governed in large part by the growth of the plankton on which these animals or their prey depend. The oceans cover two-thirds of the planet, but virtually all commercial fish tonnage comes from the relatively shallow areas flanking the continents, where plankton growth is most vigorous.

To the biologist who looks at the entire marine world, plankton is clearly the principal life form, and Puget Sound is an ideal place to study it. This book will describe the unique characteristics of plankton that make it abundant, ubiquitous, and vital to life in Puget Sound. Far from being exotic and abstruse, plankton research is the very heart of marine biology.

Plankton—The Drifters

"Plankton" is derived from a Greek word which means "free-floating." While many plankters can swim as well as float, plankton includes any aquatic—in this case, marine—organism living unattached and having swimming power insufficient to resist most water currents. But there is more to the definition, as described by Hardy:

> "Plankton" is one of the most expressive technical terms used in science and is taken directly from the Greek. It is often translated as if it meant just "wandering," but really the Greek is more subtle than this and tells us in one word what we in English have to say in several; it has a distinctly passive sense meaning "that which is made to wander or drift," i.e. drifting beyond its own control—unable to stop if it wanted to.

Plankton includes bacteria, plants, animals, and even some organisms that seem both plant and animal. In keeping with their weak mobility, most planktonic organisms are quite small; few are larger than a common housefly.

The term phytoplankton refers to those members of the plankton which make their own food from sunlight. All phytoplankters (except perhaps some photosynthetic bacteria uncommon in Puget Sound) belong to that group of plants called algae, which also includes seaweeds. Non-photosynthetic bacteria that live suspended in the water are called bacterioplankton. All other plankters—that is, all of the planktonic animals—are referred to as zooplankton.

Plankton contains an extremely diverse range of organisms; nearly every major group of animals has representatives in the zooplankton. Many creatures exist in the plankton only until they grow large enough to swim independently (such adults are called nekton), or until they are transformed to live as adults (the benthos) on the sea bottom. These temporary zooplankters—larval stages of such animals as crabs, starfishes, clams, and some fishes—are called meroplankton. Organisms remaining in the plankton their entire lives are called holoplankton.

Why Plankton Is Important

"Plankton" is an unusual term in biology—it classifies organisms according to their locomotion rather than their genetic kinships. The unique constraints and consequences of the planktonic lifestyle merit separate consideration in science. The most significant roles of the

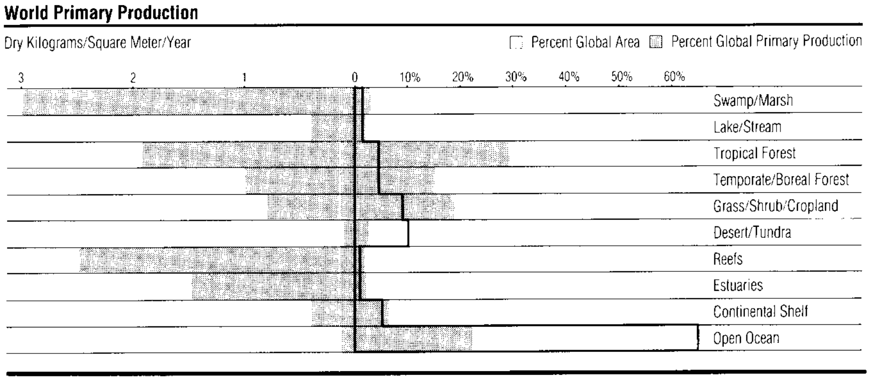


Figure 1.2 Average annual production of plant matter in different ecosystems shown by two measures: dry yield per unit area and the fraction each contributes to worldwide yield based on its global area. The oceans are mostly unproductive except near the coasts, hence the two-thirds of the earth covered by water contributes only one-third of global plant production. (After Whittaker, 1975).

plankton are as sources of food, oxygen, and energy, as ecological and paleoecological indicators, and as poison.

Food Source

Plankton is the nutritional foundation of the sea's biological edifice. The breadbasket of the sea is the phytoplankton; phytoplankton is food for zooplankton, and zooplankton is food for fishes, leading finally to birds, mammals, and humans. Furthermore, the corpses and non-living organic by-products of all these organisms sink and sustain animals on the sea bottom. Outside of some in the shallowest few meters of water close to shore, virtually all marine animals are ultimately dependent on plankton. Some people believe that plankton can become a food for humans as well.

