CHAPTER FIVE

The Green Machine—Phytoplankton

Nihil vilior algae (Nothing is more worthless than algae).
Virgil

Puget Sound is a solar-powered factory in which animals are assembled from raw materials of water and the carbon, nitrogen, phosphorus, and other vital chemicals dissolved in it. The analogy is unfair in some respects, since a single cell, with its ability to replicate, is more wondrously complex than the largest factory. Much can be learned, nevertheless, by examining organisms and ecosystems as though they were mechanical.

Puget Sound's pelagic food chain, which culminates in fishes, birds, mammals, and humans, begins with the phytoplankton. This community of tiny plants is a biological antenna deployed over the entire surface of the Sound, gathering the solar energy needed for the production of animals. The phytoplankton is also a rechargeable storage battery, which photosynthetically sequesters sunlight in the chemical form of combined carbon. Solar energy stored in biomass can be called trophic energy. Thus carbon becomes the fuel and, along with the nitrogen in protein, the structural material for fabricating the entire living ecosystem.

To comprehend the Puget Sound pelagic food chain as a biological machine, and to trace the path of biomass—"food"—and the trophic energy it contains as they are transmitted through each trophic level, we must examine some of the important environmental and biological constraints which regulate that transmission. The starting point is the interface between the phytoplankton and its surroundings. Plants are directly tied to their environment, whereas animals are, to some extent, segregated from it, buffered by their position on the food chain.

The Physical Setting

The understanding of primary production in Puget Sound depends as much on physics as on biology. Like terrestrial plants, planktonic plants need only enough light and enough nutrients and they will grow. Unlike the land, however, Puget Sound is not at rest, and water motion affects the availability of both light and nutrients. Phytoplankton growth in the Sound is regulated by the interaction between sun, precipitation, and forces that set water moving, including wind. In short, as on land, plant production in water depends on the weather.

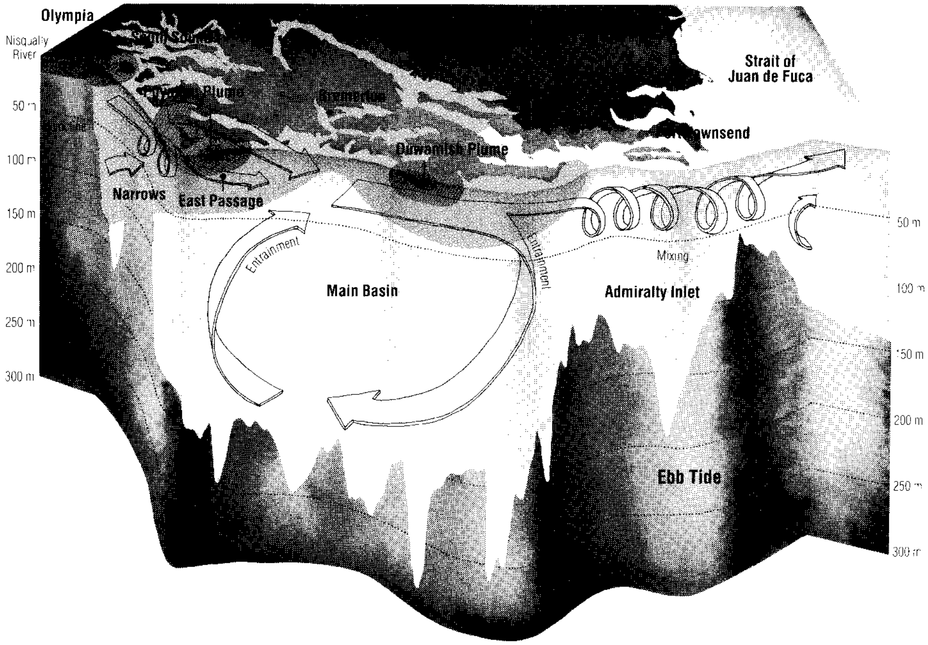


Figure 5.1B Currents in the main basin—ebb tide. In deep water, there is weak landward flow. Surface water flows seaward, entraining bottom water into its lower layers. Roughly two-thirds of the surface flow reaching Admiralty Inlet returns to the main basin as it mixes with deeper inflow. Low salinity river plumes (dark shading) are evident off the Nisqually, Puyallup, and Duwamish rivers. Currents in East Passage remain predominantly landward at all tidal stages. (After Barnes and Ebbesmeyer, 1980)

can also be beneficial because it brings nutrients from deep water, where they are plentiful, toward the surface, where they are most needed and yet likely to be scarce. The role of vertical mixing, then, is twofold: too much mixing depresses photosynthesis and disperses phytoplankton populations, but not enough mixing leads to nutrient exhaustion. A little bit of mixing is just right, and this is what makes Puget Sound such a productive ecosystem.

The agent of both horizontal and vertical mixing is moving water. When seawater stands still, the only transport processes—molecular diffusion of dissolved chemicals and sinking of suspended matter—are relatively slow. Any physical force that sets water into motion, particularly turbulent motion, greatly increases the rate of mixing.

