CHAPTER THREE

Plankton Hall of Fame

Natura nusquam magis est tota quam in minimis (Nature is to be found in her entirety nowhere more than in her smallest creatures)

Pliny

A community of similar plankton species inhabits much of the Pacific coast of North America, from California's Golden Gate to Alaska's Inside Passage. This community is exemplified by the plentiful plankters living near the center of that range, in the sheltered and beneficent waters of Puget Sound. Puget Sound is to plankton what Florida is to oranges, what Iowa is to corn, what the Cascades are to the Douglas fir. Although hundreds of species of plankton may populate the Sound at one time, or over the course of a year, most of the plankton assemblage is comprised of a relatively few important organisms.

Phytoplankton

The species of algae which comprise the marine phytoplankton are unique life forms. Although among the oldest forms of life on the planet, they are also highly specialized and well-adapted to their environment. Unlike higher plants, which can contain billions of cells, each phytoplankter consists of only a single cell. Though they sometimes link together to form chains, each individual cell is self-sufficient: the chains are colonies, not organisms.

What distinguishes an organism as a plant is the process of photosynthesis. Plants capture the energy of the sun in the green pigment chlorophyll, and use this energy to convert carbon dioxide and water into sugar. Phytoplankters do this only within the proper range of light intensity, temperature, and salinity conditions. In addition, as a garden needs fertilizer, phytoplankters need certain nutrients. The required nutrients are nitrogen, most common in the sea combined with oxygen as nitrate; phosphorus, present as phosphate; carbon, potassium, sodium, calcium, and sulfur, all plentiful in the sea; and trace metals such as iron, manganese, cobalt, copper, nickel, tin and zinc. A majority of phytoplankters also need vitamins, especially vitamin B_{12}.

According to the "limiting nutrient" concept derived from terrestrial agriculture, the supply of these plant nutrients limits both the productivity and the standing stock of phytoplankton. Nutrients are present in seawater in roughly constant ratios, which do not necessarily match the demands of phytoplankton, the theory continues. One nutrient will be exhausted before the others, and it—the limiting nutrient—will place a ceiling on plant growth. The limiting nutrient in fresh water is usually assumed to be phosphorus. In salt water, however, nitrogen is believed to be in shorter supply, sometimes consumed by phytoplankton to levels of virtual undetectability at the sea surface.

Nitrogen supply is only one influence on phytoplankton growth in Puget Sound, and is believed to be less important in most instances than the availability of light. The effects of the trace nutrients, such as minerals and vitamins, have received little study and may also have an influence. Furthermore, when the complexities of multiple phytoplankton (and zooplankton) species and multiple nutrient sources in a turbulent fluid are considered, the limiting nutrient theory can play only a partial role in controlling phytoplankton abundance in the Sound.

All phytoplankton cells have an outer cell membrane and an inner, jelly-like cytoplasm. Many also possess an armored cell wall. All reproduce asexually by simple cell division, called binary fission. A parent cell expands its size, duplicates all its intracellular contents, forms a wall through its midsection, then separates into two sibling cells. The siblings are genetic duplicates (clones) of each other, and the parent ceases to exist. Binary fission is a powerful process: it expands the population by doubling again and again, creating from a single cell first two, then four, eight, and sixteen cells. Propagating in this fashion, once a day, a single cell can produce a billion copies of itself in a month. Binary fission is the means by which the cells of all larger organisms reproduce. Only in unicellular organisms such as phytoplankton, however, do single divisions produce complete offspring.

Phytoplankters can also undergo sexual reproduction, in which a cell dissolves into tiny, swimming sperms or eggs, which unite in the water to form zygotes. The new cells that form are genetic crosses between the parents, rather than duplicates of a single parent. Sexual reproduction has received little study, but is believed to be triggered by a sudden deterioration in such environmental conditions as light intensity, temperature, or nutrient concentrations. The exact cues are likely to be different for each species.

An unfavorable environment may also trigger the formation of any of a variety of resting spores or cysts, with hardened walls and slowed metabolism. These sink to the bottom where they are less likely to be eaten, then regenerate vegetative cells when favorable conditions return, possibly months or years later. Cyst formation is poorly understood and may be associated with the sexual cycle. It is observed only in species inhabiting coastal waters sufficiently shallow that storms and currents can resuspend bottom sediments and cysts into lighted waters where growth can resume. The triggering of phases of the sexual and cyst cycles simultaneously in entire populations of a phytoplankton species is suspected of accounting for very rapid shifts in phytoplankton species composition occasionally observed in Puget Sound.

Of the many diverse phytoplankters in the sea, those most common in Puget Sound can be lumped into three broad categories. The customary unit for such classifications of both plants and animals is the phylum, the coarsest taxonomic division after the kingdom. Below the rank of phylum, in order of increasing specificity, are class, order, family, genus, species, and race or strain. Scientists can debate endlessly over such distinctions, however, and for our purposes it is more meaningful to define pragmatic ecologically based groupings, which cut across strict phyletic lines. In addition to diagnostic external features such as size and cell wall structure, the most useful characteristic for differentiating the three groups of phytoplankton in Puget Sound is locomotion, which is found in the plant kingdom only in certain microalgae.

The possession of one or more whip-like swimming appendages called flagella is common to many groups of unicellular organisms not far from the fork in the road of evolution separating plants and animals. These organisms are called flagellates, and the phytosynthetic forms are called phytoflagellates. Their swimming speed—at most a few meters per hour—does not threaten their status as plankton. The dinoflagellates, including both plant and animal forms, have two uniquely arranged flagella and a distinctive cell shape. The term phytoflagellates will be used below to refer only to the remainder of the phytosynthetic flagellates, a heterogeneous assortment sharing similar size and cell wall characteristics.

The diatoms have no flagella (except on their male reproductive cells), and therefore planktonic diatoms have little if any locomotion. Other species of non-planktonic diatoms important in shallow benthic environments have a snail-like gliding ability not involving flagella. Varying widely in size, diatoms also have a unique hardened cell wall.

Diatoms (Bacillariophyceae)

Diatoms (Figure 3.1) are widely assumed to be the most common plants in the sea, although new findings on flagellates may challenge this belief. The name denotes the presence of two hard outer shells, called frustules, embedded in the wall around each cell. Shaped like two pillbox halves that fit one rim inside the other, the frustules are made of silica extracted from seawater, making silicon an additional essential nutrient for the diatoms. The casing is perforated, allowing chemical exchange between the cell and the water, and is sculpted in each species into a different exquisite pattern. Because new frustules form within those of the parent during binary fission, the cells of a diatom population steadily diminish in size during asexual propagation. Only sexual reproduction can restore the original cell size and vigor of the population; otherwise the cells die out.