Oxygen Source

All of the oxygen that animals and plants respire is generated by the photosynthesis of plants, from the splitting of water molecules using solar energy. Photosynthesis also removes excess carbon dioxide from the atmosphere. Primitive phytoplankton in the primordial sea changed the world forever by introducing oxygen into the atmosphere over a billion years ago. Phytoplankton today produces 95 percent of the oxygen generated in the sea, and a third of the earth's oxygen (oxygen of terrestrial origin could still sustain the earth if plankton disappeared). While most marine oxygen comes from the expanses of the open oceans, areas such as Puget Sound are more than ten times as productive for their area (Figures 1.1 and 1.2).

It is also a paradox that these organisms that supply oxygen sometimes also cause oxygen shortages in waters of the Puget Sound area. The decay of dead phytoplankton can strip the oxygen from stagnant waters. In a few places in Puget Sound, following rapid outbursts of phytoplankton growth probably aggravated by pollution and other human activities, acute episodes of oxygen depletion cause problems for fishes and other animals. Some inlets in the area also have natural, chronic oxygen shortages to which certain animals seem to have adapted.

Energy Source

Settled to the ocean bottom, buried, compressed, and heated under just the right geological conditions for millions of years, plankton becomes the viscid stew we now tap as petroleum. In crude oil are found hydrocarbons, mostly derived from the lipids of phytoplankton, that are the remnants of blooms millenia ago. Traces of plant pigments still appear in oil. Fossilized zooplankton droppings are found in oil shale deposits, and many of the components of oil have properties, such as the predominance of light isotopes of carbon and the ability to rotate the plane of polarized light, that can be directly related to planktonic origins.

Oil today is generated continuously on the ocean floor by the liquefaction of plankton sediments, but this renewable resource is far from boundless. If all the plankton produced in the world in a year became oil (which it does not), it would supply the United States—assuming a rate of consumption of nearly 20 million barrels a day—for less than a week. Oil is found where plankton was most productive during geologic history, along the ancient continental shelves, reefs, and inland seas and lakes. Puget Sound might be an outstanding location for drilling operations in a few million years, if it isn't wiped out by another ice age.

Ecological and Paleoecological Indicator

Geologists obtain from fossils information about the nature of the environments in which fossils form and the relative ages of the rocks containing them. Certain planktonic species are known to have existed only at certain geologic times, and to have been associated with known sets of conditions. By analyzing the shapes and chemical makeup of tiny shells left by plankters millions of years ago, paleontologists can trace ancient fluctuations in global climate, and chart historical changes in ocean currents and salinity.

Biologists can also tell a great deal about today's water bodies from their plankton communities. A particular composition of plankton is a signal, for example, of deterioration of water quality. The eutrophication of Lake Washington due to sewage during the 1960s was diagnosed by the appearance of eutrophic-type plankters in time to avert widespread beach closures and loss of fish populations. Lake Washington is now being rehabilitated, as demonstrated by the return of plankton that is characteristic of cold, clear, clean lakes.

Poison

In the autumn of 1978 several persons became ill after eating shellfish gathered from Whidbey Island beaches. State health officials sampled the shellfish and immediately closed the affected beaches, because of the presence of paralytic shellfish poisoning (PSP). The illness is caused by toxins formed by a species of phytoplankton and accumulated in the tissues of mussels, clams, and oysters feeding on the plankton. Such outbreaks are called "red tides." Plankton sometimes does grow densely enough to tint the water red, but the relationship between red tides and PSP is not so simple.

PSP toxins are some of the many chemicals—including ordinary mineral nutrients—that can be transferred from plankton to higher animals. Of particular concern are those toxins which concentrate in living tissues. Now banned in the United States, the insecticide DDT is a classic example. DDT was found in higher concentrations in fishes than in the plankton they eat, and in some locations reached harmful levels in certain fish-eating birds. The plankton occupies a crucial role in the pathways by which the growing number of such industrial chemicals now finding their way into the marine environment reach higher animals and people.