Currents, including tidal currents, are the dominant water motions in Puget Sound. The pattern of net circulation, averaged over at least several tidal cycles, is typical of an estuary (Figure 5.1). River runoff drives fresh water seaward at the surface, and pulls along (entrains) several times its own volume of the underlying salt water. Deeper water, as a consequence, flows landward from the Strait of Juan de Fuca to replace the salt water entrained in the surface outflow. The net flow changes from seaward to landward at a depth of roughly 50 meters. The inexorable skimming off and replacement from below of the water in this transition zone produces a gradual upward mixing of nutrients.

At any given moment, the mean current condition is hidden amidst the much stronger twice-daily rhythm of tidal currents, which can completely reverse the estuarine outflow. Surface water flows two steps seaward on the ebb tide (Figure 5.1), then one step back on the flood tide. Likewise, deep inflow is retarded by the ebb and reinforced by the flood. This seesawing of waters from the rivers and the sea produces both horizontal and vertical mixing where the two meet.

Tidal currents and the mixing they cause vary in strength with the tidal amplitude. Each month there are two periods of "spring" tides (periods of especially high and low tides) associated with the new and full moons, and two "neap" tides of low amplitude during the quarter moons. The spring tides during the months of April, May, and June are of particularly large amplitude, and thus cause bimonthly periods of especially vigorous mixing when the growth season is just beginning.

Vertical mixing is strongest where the ebb and flood rush over shallow shoals. The forcing of currents over sills and through narrow constrictions propels deep water upwards, causing strong mixing often visible as surface turbulence. The sill at Admiralty Inlet, in fact, obstructs the continuous inflow of deep water, which pulses intermittently instead. Although this process occurs at only a few places, these are the dominant areas of mixing for the entire Sound.

Winds also cause mixing. Puget Sound is more sheltered from wind action than coastal and open ocean waters, but in some cases—the storm that destroyed the bridge over Hood Canal in February, 1979 is an outstanding example—its effects on the surface can be severe. The wind acts by raising waves, which stir the surface layer. The wind also generates currents in the direction it blows, and since the wind direction may not be the same as that of the underlying surface current, it can alter the existing water flow and the resultant mixing. The effects of winds are most pronounced when their direction is parallel to the long axis of a body of water—that is, when they have a long fetch over which to act. The 1979 storm was devastating because the wind blew directly down the long axis of Hood Canal, in opposition to an incoming tide, and built the water up to an extreme crest. In most of Puget Sound, northerly and southerly winds have the greatest effects.

Given enough light and nutrients, rapid phytoplankton growth can commence at Puget Sound's surface simply due to the absence of strong mixing. Mixing forces are pervasive, however, and little growth usually occurs unless mixing is counteracted by some stabilizing force that permits phytoplankters to bask undisturbed in surface sunshine. Surface water stability—its resistance to vertical mixing—is the result of strati-

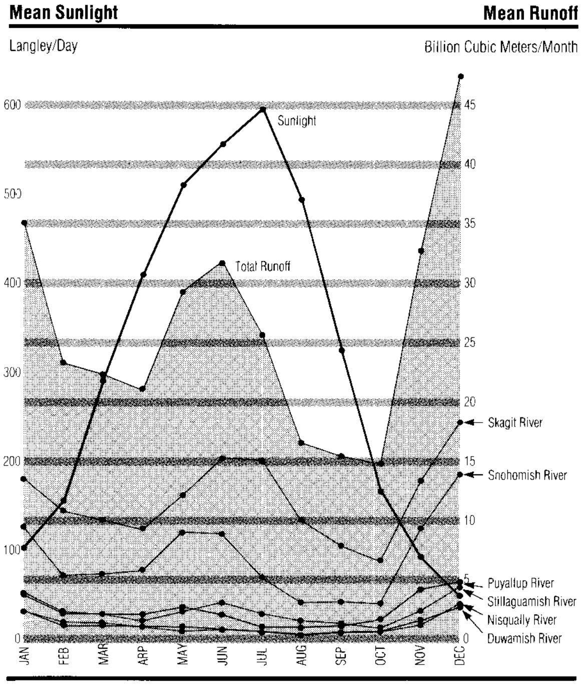


Figure 5.3 The growing season in Puget Sound. Increased sunlight caused by longer days, clearer skies, and a higher sun angle coincides with stratification at the surface, making May to July the peak growing season in the main basin. Freshwater runoff accounts for stratification, and is shown here as outflow from individual rivers and as total input to the main basin. (After Dexter et al., 1981; and Ebbesmeyer and Helseth, 1977)

There are further complexities to the regulation of primary productivity in the main basin, however. The onset of phytoplankton growth occurs later here than in other estuaries at the same latitude, or even in other regions of the Sound; yet on an annual basis the main basin is more productive than these other areas. Furthermore, the growth occurs as blooms, which like sunshine and runoff are discrete events whose timing and intensity differs considerably between years and may have little resemblance to a long-term average condition. To understand these irregularities requires a closer examination of the unique physical environment of the main basin.