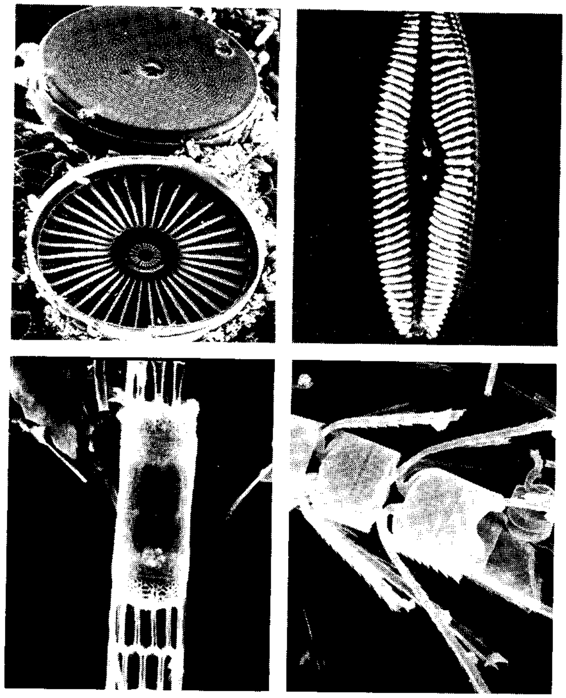


Figure 3.1 Diatoms

Top left: Separated pieces of the frustule of the solitary centric diatom *Coscinodiscus*. Actual diameter approximately 100 micrometers. (Courtesy National Marine Fisheries Service (NMFS), NOAA, micrograph by Michael Eng).

Top right: The solitary pennate diatom *Navicula*. Actual length approximately 100 micrometers. (Courtesy School of Oceanography, University of Washington)

Bottom left: A portion of a chain of the centric diatom *Skeletonema*. Actual cell diameter approximately 25 micrometers. (Courtesy B. Dumbauld)

Bottom right: A segment of the centric diatom *Chaetoceros*. Actual cell diameter approximately 35 micrometers. (Courtesy Beatrice C. Booth)

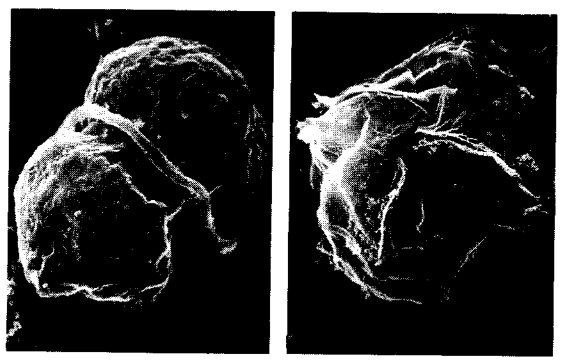


Figure 3.2 Dinoflagellates

Left: The unarmored dinoflagellate *Gymnodinium*. Note the flagellum in the transverse groove. Actual cell length approximately 6 micrometers.

Right: The armored dinoflagellate *Gonyaulax*, cause of paralytic shellfish poisoning. Actual size approximately 30 micrometers. (Photos courtesy Susan B. Stanton)

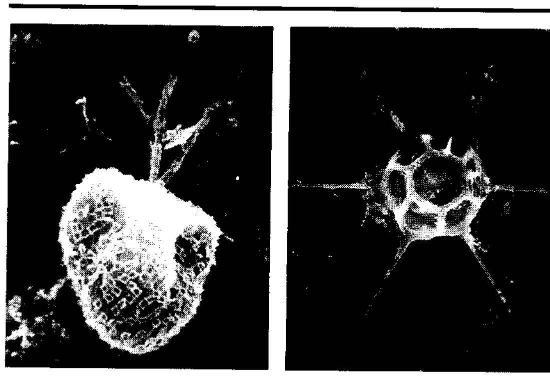


Figure 3.3 Phytoflagellates

Left: A green flagellate (probably *Pyramimonas*). Note flagella and surface scales. Actual size approximately 8 micrometers.

Right: The skeleton of the golden-brown silicoflagellate *Dichtyocha*. Actual size including spines approximately 50 micrometers. (Photos courtesy Beatrice C. Booth)

The opaline diatom frustules are a major constituent of marine sediments at high latitudes, since they are heavy and slow to redissolve as they sink. Useful as fossil indicators, they compose the fine mineral diatomaceous earth (diatomite), which because of its large surface area and abrasiveness has a wide variety of commercial uses, such as in wine filtration and in scouring powder. Diatomite deposited before the Cascade Mountains rose from the sea has been mined in the Columbia River basin near Vantage, Washington.

Two classes of diatoms, centric and pennate, are distinguished by shape. Centric diatoms are radially symmetrical like a wheel. Pennate diatoms are bilaterally symmetrical or asymmetrical, and elongated along one axis like an almond. Both classes contain some species which are solitary and others that link together to form chains. Long spines may also be present in some colonial species.

Dinoflagellates (Dinophyceae)

The dinoflagellates (Figure 3.2) are a highly contradictory group about which it is difficult to make generalizations. Most are plants, but some are animals, parasites, or other innovative forms. The prefix "dino-" (as in dinosaur) refers to a cell wall armored with cellulose plates, but many species are naked. Most dinoflagellates have a basic body plan resembling two cones joined at their bases, with a groove in between. One flagellum lies in the groove and its beating makes the cell spin like a top. The other flagellum lies in a second, perpendicular groove on the lower cone and its beating propels the cell forward. A major subgroup of dinoflagellates, however, is almond-shaped, with both flagella inserted at one end. Some dinoflagellates, like some diatoms, drastically modify their basic body plan by forming chains, or (more commonly) by having prominent spines.

Dinoflagellates have a peculiar trait of migrating vertically in the water. During the daytime, they are found near the surface photosynthesizing. In the evening, however, they may be found a few meters below the surface, and as dawn approaches they swim back to the surface en masse. They form dense swarms at times and places where conditions are right, resulting in a "red tide." Some dinoflagellates are luminescent and are one cause of the glow of stirred water on summer evenings, and some can sicken or kill marine animals and even humans.

Phytoflagellates

The most common species of the other phytoflagellates (also sometimes called nanoflagellates) in the Puget Sound area are mostly unarmored, usually unicellular, come from many different taxonomic groups, and are distinguished mainly by being the smallest of the phytoplankton (Figure 3.3). They have been overlooked for many years because their size makes them difficult to capture and preserve. Little is yet known of their habits or abundance in Puget Sound. Through careful sampling, however, phytoflagellates have been discovered in a wide variety of habitats, and may prove to be very important.

Zooplankton

The zooplankton is an extremely diverse group of animals, containing at least one developmental stage of dozens of phyla. Zooplankton lifestyles are far more varied than those of phytoplankton. Animals must have senses to detect, propulsion to pursue, appendages to apprehend, and mechanisms to ingest, digest, and egest food. Animals also use sophisticated strategies to avoid becoming food. Some zooplankters, the protozoans, are unicellular, but most are multicellular metazoans. Animal reproduction, especially that of the metazoans, is more complex than that of plants. In most cases, asexual reproduction has been replaced by sexual reproduction, and more advanced animals have prolonged stages of immaturity and more carefully programmed behavior for bearing young to increase their odds for survival.

Protozoans

Most of the unicellular members of the phylum Protozoa (Figure 3.4) reproduce as phytoplankters do, by simple binary fission. Most protozoans also feed on very small phytoplankton, especially phytoflagellates, or on bacteria. Four types of protozoans are encountered in Puget Sound: foraminiferans and radiolarians are uncommon, and dinoflagellates and ciliates are more abundant.

The mouthless foraminiferans (forams) and radiolarians eat by simply engulfing their food, as an amoeba does. Both possess skeletons: foram shells are external, calcareous, and whorled like those of a tiny snail, while radiolarians have star-shaped inner silica skeletons. Both types of skeleton form thick oozes over wide areas of ocean bottom. The white cliffs of Dover are 500-foot-thick piles of ancient forams.