The chapters that follow will elaborate on the roles of plankton in food production and in pollution in Puget Sound. First, however, we will gain some familiarity with plankton, the world it inhabits, and how scientists study it.

CHAPTER TWO

Studying Plankton

> The first requirement of a scientist is that he be curious. He should be capable of being astonished and eager to find out.
>
> Erwin Schroedinger

The waxing and waning of plankton in Puget Sound are scarcely visible to the naked eye. We cannot see that plankton swarms drift across its surface like clouds across the sky. At times we may see faint gradations of color, from wintry blue to muddy brown to spring green, or occasional prominent red tides, but most of the affairs of the plankton are as private as those of deep-sea creatures. SCUBA divers have a closer perspective, but what they gain from proximity, they lose in breadth and depth of vision. Fortunately, with the aid of ships and instruments, we can crudely construct what our eyes fail to perceive directly.

Sampling

Sampling is the central art of the outdoor sciences, and of biological oceanography in particular. What is known about plankton is dictated ultimately by the act of sampling, for we can learn little about organisms we cannot capture. A plankton sample is a window for viewing microscopic sea life. If some plankters escape sampling, then that view is obscured or distorted.

Plankton nets are used to capture and concentrate organisms living in a dilute suspension in the upper layers of sea. Used by fishermen for centuries, nets were adapted to fish for microorganisms only with the advent of the microscope. In 1828 J. Vaughn Thompson of Cork, Ireland sewed silk cloth of the type used for sifting flour into a cone. When pulled through the water, the cloth strained out tiny organisms and deposited them in an open jar sewn onto the pointed end. Thompson called his device a tow-net, and modern plankton nets are hardly different. Charles Darwin used a tow-net aboard the *Beagle*, on the cruise which stimulated his 1859 *Origin of Species*. Tow-nets were also standard equipment aboard the *H.M.S. Challenger*, which departed England in 1872 for four years at sea, on a voyage commonly regarded as marking the birth of modern oceanography.

To Darwin and his peers, nets and microscopes revealed nothing more than smaller members of the known groups of plants and animals. It was not until 1887 that Victor Hensen of Kiel, Germany thought of the organisms caught in tow-nets as a distinct biological community and coined the term plankton. It was an innovative way to classify organisms—by their habitat and locomotion rather than by their ancestry—and it grew out of sampling technology.

No single net can faithfully sample all types of plankton. Plankton nets come in two varieties, those used for capturing phytoplankton and zooplankton. Phytoplankton nets, now seldom used, are small with a fine mesh for capturing abundant (up to several million per liter) tiny cells. Zooplankton nets are larger and coarser-meshed, for pursuing larger and scarcer organisms (Figure 2.1). They offer less resistance when pulled through the water, and the mesh is large enough to allow phytoplankters and some of the smaller animals to pass through to reduce clogging. This permits the net to be towed at the higher speeds necessary to capture large animals with some swimming ability.

Numbers and types of plankters differ from surface to deep water. The earliest plankton nets could not realistically sample deep-water plankton, because the open net would be contaminated with surface

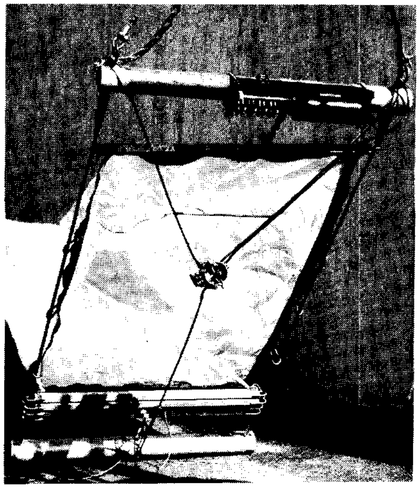
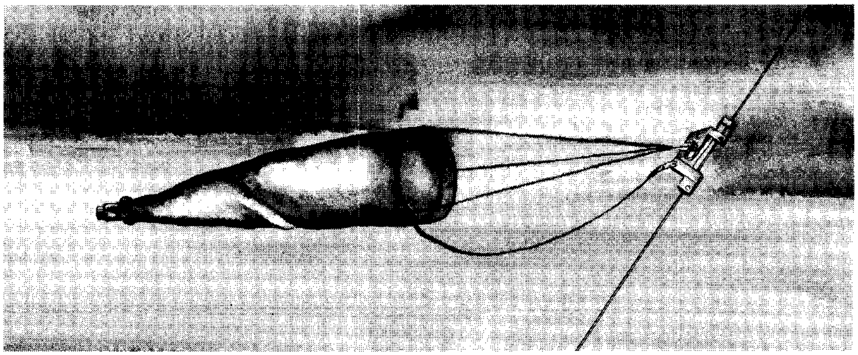