Sills and Residence Time

The main basin of Puget Sound is bathymetrically embraced, as though by a pair of bookends, by shallow sills at its northern and southern ends. The sills alter the normal pattern of estuarine circulation by causing mixing and by restricting the exchange of water with adjacent basins, and these alterations contribute to the singular patchiness and productivity of the main basin.

Not all of the surface outflow in the main basin comes directly from rivers. Fresh water from the southern Sound must pass through The Narrows on its seaward course. From The Narrows outflow traverses Colvos Passage and encounters another sill near Blake Island before entering the main basin. Along this route water from a depth of 120 meters (80 meters below the sill depth) is completely blended with surface water, producing roughly a quarter of the main basin's outflow. This disruption of stratification dilutes whatever phytoplankton grows in the southern Sound, and suppresses primary productivity at The Narrows throughout the year. It also accounts for the delay of blooms until April and May in the main basin, compared to estuaries with similar runoff and sunlight characteristics, such as Long Island Sound, where blooms begin in March.

In the open main basin, mixing forces are weaker, and phytoplankton can grow using the rich nutrients pumped to the surface at The Narrows. Once sunlight is sufficient to compensate for the weak stability, these nutrients sustain primary productivity at a high level through the summer. The annual production of the main basin exceeds that of Long Island Sound by a third or more. This, then, is the secret of the main basin's high productivity: vigorous mixing is patchy, restricted to a small upstream area, and growth proceeds undisrupted in the open basin.

The surface water in the open main basin is also quite patchy, coming as it does from two different sorts of sources. Highly stratified river runoff flows seaward side by side with less stratified but nutrient-rich Narrows water. These discrete waters appear as "stripes," greener as they drift north, which are generated twice a day by the ebbing tide. Depending on the strength of tidal and other currents, the stripes are about nine kilometers long, and can be visible from a ship or an airplane (Figure 5.4). The two different source waters represent the two extremes of physical conditions for phytoplankton growth, mixed waters and stratified waters. Seemingly the most favorable spots for phytoplankton growth would be where these streams make contact, where both nutrients and stratification are in close proximity. Perhaps such contacts could even be traced by locating an optimal salinity that marks their boundary. Such speculations aside, it is clear that "stripes" make the surface of the main basin a highly heterogeneous environment.

To understand patchiness in time, some further details of the circulation in the main basin are needed. Stripes have a finite life span. Oscillating with the tides, surface water traverses the length of the main basin and reaches Admiralty Inlet in roughly six days—faster when runoff is profuse, slower when held back by northerly winds. There the stripes encounter another sill, which once again homogenizes surface and deep waters and disperses surface patchiness, stratification, and blooms. This disruption further alters the classical picture of estuarine circulation. A major fraction of surface outflow is believed to be diverted back into the Sound, rather than to the Strait of Juan de Fuca. About two-thirds of the deep water entering the main basin, in fact, is thought to be main basin surface water caught in the deep inflow during mixing at Admiralty Inlet, rather than water from the Strait.