There are few common or well-studied zooplanktonic flagellates in Puget Sound. The most prominent is an animal dinoflagellate, *Noctiluca*. Mostly water like a jellyfish, *Noctiluca* is unarmored and is either transparent or pigmented a faint pink. It has one flagellum for swimming, while the other, next to its simple mouth, is used as a tentacle for grasping food. It can reproduce rapidly enough to form a luminescent animal red tide, and it is a voracious feeder on all types of phytoplankton and even on small animals, some of which can be seen inside its diaphanous body before they are digested.

The ciliates, the most consistently abundant protozoans in Puget Sound, derive their name from the rows of tiny hair-like cilia that they use for both propulsion and food-gathering. Some ciliates, in addition, have forms of armor. The tintinnids have a tough outer shell called a lorica, always a variation of the basic ice-cream-cone shape, which they adorn with cemented bits of sand. When threatened, a tintinnid will abandon its lorica. Less armored than the tintinnids are the oligotrichs, which cannot abandon their sheaths and sometimes have none at all. Holotrich ciliates are represented in Puget Sound principally by one species, *Mesodinium rubrum*, which can at times form red tides. *Mesodinium* has only a vestige of a mouth, and instead of eating lives off symbiotic phytoflagellates within its body: it is an animal which has reverted to a plant-like existence.

Crustaceans

The class Crustacea (Figure 3.5) of the phylum Arthropoda clearly dominates the zooplankton of Puget Sound and the sea as a whole. The marine equivalent of the insects (another Arthropod class, which outnumbers all other animal species combined) is an order of crustaceans called the copepods. Copepods are superfically shrimp-like, with segmented, torpedo-shaped bodies, antennae and mouth parts at the front, and swimming appendages dangling below. Corkett and McLaren have surmised that the copepod *Pseudocalanus* may be the most populous metazoan genus in the world, and Hardy has ventured that the number of copepods may exceed the numbers of all other metazoans in the sea combined.

Most copepods have preferences for either plant or animal food, and their sizes and feeding structures differ accordingly. *Calanus*, a moderate-sized animal that can contribute a large fraction of the copepod biomass in Puget Sound, is a grazer that as an adult eats primarily diatoms, although given the opportunity it will prey on some small protozoans and larvae. While its precise feeding mechanism is not yet clear, *Calanus* appears to draw water toward its mouth using feeding appendages with fine branches, which concentrate masses of small food particles as a phytoplankton net does. This type of strategy is called suspension feeding.

Contrasting with *Calanus* are some strictly carnivorous copepods. The largest copepod in the Sound, about the size of a grain of rice, is *Euchaeta*, which finds the smaller herbivore *Pseudocalanus* an ideal prey. A unique predator is the smaller *Corycaeus*, often the most numerous in the Sound. It has sharp, pincer-like appendages for grasping individual prey, and even has primitive eyes. Such carnivorous copepods also have blunt, molar-like grinding surface on their jaws for chewing muscle, while more herbivorous animals such as *Calanus* have sharp, incisor-like jaws for cracking open diatom frustules.

Crustaceans rely exclusively on sexual reproduction. A few hours after copepod eggs are laid, they hatch into larvae called nauplii, which swim and like the protozoans feed on the tiniest phytoplankton. In copepods, the larva molts eleven times before reaching adulthood, passing through an additional series of copepodite stages. The entire life cycle, depending on temperature and the availability of food, takes about a month in the summer, or several months in the winter.

Members of orders of larger shrimp-like planktonic crustaceans—the euphausiids, mysids, and hyperiid amphipods—are second in abundance to the copepods. In addition, one true shrimp, the small *Pasiphaea*, is planktonic; but the Puget Sound commercial and sport shrimp *Pandalus* is too large to be a plankter except in its larval stages. Euphausiids, mysids, and amphipods live deeper in the water than many of the copepods, feeding on the largest phytoplankton, protozoa, copepods, and other medium-sized zooplankters including fish larvae. Many of them also migrate a hundred meters or more below the surface during the daytime. The euphausiids, especially the genus *Euphausia*, are "krill," the staple diet of baleen whales in the Arctic and the Antarctic. These larger and more complex organisms pass through more stages of immaturity than the copepods. Euphausiids usually take an entire year to mature as plantonic larvae, and live for two years or more. Larval mysids and amphipods, in contrast, are reared in a kangaroo-like maternal brood pouch before becoming free-living.

Two minor orders of crustaceans, both of which are more common in fresh water, are the ostracods and the cladocerans. Ostracods have a shell shaped into two clamshell-like cups, in which they hide as they float, emerging only to swipe at passing food. Cladocerans, the marine relatives of *Daphnia* (the water-flea of lakes and ponds), have a prominent eye-spot, and long limbs used for both swimming and feeding.

Rotifers

The phylum Rotifera (Figure 3.6) includes mostly freshwater members, but the genus *Synchaeta* appears regularly in Puget Sound. Rotifers are multicellular, but similar in size to the larger protozoans. They feed on large phytoplankton and small animals, using a ring of beating cilia which surrounds powerful jaws.

Coelenterates

The phylum Coelenterata, also called Cnidaria, (Figure 3.7) is best known, perhaps, for corals and anemones. Its local planktonic representatives are species of floating or swimming jellyfishes, called medusae. The medusa is but one stage of the animal's life cycle, alternating with a sedentary form called the hydra. For many years the medusae and hydras were thought to be different species entirely, but through slow, painstaking observation the matching life stages were pieced together. Hydras are asexual and bud off large numbers of medu-

Figure 3.4 Protozoa

Left: The dinoflagellate protozoan *Noctiluca* that causes nontoxic luminescent red tides in Puget Sound. Note the flagellum. Actual diameter approximately 100 micrometers.

Right: The lorica of the ciliate protozoan *Tintinnopsis*. Actual length approximately 100 micrometers. (Photos courtesy Alexander J. Chester)

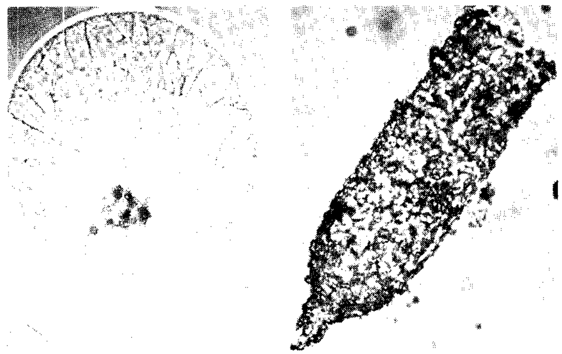
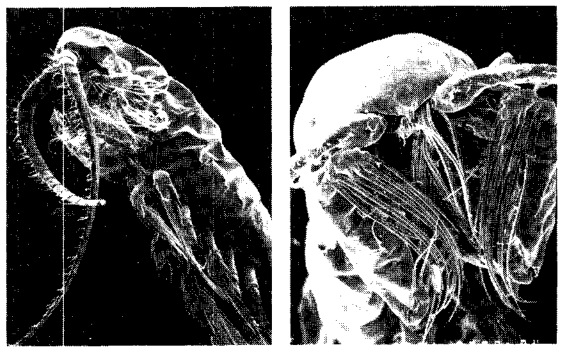


Figure 3.5 Crustaceans

Left: The herbivorous copepod *Calanus* showing the antennae and feeding (upper) and swimming (lower) appendages. Actual length approximately 3 millimeters.