Figure 2.1 The simplest and oldest zooplankton net (below) is a cone about one meter across, six meters long, with 0.3–0.6 millimeter mesh. The modern Tucker trawl (left) is two meters square, has a flow meter, and is really several accordion-like nets opened by electronic signals to sample sequential depth strata. (Courtesy B. W. Frost)



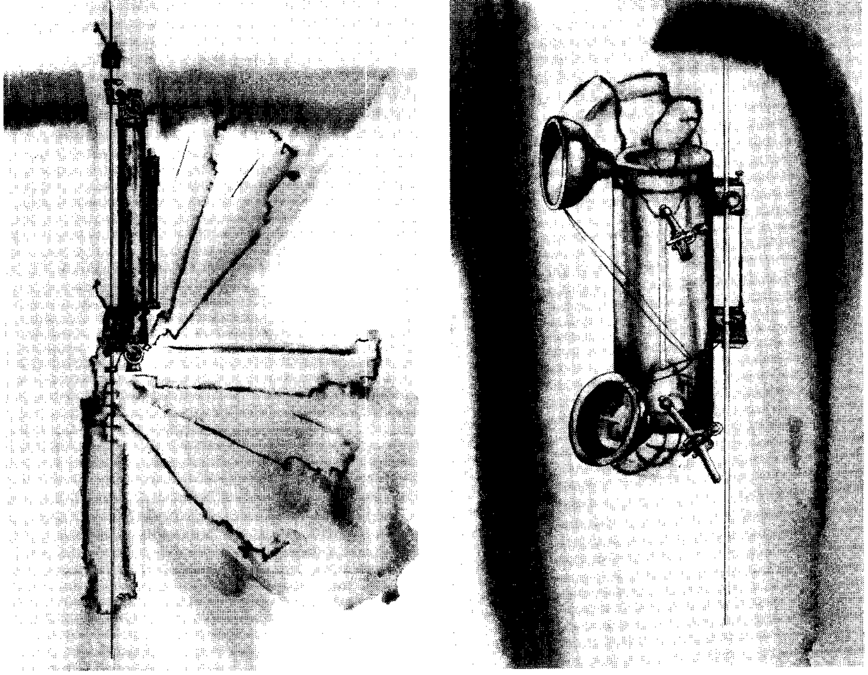


Figure 2.2 An early standard sampling bottle (left) was named for Norwegian explorer Fridtjof Nansen, who froze his ship in arctic ice for three years to follow the currents. The one-liter Nansen bottle, made of galvanized steel, inverts to close and trap the sample. The Van Dorn bottle (right) is larger and made of nontoxic plastic to reduce inhibition of plankton growth. It is closed by a weight that releases two rubberband-loaded plugs.

plankton as it was retrieved. Thus an early improvement to net design was a capability for closing the net and isolating deep-water samples.

A modern net may also have a flow meter to measure the volume of water sampled, permitting a count of animals per unit volume. Small zooplankton nets can capture animals the size of copepods, while larger and faster midwater trawls must be used to capture the strongest swimmers, such as planktonic shrimps and larval fishes.

Two recent innovations have brought the zooplankton net to a high state of sophistication. The Tucker trawl has several compartments which can be opened and closed automatically at different depths by an electronic signal. It can thus provide sequential pictures of the zooplankton communities in several depth strata. With any net, however, it is difficult to determine whether some animals, perhaps warned by the vibrations of the cable towing the net, are escaping capture. A new net developed on Puget Sound avoids this problem by sampling while it sinks under its own weight, instead of while being towed surfaceward.