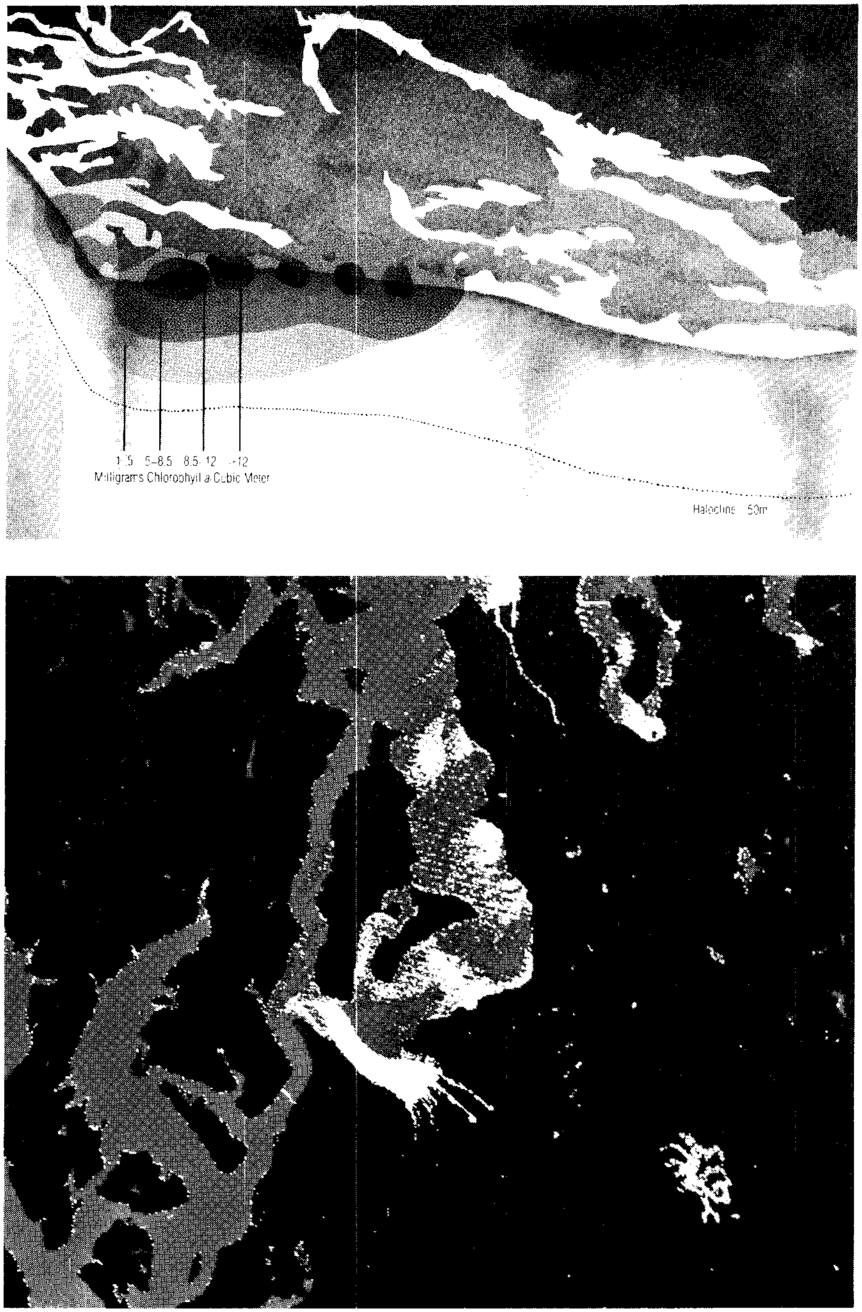


Figure 5.4 Patchiness in the main basin. Top: Tidal striping of surface chlorophyll patches as derived from continuous fluorometric measurements on May 15, 1969 (After Munson, 1970).

Bottom: Computer-enhanced satellite (LANDSAT) photograph of the main basin on June 13, 1974, showing surface tidal striping off the Puyallup River. The photo shows light of wavelengths of 600–700 nanometers (billionths of a meter) and detects both chlorophyll and nonliving suspended sediment. (Photo courtesy Smyth Associates, Inc.)

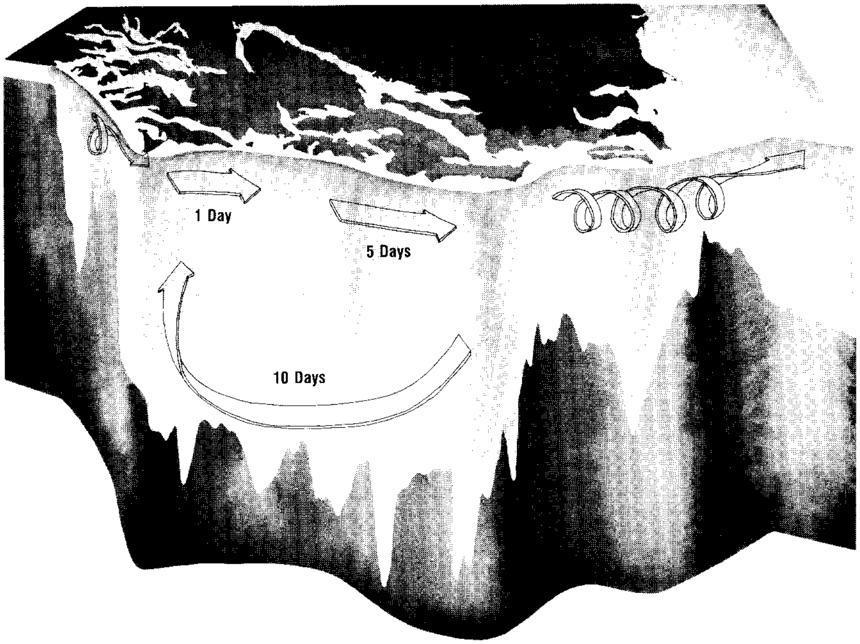


Figure 5.5 Entrainment of surface water by intrusions from the Strait of Juan de Fuca and of deep water by upwelling at The Narrows produces a semi-closed loop in the average circulation pattern of the main basin. Water and plankton average one trip through the deep portion of the loop before exiting at Admiralty Inlet (After Ebbesmeyer and Helseth, 1977).

Thus the mixing at Admiralty Inlet partially short-circuits the two-layer estuarine circulation pattern. Water that enters the Sound at a river mouth might receive an infusion of Pacific salt water at Admiralty Inlet, be carried back through the cold, dark depths of the main basin to The Narrows, then be spurted back to the surface, perhaps repeating the cycle several times before finally exiting seaward (Figure 5.5). The travel time through the deep basin is longer—ten to twenty days—than at the surface. This semi-continuous loop pattern of circulation resembles a conveyor belt, carrying water, salt, nutrients, and phytoplankton back and forth between The Narrows and Admiralty Inlet, between the surface and the depths.