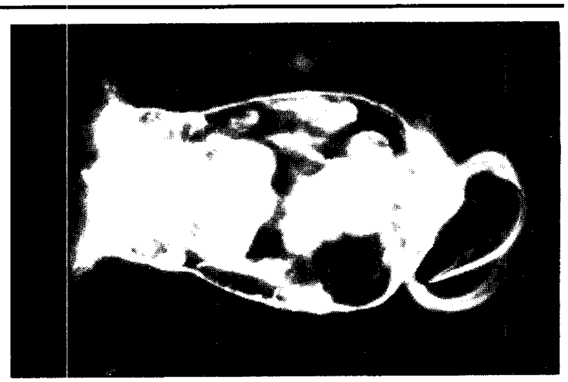
Right: The carnivorous copepod *Euchaeta*, with coarse feeding appendages adapted for grasping, in contrast to the filtering apparatus of *Calanus*. Actual length approximately 1 centimeter. (Photos courtesy Charles H. Greene)



The euphausiid "krill" *Euphausia*, which is mostly herbivorous in Puget Sound. Actual length approximately 2 centimeters. (Courtesy Mark D. Ohman)

Figure 3.6 Rotifers

The brackish-water rotifer *Brachionus*. The blur is caused by beating cilia. Actual length approximately 200 micrometers. (Courtesy Richard Kaiser)



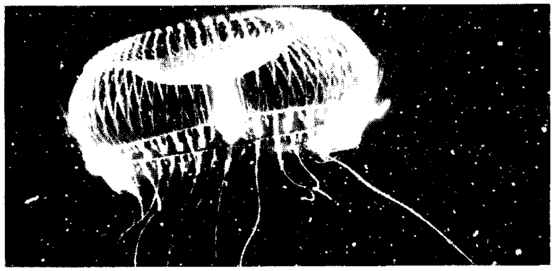


Figure 3.7 Coelenterates

The luminescent medusa stage of *Aequorea*. Actual size approximately 7 centimeters. (Courtesy William D. Waddington)

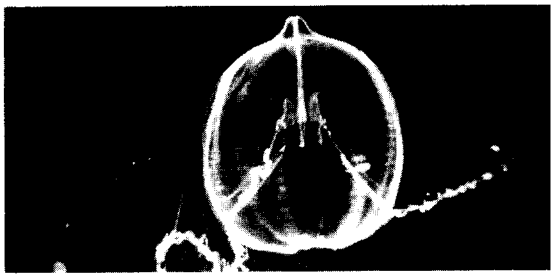


Figure 3.8 Ctenophores

The ctenophore *Pleurobrachia*. Note the comb rows and tentacles. Actual diameter approximately 3 millimeters. (Photo courtesy School of Oceanography, University of Washington)

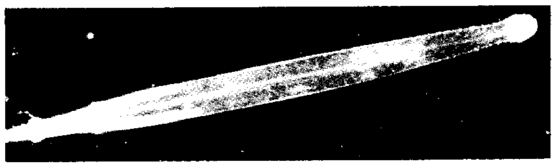


Figure 3.9 Chaetognaths

The chaetognath *Sagitta*. Spines at head are retracted. Actual length approximately 2 centimeters. (Courtesy Mark Ohman)

Figure 3.10 Molluscs

The naked pteropod *Clione*. Note "wings" (actually the "foot"). Actual length approximately 3 centimeters. (Photo courtesy School of Oceanography, University of Washington)

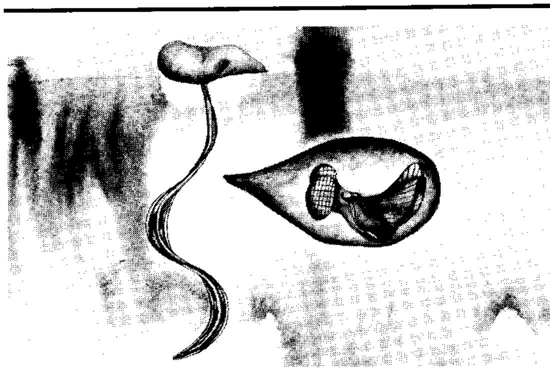


Figure 3.11 Chordates

The larvacean *Oikopleura*. The animal's head is at center. Its waving tail draws water through the surrounding mucous "house" to catch food on two sets of screens. Actual length including house approximately 2 centimeters.

sae, which carry out sexual reproduction as they drift. Coelenterates feed by using special organelles called cnidoblasts, which eject a thin cord tipped with a poisoned dart to embed itself in the prey. At times in the summer, medusae can float by the thousands near the surface and decimate the populations of their zooplankton prey.

Ctenophores

The phylum Ctenophora (Figure 3.8) was long included in the Coelenterata because its members have soft, transparent bodies and tentacles. Their delicate form makes them difficult to sample and preserve, so less is known about them than about most zooplankters. Ctenophores are nicknamed "comb jellies" for the eight rows of paddle-like fused cilia which divide their spherical bodies like the sections of an orange. These comb rows, which may be brightly luminescent, are the animal's means of propulsion. *Pleurobrachia*, the dominant ctenophore on Puget Sound, also has a long pair of tentacles with adhesive cells for snaring zooplankton prey, but it lacks the "stingers" of the coelenterates. Ctenophores have a tremendous appetite—up to tens of times their body weight per day—and when food is plentiful they can form dense, glowing swarms at the water surface.

Chaetognaths

The principal genus of the phylum Chaetognatha in Puget Sound is *Sagitta* (Figure 3.9), which can reach a length of two centimeters. The nickname "arrow worms" comes from the long, streamlined bodies and the feeding habits of the chaetognaths, which resemble those of a barracuda. Chaetognaths are voracious predators on all other zooplankters and larvae, even on some animals larger than themselves. They dart at high speed, snatch their prey with a lightning-quick strike, and swallow it whole. The chaetognaths, as well as the ctenophores, are hermaphroditic.

Molluscs

Like the Coelenterata, the phylum Mollusca is better known for its non-planktonic representatives: squid, octopi, clams, mussels, snails, and slugs (Figure 3.10). The nudibranch snails, known for their beauty, are sometimes found floating freely in the water but are dependent on rooted subsurface vegetation and attached animals, and so are not plankton. The truly planktonic molluscs, nicknamed "sea butterflies," are the pteropods. They include the shelled *Limacina* and the naked *Clione*. *Limacina* leads a life like other tiny shelled plankton; it has little swimming power and is a passive filterer of phytoplankton. It captures food by secreting a huge parachute of mucous, free-falling through the water, then eating the catch, mucous and all. *Clione* is a large carnivore (up to seven centimeters), which swims by making water wings of the flaps of skin that form the "foot" in its cousin, the snail.

Chordates

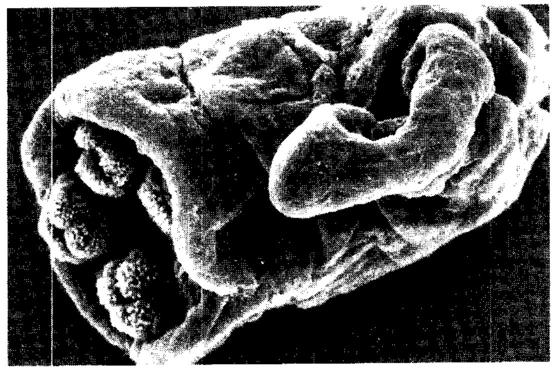
Some plankters belong to the same phylum as humans, the phylum Chordata (Figure 3.11), which includes the subphylum Vertebrata. In addition to the vertebrate fish larvae that exist in the plankton, there are adult organisms, such as the larvacean *Oikopleura*. It is a small, worm-like creature, which secretes a balloon-like, luminescent, mucous "house" that doubles as a filter for capturing phytoplankton. *Oikopleura* waves its tail to propel a stream of water through two sets of windows in the house, where food is caught on screens. When the screens clog, the animal simply abandons its house and erects a new one, sometimes as often as every four hours. The filter is fine enough to capture even the smallest phytoplankton and bacteria, making *Oikopleura* perhaps the only animal of its size to do so. It is a hermaphrodite, and a newborn can have its own house built and functioning within one day.