For sampling phytoplankton, nets have been largely replaced by closable bottles (Figure 2.2). The advantage of using bottles is that they capture even the tiniest cells, which slip through nets. Furthermore, sample depth and volume can be accurately determined, several depths may be sampled simultaneously, and water is collected for chemical analysis along with the plankton. The disadvantage is that bottle samples do not concentrate the plankton as nets do. This must be done after collection, most commonly by killing the plankters with formaldehyde or iodine in a special chamber, and examining them after they sink onto a microscope slide that forms the chamber bottom.

A third method of sampling is to pump water directly aboard ship. In many ways this is an ideal method—a hose is lowered to the desired depth, the pump is switched on, and liter after liter of water is instantly available. Pumps and hoses are difficult to handle in rough seas or at great depths, however, and even the best pump processes only a fraction of the volume sampled by a large zooplankton net. Modern vessels use pumps mainly as a convenient method of surveying a large area quickly.

The most serious problem with plankton sampling is the artificiality of observing plankton out of its natural element. In describing the first observations of deep-sea creatures—including plankton—from a submersible vehicle, and reflecting on the shackles which bind most marine scientists to the surface, Jacques Cousteau said: "Oceanographers, bless them, are blind beggars, tottering about on crutches of cables." Indeed, some of the most dramatic recent discoveries about plankton—the habits of delicate gelatinous zooplankters, for instance—have resulted when oceanographers immersed themselves in the sea, and observed directly what their crude sampling devices had for decades been destroying in the process of capture. This problem is common to all sciences; the process of observation alters what the scientist wants to observe.

Early Research on Puget Sound

The first published scientific observations of plankton on Puget Sound were conducted on jellyfish (Figure 2.3) by Louis Agassiz and his son Alexander, who cruised the area in the summer of 1859. The elder Agassiz, America's foremost naturalist, also founded Harvard's Museum of Comparative Zoology that year, and in 1873 set up America's first marine lab on Penikese Island off Cape Cod.

After his father's death, Alexander Agassiz returned to Puget Sound several times between 1888 and 1905, aboard the renowned U.S. Fish Commission steamer *Albatross*, from which he and his crew routinely sampled with a plankton net.

Other early plankton studies were performed by biologists from Columbia University who booked quarters near Port Townsend in 1896 hoping to encounter species from both the protected waters to the south and the more open waters to the north, and who learned about oceanic waters by persuading a tugboat captain to take them out to Cape Flat-

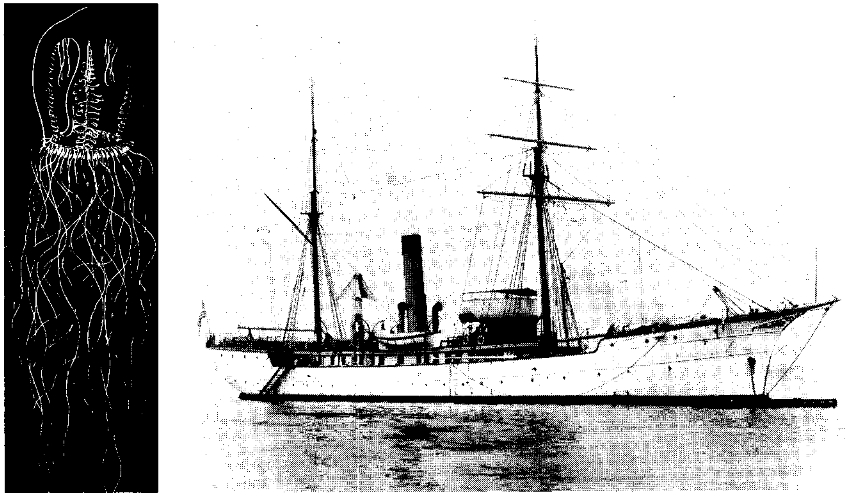


Figure 2.3 The medusa jellyfish *Polyorchis*, pictured in this woodblock print by Alexander Agassiz (1865), was among the first plankters studied on Puget Sound. The *Albatross*, one of the nation's first vessels built for marine research, visited Puget Sound near the turn of the century. (Photo courtesy Puget Sound Maritime Historical Society)

tery. They were visited by Trevor Kincaid, who later supervised the first indigenous plankton research on the Sound. The same group visited Port Townsend again in 1897, along with a contingent from England.