The retention and recycling of water within the main basin have several biological consequences. The salinity and nutrient content of deep water are lower than they would be with more inflow from the Strait of Juan de Fuca, reducing stratification, nutrient content, and productivity of surface waters past the spring and into the summer. At the same time, because phytoplankton is carried into deep water, there is more total chlorophyll below the euphotic zone than within it. This reservoir tends to offset the reduction in productivity by retaining some of the phytoplankton generated, and by seeding water upwelled at The

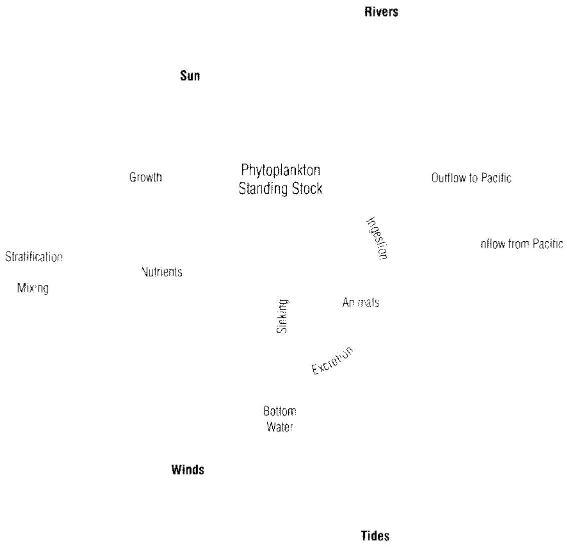


Figure 5.6 Physical forces produce both positive and negative effects on phytoplankton growth, and blooms occur when the forces are balanced. Phytoplankton standing stock is increased by photosynthesis and nutrient uptake, which are regulated by sunlight, stratification, and mixing. Standing stock is decreased by animal consumption, sinking, and flushing by winds, tides, and runoff.

Narrows with an increased stock of cells that survived suspended animation deep in the water. Such a cycle, enhanced by the vertical migration of dinoflagellates, has been observed in another, shallower estuary, Chesapeake Bay. The greatest biological consequence, however, is the effect of the liquid conveyor belt on the timing of blooms.

Residence time (also called retention time or flushing time) is a third major factor, in addition to sunlight and stratification, that governs phytoplankton blooms in the main basin. Surface residence time is the duration of the transit along the surface portion of the liquid conveyor belt, from a river mouth or from The Narrows, where surface water is generated, to Admiralty Inlet, where it is dispersed. While the interplay between sunlight and stratification controls the rate of photosynthesis, the residence time controls the standing stock, which accumulates as a product of photosynthesis. Residence time effects have also been observed in estuaries in Maine, off New York, in San Francisco Bay, and in India, as well as in Puget Sound marinas.

The effects of residence time on phytoplankton growth resemble those of mixing. As with mixing, intermediate residence, rather than long or short, is optimal. Phytoplankters need several days of uninterrupted growth to build their standing stock to bloom proportions, especially when beginning from the sparse populations of a Puget Sound winter. A short residence time means a short exposure to sunlight, and a low resulting standing stock. When both sunlight and stability are favorable, very long residence time, in contrast, leads to a slow rate of nutrient input at The Narrows, nutrient depletion, and inhibition of phytoplankton growth.

There are no measurements of its variability, but the residence time of main basin surface water is governed, in complex fashion, by the same agents of water motion that cause mixing: river flow, tides, and winds. Productivity in the main basin might be even higher if runoff and residence time effects did not often tend to counteract each other. Heavy runoff, which reduces mixing and creates a stable layer for phytoplankton growth, also flushes nascent blooms rapidly out of the main basin. Weak runoff and longer residence coincide with weaker stability. Tidal effects on residence times parallel those on mixing—the stronger currents during the bimonthly spring tides increase the rates of both flushing and mixing, and so reduce the potential for blooms. Finally, all winds increase surface mixing, but the southerly winds of winter and of storms accelerate surface outflow and reduce residence time in the main basin, while the northerly fair weather winds that accompany sunshine also benefit productivity by lengthening residence time.

All of these influences are highly variable in time, and produce the extreme temporal patchiness of phytoplankton growth and abundance in the main basin characterized as blooms. The effects of all these physical forces on primary productivity are summarized graphically in Figure 5.6. The occurrence of a bloom depends on the coincidence of sunlight with some or all of the physical forces that favor intermediate stability and residence time: moderate runoff, neap tides, and light northerly winds. An abrupt alteration in one or more of these beneficent influences could prevent a bloom, or cause a nascent bloom to collapse.