Planktonic Larvae

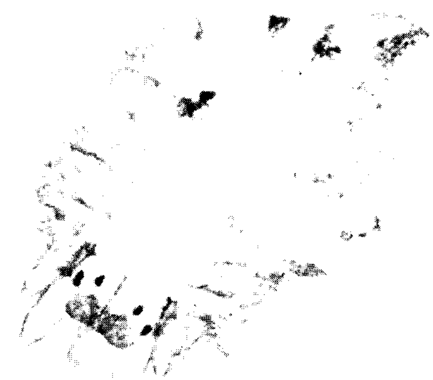
The animals above, except the medusae, spend their entire lives, including any stages of immaturity, in the plankton. About three-fourths of all the remaining animals in Puget Sound (nekton and benthos) have meroplanktonic larvae (Figure 3.12). At the surface the young find the food more abundant, the water warmer, and the currents for transporting them to new territory stronger than in most subsurface habitats. A piece of bare rock or wood exposed to the surface waters of Puget Sound will, within a matter of days, have a thin glaze of larval colonists: shipworms, barnacles, mussels, bryozoans, sponges, and other creatures. Many other larvae settle to the bottom in deeper water, responding to subtle chemical and biological cues. Millions of these ciliated floaters are released to ensure that a few survive. Although an animal might spawn but once a year, and spend only a few days in the plankton, in aggregate the planktonic larvae form an important component of the zooplankton from spring through fall. Although crustaceans are probably most numerous, many larvae are also contributed by animal groups such as the annelids, the molluscs, and the echinoderms.

Annelids are segmented worms that live on or in the bottom. Their larva is called a trochophore. Molluscs have a veliger larva with two wing-like lobes resembling those of an adult pteropod. Echinoderms, a highly specialized phylum that includes the sea urchin, starfish, sand dollar, and sea cucumber, also have a variety of highly specialized larvae. All of these larvae, while present in the plankton, occupy a niche similar to that of a large protozoan or a small copepod, feeding on phytoplankton near the surface.

Figure 3.12 Larvae

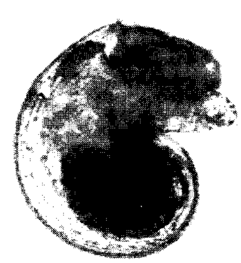


A larval sea cucumber. Actual length approximately 0.8 millimeters. (Courtesy NMFS, NOAA, micrograph by Carla Stehr)



A larval annelid (polychaete) worm. Actual diameter approximately 0.5 millimeters. (Courtesy Alexander J. Chester)

A larval hermit crab, with a small copepod (foreground). Actual length approximately 6 millimeters. (Courtesy NMFS, NOAA, micrograph by Carla Stehr)



A late-stage larval gastropod mollusc. Actual diameter approximately 0.5 millimeters. (Courtesy Alexander J. Chester)

Larvae of such well-known nekton as smelt, herring, cod, rockfish, greenling, and flatfish also can be considered zooplankton during their earliest stages. Called ichthyoplankton, they are most common during winter and spring. They can be extremely abundant, and are important as a critical phase in the lives of economically valuable fishes.

This assemblage of planktonic organisms, with its diverse lineage, also exhibits a great variety of survival strategies. In part these strategies reflect the fundamental ecological duties of food production by phytoplankton, and consumption of and competition for that food by zooplankton. (These two roles will be examined in Chapters Five and Six.) But plankton must also contend with the unique environment in which it is immersed. The fluid nature of Puget Sound not only provokes many of the innovative adaptations of individual plankters, it even dictates the unique ways in which these organisms interact.

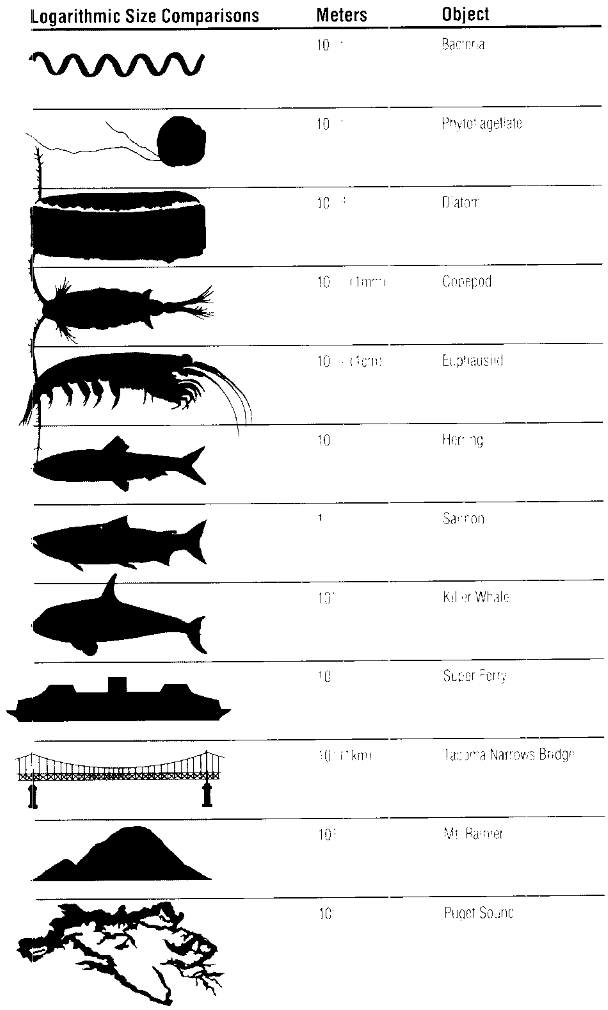


Figure 4.1 The lengths of common Puget Sound organisms and objects are compared here on a scale of powers of ten. Each object pictured is ten times the size of the one above it, and a tenth the size of the one below it. The euphausiid is shown actual size, 2 centimeters.

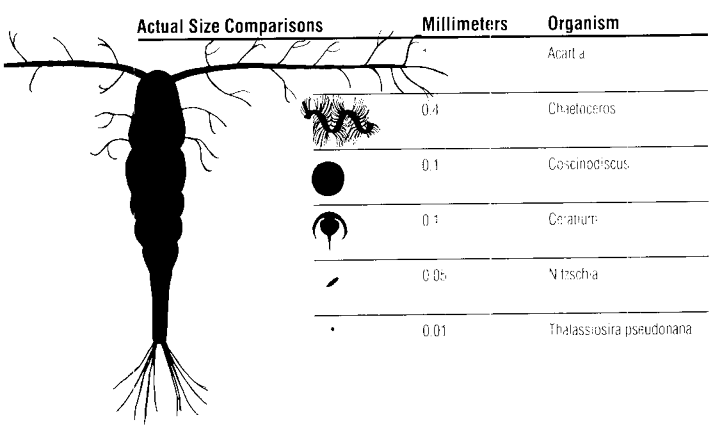


Figure 4.2 The size of a small copepod is compared to that of typical phytoplankton cells, all enlarged about forty times.