The Laboratory and the Field

With the founding of the University of Washington Friday Harbor Laboratory by Trevor Kincaid (Figure 2.4) and T. C. Frye biological oceanographic research on Puget Sound began to diverge into two channels: those studies carried out on location in the field (in this case, water), and studies in the laboratory. Laboratory and field studies differ in scope: there is a broad landscape focus in the field, versus a narrow portrait focus in the lab. Seagoing studies encounter all the complicated variables of ecosystems—light, temperature, weather, currents, and water chemistry—in a complex, intermeshing natural machinery. Field studies must integrate. Laboratory studies segregate, trimming problems down to size by eliminating or controlling as many variables as necessary or possible. Studying an ecosystem is like assembling a jigsaw puzzle. Field studies stand back to fit the pieces to a grand design, whereas laboratory studies move in close and fit pieces according to their shapes. Field studies sketch out a skeleton; laboratory studies put flesh on its bones.

An entire battery of subsciences has arisen from laboratory work. Perhaps the earliest laboratory work done at Friday Harbor was the study of morphology, the anatomy and external structure of organisms—shape, size, color, texture, and arrangement. When a new spe-

Figure 2.4 Trevor Kincaid, a precocious bug collector, was appointed a zoology professor at his University of Washington graduation. In 1904 he and botanist T. C. Frye founded the Puget Sound Biological Station (now the Friday Harbor Laboratories), where they pioneered research on local plankton and other marine life. Kincaid also founded the University of Washington Fisheries College in 1919 and helped revive the state's failing oyster industry in the 1920s. He died in 1970 at age 97. (Photo courtesy Friday Harbor Laboratories)

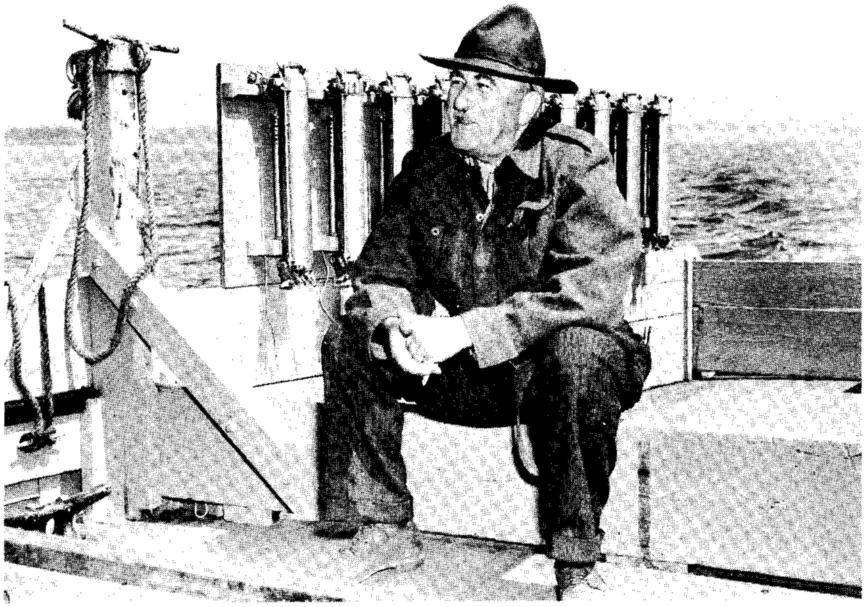


Figure 2.5 Thomas G. ("Tommy") Thompson was a University of Washington chemistry professor with an interest in seawater who in 1930 was appointed to transform the biological station at Friday Harbor into an oceanographic laboratory. His comprehensive and systematic research methods brought fresh and valuable insights into the physics, chemistry, and biology of Puget Sound, and he created a world-class oceanographic institution. He was the UW's first member of the National Academy of Sciences. After his death in 1961 the University's new ocean-going research vessel was christened in his honor. (Photo courtesy Friday Harbor Laboratories, University of Washington)

cies is identified (as many were at Friday Harbor), a full description of its morphology is published, in detail sufficient for other scientists to recognize the organism. Morphology is intimately bound up with taxonomy, the subscience of evolutionary and genetic classification.