The prime season for blooms is in the spring, because these physical influences do not occur completely randomly or independently of each other, but tend to co-occur. Increasing springtime sunshine is associated with both increased runoff and northerly winds. The balance of these influences is delicate enough that the bimonthly advent of the neap tides can trigger a bloom most often in late April or early May. The variability of blooms in a given year and in different years, and the sensitivity of the main basin ecosystem to its various physical influences, are illustrated by case studies of individual years.

The Spring Bloom

Blooms have a strong element of randomness to their appearances. Although the timing of the spring bloom depends on some quite predictable events, such as neap tides, and on fairly reliable increases in sunlight, runoff, and northerly winds, these seasonal trends only specify an envelope of probabilities. The exact timing of a clear spell, or the onset, magnitude, and duration of a consequent bloom, are largely matters of chance. As important to understanding primary production in the main basin of Puget Sound as a listing of the driving forces, is a knowledge of their variability. One day does not necessarily look like the next, one year does not look like another, nor is any of them likely to match the long-term average condition. Furthermore, the ability to comprehend this variability is confounded by the practical limitations on sampling.

Figure 5.7 shows the smallest scale of time variability: sunshine, runoff, stratification, tides, and phytoplankton at a single location can change markedly within a few days. Blooms—outbursts of growth lasting ten days or less—appear at intervals during the study period, April through June. They appear at different times in each of the years illustrated, reflecting the different timing of tides and weather.

The brief period of observation during 1969 appears to have been ideal for bloom formation. Bright sunshine, moderate runoff and stability, and gentle northerly winds all coincided with a neap tide. Although the conditions (or the data collection) did not continue long enough to furnish a high biomass, the primary productivity (nearly ten grams of carbon per square meter on May 10) approached the highest ever measured in marine phytoplankton. The bloom appears to have been terminated by an abrupt increase in runoff, which although increasing the stability also flushed the surface waters rapidly seaward.

The opposite extreme, a very unproductive spring, occurred in 1975. Low sunlight and high runoff that year dictated small blooms, which nevertheless corresponded fairly closely with neap tides and high stability.

Perhaps 1966 was a more representative year, and one in which the interaction of the various bloom-forming forces is well illustrated. Although the first and most extensive bloom of that season also appears to have been flushed away, the ensuing four phytoplankton peaks correspond closely to moderate peaks in stability. Runoff was generally low, sunlight generally high (especially in early June), and tidal ranges low (if not exactly neap) at the time of each bloom.

Each of these examples differs significantly from the composite seasonal picture obtained by summing a decade of data. This is the statistical envelope of bloom probability; it is an average year, but not a typical year, because sun and phytoplankton arrive in discrete events, not in smooth continuous gradations. Nevertheless, the graph presents useful information concerning the entire year's primary production. In the average year, 465 grams of carbon are fixed by phytoplankton over each square meter of the main basin's surface. The most productive period is likely to be during May, and 86 percent of the year's production can be expected from April through August. The midpoint of the growing season falls around the summer solstice, and the average stratification is symmetrical about that date. Yet there is consistently reduced production around that date, and again later in the season. Although