CHAPTER FOUR

Seascapes

> As soon as you have entered this pelagic wonderland, you will see that you cannot leave it.
>
> Johannes Müller

Puget Sound, like the sea at large, is a wilderness at our doorstep, in which no people live and through which no trails pass. Most people who see or traverse Puget Sound know little of its creatures or their lives below the surface. To learn the inner workings of the ocean requires an imaginary journey like that of Lewis Carroll's Alice. We must step through the looking-glass surface of the sea, become very small, and see life from a plankter's point of view. Doing this, we indeed enter a wonderland.

The world of the plankton is alien to our own. Underwater life constrains plants and animals into adaptations and lifestyles very different from those on land. This is true not only in individual organisms, but also in the fundamental structure of underwater ecosystems. To understand what makes Puget Sound such a productive place, we must first look at some of those differences.

Size

Let us begin by putting oceanic dimensions in perspective. Puget Sound, at its deepest point, was scoured by glaciers to a depth of 275 meters; its bathymetry essentially mirrors the surrounding foothills. As on land, this relatively small departure from sea level produces dramatic physical, chemical, geological, and biological effects. The size of the environment is, however, not so important as the size of the plankton itself—this is the greatest difference between terrestrial and aquatic ecosystems. In the sea there are many advantages to being small, and few to being large. Although the largest animal ever to have lived—the blue whale—lives in the sea, on the whole marine organisms are much smaller than those on land (Figure 4.1).

Phytoplankton cells, from the smallest phytoflagellate to the largest diatom, range from about 5 to 200 micrometers (millionths of a meter) in diameter (Figure 4.2). Some diatoms chains can reach 500 micrometers in length. Phytoplankters fall into two size classes, the nanoplankton (less than 20 micrometers in diameter), and the net plankton (greater than 20 micrometers and large enough to be caught with nets). The phytoplankton spans a range of one millionfold in weight—the same range that encompasses all terrestrial mammals, from mouse to elephant. It is difficult, however, to grasp how small single cells really are. It would take about one trillion large phytoplankton cells, 100 micrometers across, to occupy the same volume as an average six-foot man. The same number of humans could be stacked into a cone the volume of Mt. Rainier. Plankton inhabits a Lilliputian world that even the power of the microscope can hardly make familiar.

The phytoplankton world, furthermore, is one of evanescence. Due to the simplicity and homogeneity of its environment, a phytoplankter has no need of roots, stems, trunks, branches, leaves, or flowers. The adaptations of the phytoplankton are simple: small size to absorb nutrients and retard sinking; spines to slow sinking and to discourage hungry animals; and the ability to propagate rapidly when conditions are favorable, as well as the tenacity to endure when they are not. Primary productivity rivals that of the nearby forest, but individual plants don't persist—phytoplankters live for days, not centuries. There is no place to store growth except in tiny cells; the biomass of living plant material below a square meter of Puget Sound surface is but a thousandth of that above a square meter of forest floor.

Zooplankters, too, must cope with these facts of scale. Planktonic animals fall into three size classes: the micro-zooplankton, including the protozoa and rotifers; the meso-zooplankton, including the copepods, medusae, ctenophores, chaetognaths, and larvaceans; and the micronekton (animals almost large enough to be true swimming nekton), including the euphausiids, mysids, amphipods, and pteropods. Each of these zooplankters must be the right small size to extract its particular diminutive food from the dilute soup in which they all are suspended. In addition, each must be adapted to the fluctuations in its food supply, which could be bountiful one week and nearly nonexistent the next. These adaptions are reflected in animal reproductive cycles— the more variable the food supply, the more frequent the population's adjustment by means of reproduction. Microzooplankters eat the tiniest plants and multiply every few days. Animals of the micronekton, in contrast, capture prey as large as fish larvae and live for more than a year. These fundamental adaptations are the foundation for the functioning of Puget Sound as a unified ecosystem.

Sink or Swim

Plankton concentrates in and depends upon the score of meters just below the water surface, where life is first generated phytosynthetically. To stay alive all plankters must stay afloat; but plankters are heavier than water, and without compensating mechanisms will sink to a deep, dark death. Any species of plankton existing today must have evolved a means of staying off the bottom at least long enough to propagate itself.

The struggle of plankters to stay afloat has a critical relationship to their sizes. The greater the surface area of an organism, relative to its volume, the greater its friction as it moves through the water, and so the slower it sinks—a "parachute" effect. One way to increase relative surface area is to grow eccentric horns, spines, and wings. Another—the strategy intrinsic to all plankton—is to be small. Indeed, the swimming abilities of plankters have a nearly perfect inverse relationship to their sizes.

Phytoplankters combine their strategies to stay afloat with their strategies to obtain and store nutrition. Small size increases the surface area through which dissolved nutrients may be absorbed from the surrounding water. Odd shapes cause cells to spin and tumble as they sink, stirring the water to bring in nutrients. Some phytoplankters have a large cavity, or vacuole, at the center of each cell, reducing its mass and density relative to its surface. The cell's enzymatic machinery can exchange chemicals between the vacuole and the surrounding water, pumping out heavy ions (magnesium, copper, sulfate) and pumping in lighter ions (nitrogen, potassium, sodium, chlorine). Many microalgae are also buoyed by their intracellular energy stores of fat and oil.

Planktonic plants face a particular dilemma, because the sunlight they need is above, and the nutrients are below. The bottomward trickle of phytoplankton cells and the nutrients they have absorbed causes nutrients to be chronically less abundant near the surface than deeper in the water. A cell cannot float indefinitely at the surface, but must remain in motion lest it completely exhaust the nutrients from the small sphere of water around it. The nonmotile diatoms can do this only by allowing themselves to sink, at an average rate of about one meter per day—slow enough to divide several times before losing sight of the sun, but still sufficient to deplete their populations. Diatoms can only thrive when assisted, both in staying afloat and in finding nutrients, by vigorous stirring, as found in the waters of Puget Sound. In calm waters, therefore, an advantage is conferred on the swimming flagellates, which can regulate the depth at which they grow.

Zooplankters are affected less by sinking, since they have more swimming ability. Large copepods have been observed to cruise at a speed of thirty body lengths (10 centimeters) per second, and in short bursts they may spring 150 body lengths (50 centimeters) in a second. The outstanding feat of swimming, and the most perplexing, is the phenomenon of diel vertical migration. Many groups of zooplankton—some copepods, the chaetognaths, and the micronekton—swim up and down in the water on a 24-hour cycle. Euphausiids and chaetognaths spend the day at depths of 100 to 200 meters, rise to the top 100 meters during the night, then return to the depths before dawn.

Various theories about vertical migration have been proposed: that zooplankters save energy by spending days in cool subsurface water; that they avoid predators by staying in the dark; that they are bothered by bright light; or that they allow plants to grow unmolested by day to harvest a larger crop by night. No experiment or theory, however, has done more than demonstrate that any or all of them are possible.