Another early pursuit that led to an interest in plankton (especially the meroplankton) was embryology, the study of maturation from fertilized egg to maturity. The usefulness of this subscience had been demonstrated by J. Vaughn Thompson with his newly invented tow-net. A small zooplankter resembling a young crab was maintained in the laboratory and matured to become a barnacle. This dispelled the notion that the barnacle was a relative of the clam.

To maintain living organisms in the laboratory it was necessary to artificially duplicate natural living conditions. So began the study of physiology, the subscience of organisms' metabolic machinery. Phytoplankton can be grown just like a marine houseplant, with the proper temperature, light, salt, water, and fertilizer, although it took decades to find the correct recipe. The ability to culture phytoplankton made it much simpler to grow zooplankton in the laboratory as well, yielding knowledge of food preferences and requirements in the animals. Along the way, lab researchers discovered reactions of organisms to such unusual and stressful conditions as lack of food and extremes of temperature and salinity.

Field studies of plankton depend for their success on careful planning. The composition of the plankton can vary tremendously, so the location and timing of sample collection, as well as the equipment used, affect how well the samples represent the intended populations. Systematic field studies of Puget Sound plankton accelerated with the arrival at Friday Harbor of Thomas G. Thompson (Figure 2.5). During the decade from the mid-1920s to the mid-1930s, Thompson's research detailed plankton abundance in the Sound, using a logical and organized approach designed to illuminate the variability of plankton production at different times and places.

Thompson and his co-workers began their study by surveying the seasonal changes in the plankton from the pier at the Friday Harbor Lab for several years, comparing one year to the next. Their next step was to compare the plankton at Friday Harbor to that found at neighboring sites near Orcas Island and in the Strait of Juan de Fuca. Finally, spatial and temporal changes were charted on a multi-day cruise over the entire Sound. They observed significant differences in the plankton community over distances of a few kilometers horizontally and a few meters vertically. There were also radical changes at one location over the few hours it takes for the tide to change, over the few days it takes for the weather to change, and between the same date in different years.

Standing Stock and Productivity

To describe the changes in plankton abundance over time and by location, two fundamental questions need to be answered: "How much is present?" and "How quickly is it changing?" As a moving body is characterized by its position and its velocity, so a plankton community is described by a static quality, the standing stock, and a dynamic quantity, the rate of production per unit time, called the productivity, which will determine the future standing stock.

Standing Stock

Standing stock can be measured as either the number of organisms, the population, or their combined weight, the biomass. Neither by itself is a complete index of abundance, however, and no measurement of standing stock can be more reliable than the sampling methods from which it is determined.

The simplest method of assaying plankton standing stock, requiring only a microscope, is to count the population of organisms in a known volume of water. By microscopically counting plankters, the organisms can often be catalogued by genus and species, and even by age. The observer can judge the health of the organisms, and separate living organisms from dead ones. But counting has one disadvantage—it is tremendously slow, and thus quite expensive.

Biomass can be measured more rapidly than population, and by a less experienced observer. The simplest method is to measure the volume of settled plankton captured with a bottle or net. Inaccuracies due to the presence of water and other non-biological matter can be reduced by drying and weighing the sample, or by burning it and estimating organic matter from the amount of carbon dioxide driven off. The problem with any method for measuring biomass is the quality of the information it yields. There are no details of species present, no distinction between living and dead material, nor even a way to separate plants from animals.

The problem of separating plant from animal, and living cells from inert matter, has been at least partially solved, however. The plant pigment chlorophyll *a*, when routinely extracted and purified, has a distinctive green color that can be precisely sensed by an instrument called a spectrophotometer. The instrument detects the amount of pigment in the sample, and a simple correction can be made for the presence of non-living pigments. The method was developed at the University of Washington by Francis Richards with Thomas G. Thompson, and it has become an indispensable tool of the oceanographer's trade.

More recently, a faster and more sensitive (if less accurate) instrument has been developed for assaying chlorophyll: the fluorometer, which can detect the fluorescence of phytoplankters bombarded with light. This instrument can be combined with a pump, at some loss of sensitivity, to monitor the fluorescence of living phytoplankton in a continuous stream of seawater. It furnishes a powerful tool for rapid estimation of phytoplankton biomass over wide areas, like an EKG of the sea. Further promise is held by aerial and satellite photography.