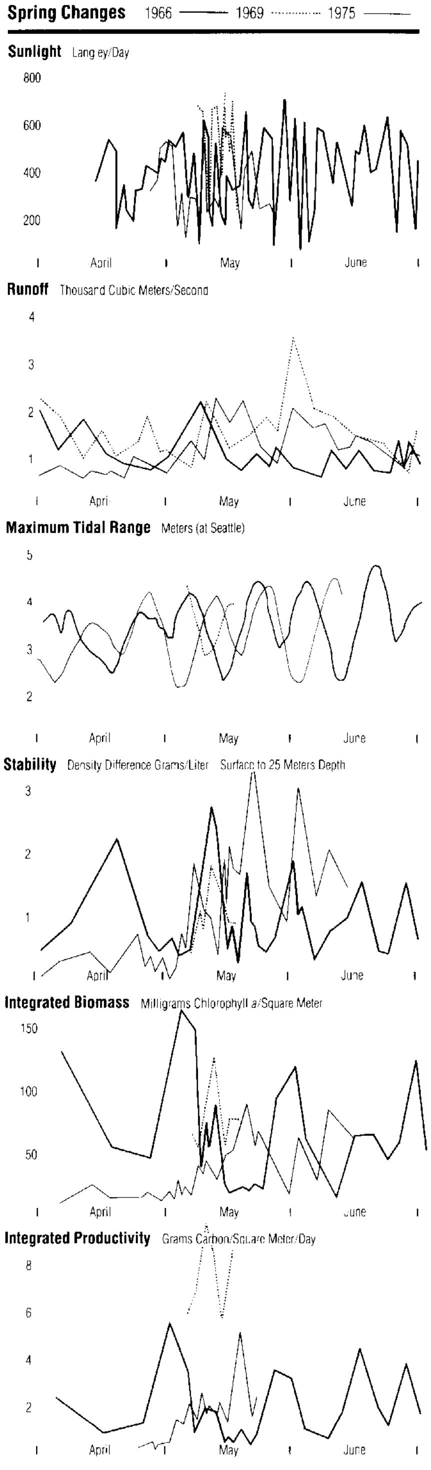


Figure 5.7 Temporal variability of phytoplankton and environmental forces in the main basin. Measured sunlight, estimated total Puget Sound river runoff, predicted maximum tidal range, measured stability (the density increase from the surface to 25 meters depth), and the resulting measured phytoplankton production and biomass are shown as they vary on three time scales. The first is the 90-day spring bloom period in three representative years. The second is the mean annual pattern obtained by averaging data by month for the decade 1966–1975. The third shows differences between years in the same decade, from either monthly or annual averages. (After Campbell et al., 1977; Coomes et al., in press; Ebbesmeyer and Helseth, 1977; Harris, 1981; METRO, unpublished; Munson, 1970, U.S. Environmental Data Service; and Winter et al., 1975).

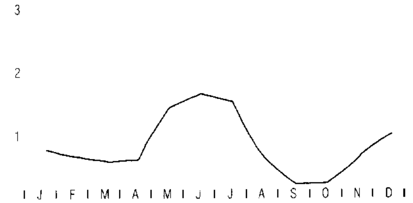
Monthly Changes

Sunlight Langley/Day

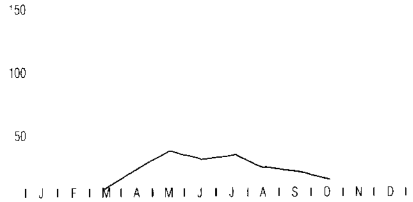
Runoff Thousand Cubic Meters/Second

Maximum Tidal Range Meters (at Seattle)

Stability Density Difference Grams/Liter Surface to 25 Meters Depth



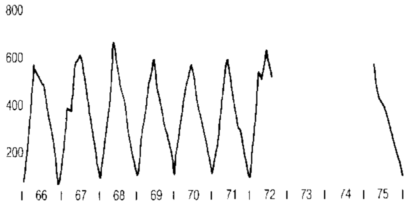
Integrated Biomass Milligrams Chlorophyll *a*/Square Meter



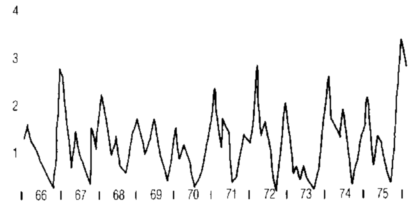
Integrated Productivity Grams Carbon/Square Meter/Day

Yearly Changes

Sunlight Langley/Day (By Month)

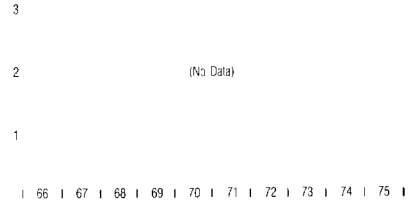


Runoff Thousand Cubic Meters/Second (By Month)

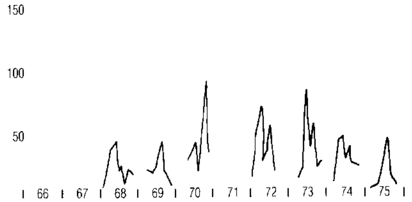


Maximum Tidal Range Meters (at Seattle)

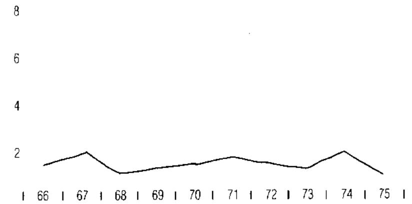
Stability Density Difference Grams/Liter Surface to 25 Meters Depth



Integrated Biomass Milligrams Chlorophyll *a*/Square Meter (By Month)



Integrated Productivity Grams Carbon/Square Meter/Day



there is more sunlight after the solstice, lower production may result from increased zooplankton populations.

Figure 5.7 also shows the total annual production in the main basin for the individual years of the decade averaged above. As on land, there are good years and bad years for plant growth. The magnitude of spring blooms plays an important role in determining how productive the year will be as a whole, and there is also some relationship between a year's production and its environmental conditions.

That clearer cause-and-effect relationships are not evident in these figures is not surprising, considering the sparse quality of data. Samples were taken at a single location, at intervals of a few hours to a week, depending more on convenience than on oceanographic conditions. They are mere arbitrary grabs from amidst the chaos of oscillating stripes. While it may be overstating the case to infer that apparent blooms may just be artifacts of passing patches, nevertheless it is impracticable, by the methods used here, to completely separate spatial and temporal variability.