Sinking and swimming, for both plants and animals, are also tied to reproduction. To maintain their populations in Puget Sound, phytoplankters, besides staying afloat, must avoid being washed by currents out to the Pacific Ocean. Cysts in the sediments persist through periods of arrested growth to reseed the surface waters. Planktonic animals play the enormous odds against survival in the lighted upper layer of the sea—which does not lend itself well to protection of young—by producing hordes of eggs and larvae. The extent of parental care in the zooplankton is the harboring of eggs (or larvae by mysids and amphipods) until they can be released in the surface waters where and when food is available, often under cover of darkness. Many zooplankters may also use their migratory strategies, both daily and seasonally, to avoid the strong surface currents which could carry them far offshore. In contrast, planktonic larvae instinctively seek the surface for a free ride to new territory.

Soil in the Sea

Besides plants and animals, all ecosystems have a third major division, the recycling component, which closes the ecological circuit and reconverts dead material to the nutrients that nourish plants. In the planktonic recycling system, independent of the sea bottom, are bits of organic matter—scraps of uneaten food, feces, molted exoskeletons, and corpses— generated by organisms near the surface and collectively called detritus. Mixed with this debris are inorganic particles washed down from rivers and eroding shorelines. Only about one milligram of particles, less than one percent organic, is suspended in a typical liter of Puget Sound water. Though very dilute, suspended matter resembles terrestrial soil, in that it provides a food source and a physical substrate for certain specialized animals and supports bacteria, which decompose dead tissue and return needed nutrients to the water.

For their irregular appearance, detrital particles are sometimes called "marine snow." The organic particles (or organic coatings on inorganic particles) are an attractive food for some zooplankters, both for mobile animals, which snatch bites as they swim, and for more sedentary microzooplankters, which adhere and feed off them continuously. The sinking flakes accumulate by snowballing, picking up plants, animals, and bacteria as they go. Small-scale current patterns also concentrate particles and hasten their flocculation. The aggregates grow as the organisms within them multiply. When they are disrupted, the new smaller pieces begin the same growth process.

Just as important as particles to recycling in the sea, however, are dissolved chemicals. The sea surface is a broth of both inorganic and organic nutrients, in which the ratio of dissolved to particulate organic matter can exceed a factor of forty. Phytoplankters need some of these organic nutrients, including vitamins. Bacteria interconvert the essential elements of life between particulate, dissolved organic, and dissolved inorganic forms. They decompose detritus into nutrients, and they take up other nutrients into their cells, which become food for animals. Nutrients are also recycled by zooplankton and fish, which excrete highly concentrated organic nitrogen and phosphorus, the former being especially useful to plants. Phytoplankters themselves release (or excrete) some forms of organic carbon, including some vitamins, into the water (perhaps accidentally, perhaps not), and these can contribute further to bacterial growth and recycling. Regenerated nutrients sustain primary productivity when the inorganic nutrients have been depleted by phytoplankton growth.

Patchiness

Oceanographers face a major handicap in studying plankton. For all the vigorous mixing in the sea, the water and its contents are never completely homogenized. Organisms in the sea are patchily distributed; they appear like galaxies in the cosmos or clumps of mushrooms in the forest. The most familiar example of aquatic patchiness is the schooling of fishes. Plankton is found in patches as well, ones more difficult to observe than fish schools. The distribution of plankton is so variable, in fact, that the discrepancy in plankton standing stock between samples taken simultaneously, side by side, is likely to be at least a factor of two.

Patchiness arises from both physical and biological causes. Seawater itself is not uniform. The collision of waters with different origins and different chemistries—surface and deep, inland and offshore, and fresh and salt—creates distinct water blobs or "parcels" that coexist temporarily until they mix together. While parcels persist they offer diverse and contrasting habitats for the plankters they contain. Parcels may be found in any size, from millimeters to kilometers, superimposed on and contained within each other. Persistent wind-generated surface current vortices, called Langmuir cells, concentrate floating matter into visible windrows. Such patchiness can be visible in slight variations of color and texture on the Sound's surface. There is even more variation in the vertical dimension than in the horizontal, since vertical mixing currents are weaker. Detrital particles, themselves tiny patches, form inanimately as they sink, by accumulating in small eddies, and by adhering to the surfaces of underwater air bubbles.

Phytoplankton patches form as colored clouds, with daughter cells created faster than they can be stirred away. Patches of nutrients form around "snowflakes," or where animals excrete, fostering the patchiness of plants. Phytoplankters also form thin horizontal stripes at depths where growth conditions are ideal and sinking is slow. Dinoflagellates, which migrate in and out of the surface daily, are patchy in time as well as in space. Patchiness due to swimming ability, moreover, is the rule among larger zooplankters: in addition to their daily and yearly migrations, they also seem to school as fishes do. These swarms are a more efficient means of exploiting their patchy prey, they are part of reproductive behavior, and they may have some defensive value.

Patchiness is so pervasive that it has become an integral part of the way marine ecosystems function. Repeated experiments have led to the conclusion that if phytoplankton was distributed uniformly throughout the surface water it would be too dilute to support animal life. Zooplankters apparently depend on occasional high concentrations of plants—both in space and time—to find enough food, and will apparently cease feeding when phytoplankton standing stock drops below a certain threshold of abundance. At the same time, paradoxically, other studies have concluded that phytoplankters survive this intense grazing only in the refuge of patches. Like settlers on the plains, they are better defended in a protective circle.

The problem of patchiness once again demonstrates the uncertainty of the scientist. When we analyze seawater, unless we are very careful, we destroy exactly what we seek to observe—the ephemeral, fluid structure that was present. Patchiness, from one point of view, is a nuisance that obstructs efforts to construct a clear picture of the abundance and habits of plankton. But patchiness is not an obstacle to knowing what goes on in the sea—it *is* what goes on in the sea. It deserves study in its own right, since it is as much a part of the plankton's world as size, or sunlight, or the stirring action of the water.

Habitats

Oceanographers divide the sea into zones (Figure 4.3), each containing a different sort of physical or biological action. There are big zones and little zones, and zones within zones. There are, first of all, the pelagic zone and the benthic zone. The pelagic zone is anywhere and everywhere in the open water. The benthic zone is the sea bottom. Plankton, fish, and whales are pelagic, whereas clams, starfish, and other bottom dwellers are benthic.

The zone exposed by the retreating tides is benthic and is called the intertidal zone. This is a unique environment because of its periodic exposure to air and direct sun. Plants and animals that live in this zone face severe problems with heat and dehydration. Below the inter-

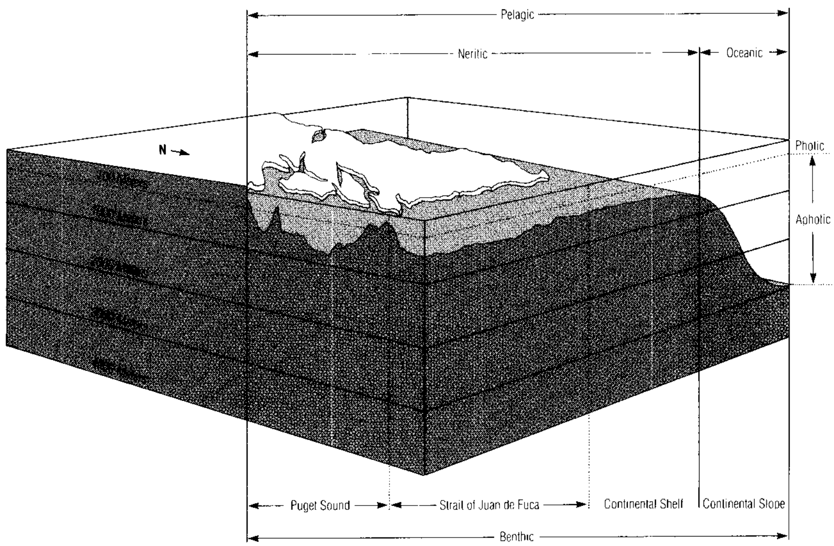


Figure 4.3 This schematic cross-sectional view shows that within the pelagic (open water) domain, Puget Sound, the Strait of Juan de Fuca, and some coastal waters are within the neritic (shallow water) zone. Neritic waters extend offshore to the edge of the underlying continental shelf.

tidal is the littoral zone, where the water is shallow enough that sunlight reaches the bottom and can support seaweeds.