There is great promise for developing an equally useful automated method for measuring zooplankton biomass, continuously and in the field. The method evolved before World War II when sailors noticed on their sonar depth soundings curious midwater blips and bands, which migrated up at night and down during the day. These echoes proved to be schools of fishes. When the frequency was stepped up to an inaudible 105 kilohertz, groups of large zooplankters could be detected. Like the fluorometer, the echo sounder unfortunately cannot distinguish one species of zooplankton from another. Together with the fluorometer, though, it might allow simultaneous acoustical and chemical surveys of great volumes of water for both plant and animal plankton. The information could be available almost immediately, without wetting a net.

Productivity

To transform a "snapshot" in time—as a standing stock measurement is—into at least a semblance of a moving picture requires some means of observing the rates of growth and reproduction of plankters, and ideally, their death rates as well. The rate of production, however, is more subtle and difficult to measure than standing stock. It requires prolonged observation and comparison of initial to final states. For this reason, methods for estimating growth rate and productivity have been slower to develop.

The simplest means of estimating productivity is to compare the standing stock before and after a fixed length of time. This yields net growth—the sum of birth, death, and migration. The accuracy of this method is likewise limited by that of the sampling methods. Small changes in standing stock due to production are likely to be invisible against the gross variations in the sea, and can be effectively monitored only under controlled laboratory conditions.

What is needed to measure productivity in the sea is a chemical whose concentration can be easily measured and has a direct relationship to growth, a chemical as characteristic of the growth process as chlorophyll *a* is characteristic of living plants. Fortunately, the unique process of photosynthesis, to which chlorophyll is vital, also provides a means by which the growth of plants (at least) may be monitored. The real business of plants is to "fix" carbon dioxide into glucose using sunlight. Carbon is the structural material and the energy currency of all biology. Measuring the rate of carbon fixation places a finger on the pulse of the phytoplankton, and of the entire ecosystem.

To measure phytoplankton productivity, a small bottle filled with seawater is injected with a shot of sodium bicarbonate (abundant in seawater, it generates carbon dioxide), in which there is an enriched proportion of radioactive carbon-14 atoms, the same isotope used for dating of fossils. The bottle is then suspended back in the water, or placed before a light of known intensity. As the algae photosynthesize, they take up the "hot" (radioactive) carbon along with the "cold" carbon already present in the water. After a few hours of incubation, the plankton is filtered, and on each filter the amount of radioactivity (above background) measured with a Geiger counter or similar device is proportional to the total amount of carbon fixed by the phytoplankton.

Unfortunately, there is no method comparable to the carbon-14 method to measure production by zooplankton, nor is there much prospect of one emerging soon. The rate at which animal standing stocks increase and decrease can be found only from consecutive biomass or population estimates, with all their imprecision. A newly developed method can, however, determine the amount of phytoplankton eaten, by assaying the fluorescence of chlorophyll in zooplankton guts.

Since World War II the study of plankton has undergone an explosion of youthful energy, during which time more was discovered than in the century before. The advent of chemical and automated methods marks planktology's scientific adolescence, but maturity is still far away. Similarly, oceanography as a whole is a superstructure assembled from other, more basic sciences, and cannot be expected to keep pace with them. As the 20th century wanes, oceanography could be compared to other sciences in their youth: medicine, for example, at the time of Louis Pasteur, or physics before Einstein. There is an understanding, but as yet no prediction or control, of major phenomena and their causes. The rate at which new knowledge emerges, while accelerating, is still slow. Textbooks of medicine are out of date almost as soon as they are printed, yet some oceanographers still use a text written forty years ago.

Biological oceanography is also a pure science. The applied sciences of fisheries and mariculture derive from it, just as horticulture and agriculture are applications of the pure science of botany. There are few practical applications to which oceanography can yet be put—we cannot yet farm the open sea or abate pollution, and we have little immediate prospect of doing either. Pure science, which inquires solely for the sake of inquiry, often seems to progress slowly, with no clear direction. A rapid advance in applied science, however, is but the tip of an iceberg buoyed by an unseen mass of pure science. Future husbandry of the seas will depend on today's primitive inquiries, as space travel was begun by Newton.