The pelagic zone is divided vertically into the euphotic zone, where there is sufficient light for photosynthesis, and the aphotic zone, where there is not. The boundary between the euphotic and aphotic zones varies in depth; the brightness of the sun and the transparency of the water make it go up and down at different seasons and locations. The pelagic zone is divided horizontally as well. Near shore is the neritic zone, and far from shore is the oceanic zone. The boundary between the neritic and oceanic zones is the edge of the continental shelf, about 50 to 60 kilometers off the Olympic coast, where the water depth does not exceed 200 meters. Thus, all of Puget Sound is within the neritic zone.

The distinction between the neritic and oceanic zones is made because the nature of planktonic life changes in deeper water. The water over much of the shelf is shallow enough that, especially during a storm, nutrients and resting cysts can be stirred from the bottom into the euphotic zone to stimulate phytoplankton growth.

Puget Sound is a special kind of zone within the neritic zone; it is an estuary. Grays Harbor, San Francisco Bay, and Chesapeake Bay are other familiar estuaries, all characterized as semi-enclosed areas where fresh water meets salt water. Puget Sound is also a fjord, an inlet created by a glacier. Fjords are deep, narrow, and steep-sided, and often have shallow plugs called sills left by the retreating glacier. Puget Sound has sills at several locations: at Admiralty Inlet, between the San

Juan Islands, at Deception Pass, at the mouth of Hood Canal, and at The Narrows (page 46).

Biologists divide the world into another set of zones, based on biological boundaries. These maps may coincide with geographical features, but the real zone boundaries are abstract and can't be drawn on paper. An ecosystem, for example, may be defined as a physical space and the living things that live in it, with the hypothetical boundary of an ecosystem drawn where creatures are not affected by either the organisms or the environment beyond its borders.

Puget Sound, neatly defined by surrounding land and narrow connections to the Pacific Ocean and the Strait of Georgia, appears to stand as an ecosystem unto itself. But the definition is not a perfect fit. Puget Sound and the Strait of Juan de Fuca are not biologically independent of either the Pacific Ocean or the Strait of Georgia nor of the lands bordering all of them. The water and organisms exchanged among these water bodies intertwine all of their ecological fates. Symbolizing this biological unity is the Pacific salmon, which makes all of the coastal and northernmost North Pacific its home. Furthermore, Puget Sound is not uniform within its boundaries—plankton behaves very differently in the shallow fingers of the southern Sound, for instance, than in the open Strait of Juan de Fuca. Nevertheless, the physical properties controlling plankton, and the biological interactions that result, are constant enough within the Sound and different enough from the open Pacific to merit separate consideration.

Within an ecosystem such as Puget Sound, the fates of plants and animals are subject to two broad biological processes, competition and predation. Each organism must contend with other, similar organisms for common needs—sunlight, nutrients, food, etc.—at the same time that animals are trying to eat them.

Superficially, the world of the plankton might seem to be a single arena in which all the species compete. If this were so, we might expect a steady disappearance of species, a winnowing of the weak from the strong. The "Competitive Exclusion Principle" states that given enough time one superior species should exclude all others with which it competes. In Puget Sound, however, as in the sea at large, different plankton species wax and wane. Although one species may dominate almost completely under some circumstances, it does not persist; other species make comebacks. Dominance in the plankton is the exception, and diversity is the rule. The Competitive Exclusion Principle is clearly inadequate to describe Puget Sound.

G. Evelyn Hutchinson, one of the grand old men of aquatic biology, called this failure "The Paradox of the Plankton." He suggested that the principle never gets sufficient time to take hold. Before a dominant species has a chance to exclude its competitors, conditions change and a new species begins to take over. Such variability is built into natural systems, on time scales of hours, weeks, and even years, and leaves the door open for multiple species to maintain their footholds.

Conditions in the plankton vary in space as well as in time, and that patchiness permits competing species to dwell contemporaneously in slightly different habitats. Furthermore, under most conditions in the sea, competing plankters may be sufficiently dilute that they do not even feel each other's presence, living within tiny spheres of influence which may never overlap. Some plankters adopt behavioral traits—migration patterns, differing nutrient and food requirements, and organism size—which partition the surface waters into delicately carved niches where species can avoid competition. Superimposed on all of these intrinsic influences are the extrinsic effects of predators. Animals can be highly selective of their food, and so can skew ecological competition toward organisms with the best defenses.

Food Chains

Various tangible objects have been used as models for visualizing the ecological relationships by which higher organisms obtain nutrition from lower ones. None of them can fully portray the complex and dynamic nature of an actual ecosystem, any more than a pencil sketch can portray a human being. A useful portrait, however, conveys the most information with the fewest lines.

The simplest ecological model is the food chain, by which each organism is linked to its sources of nutrition and to the organisms that feed on it. Food chains are linear and one-dimensional, with each organism assigned to a numbered trophic level. At the first trophic level are the plants, which as autotrophs make their own food. Heterotrophs, which must obtain food from other organisms, are assigned to the second trophic level of the herbivores and to the third and higher levels of the carnivores.

More complex and realistic is the food web, in which animals do not fall neatly into trophic levels. Omnivores (which feed on both plants and animals), animals that change their feeding habits as they mature or as food abundance changes, and predators that feed on other animals ostensibly at the same trophic level all form a second dimension of cross-links between many coexisting and changing food chains. An animal may obtain its food through several different routes simultaneously, each perhaps having a different number of trophic links. Despite this increased complexity, however, food webs are still very crude representations of systems which defy even the power of a computer to portray them.

Food chains and webs at the sea surface are unlike any other on earth. The pelagic food chain is rigidly built according to size, with pelagic animals almost always larger than their food. In forests, the largest organisms are the massive long-lived trees. In grassland and tundra ecosystems, the largest organisms are long-lived, highly mobile herbivores such as bison and caribou. In Puget Sound, however, the largest organisms are carnivores. Only killer whales—which can gang up and steal the tongue of the larger minke whale—ever use the strategy of the wolf or the lion, and hunt in packs for large prey.

Paradoxically, the trophic relationships of highly fertile Puget Sound most closely resemble those of a desert or dry prairie. In both, most plants are relatively small and patchy, their growth is intermittent, and their abundance changes at the whim of the physical elements. Many planktonic and desert animals hide during the daytime and feed at night. As in Puget Sound, herbivores of the desert (such as rodents and insects) are small and opportunistic, carnivores (such as birds) are large, fierce, and mobile, and very little biomass accumulates either in living organisms or in organic detritus.

To grasp the essential information about how animal populations in Puget Sound are controlled by both the abundance of food and the path by which it is obtained, it is necessary to begin with the simplest model, the food chain. This approach will sacrifice a great deal of interesting detail. Eventually some of the most important features of Puget Sound's pelagic ecosystem will only be explainable by adopting the more complex picture of a food web.