A case study of patchiness was made during the vigorous growth period of May 1969. A bloom, concentrated near the surface, appears around May 12 in data from single-station sampling. Surveys of surface patchiness taken through the same period, howevever, illustrate that single daily samples could be misleading, making the simple passage of a stripe resemble a bloom (Figure 5.4). There is apparently no consistent geographic pattern to these stripes as they pulse seaward in the open main basin. That is, while at a given time one spot may be greener than another, averaged over a few days or weeks all locations appear to be about equally productive. Over a period of time, the variability between locations is no larger than that at a single station.

An additional dimension of patchiness is the species composition of the phytoplankton, a fine grain beneath the gross outlines of standing stock. Surprisingly, very little information is available on phytoplankton species in the main basin. The best data (Figure 5.8), from the spring bloom of May 1967, demonstrate some important points. The dominant organisms are centric diatoms of the genera *Skeletonema*, *Thalassiosira*, and *Chaetoceros*; and populations of these organisms are extremely patchy in the main basin, fluctuating up to a thousandfold within a few days, even as total biomass varies merely by a factor of two to four.

Observations of phytoplankton species at other places and times on Puget Sound are quite scarce. In particular, there are few documented occurrences of flagellates. There is considerable evidence from other sources, however, that different phytoplankton species have very different preferences both for habitat and for environmental conditions such as temperature, light intensity, stability, and water chemistry. Di-

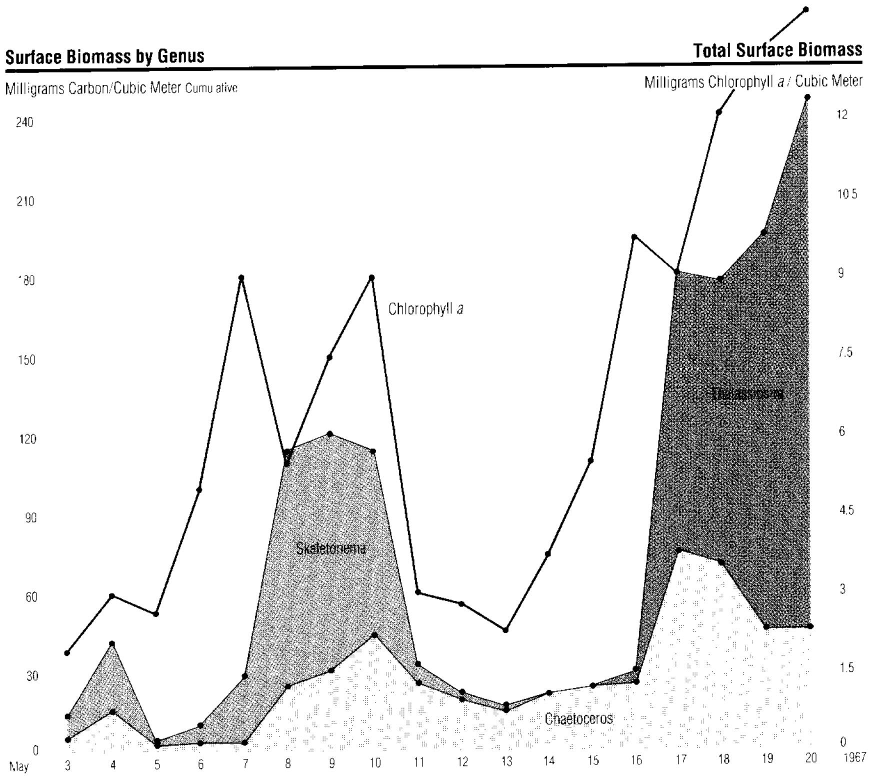


Figure 5.8 Total biomass of phytoplankton at the surface of the main basin during May 1967 is displayed as chlorophyll *a* and as carbon (estimated from cell counts of major genera). The same two blooms are evident in both sets of data, but populations vary widely: *Chaetoceros* maintained a relatively low and constant population, while *Skeletonema* bloomed after a neap tide May 5 and disappeared by the time of the *Thalassiosira* bloom at the May 20 neap tide. (After Booth, 1969)

noflagellates and phytoflagellates seem to inhabit different waters than diatoms do, being more abundant in warm, strongly stratified or poorly mixed waters. Phytoflagellates are also found in strongly mixed dark winter waters and despite their size can be the most abundant phytoplankters in both population and biomass. Observations from British Columbia suggest that while phytoflagellates may bloom at any time of year, they tend to dominate in early spring before diatom blooms have taken hold. Distinct populations of different phytoplankton groups can also coexist at different depths. Certainly the swimming ability of the flagellates must enable them to persist under conditions in which diatoms cannot remain afloat.

The importance of knowing the type of phytoplankton present, as well as the amount, will become clear when studying the food chain. Animals, including zooplankters, are selective eaters. Thus, the phytoplankton community is believed to strongly influence both the amounts and the types of zooplankton present; this in turn affects the fish community. Research on these trophic connections is just beginning to demonstrate their variability and importance.

Inlets: Variations on a Theme

The same processes that govern phytoplankton in the main basin—sunlight, mixing and residence time—operate in the rest of the Sound as well. There are variations, however, in the physical manifestations of these processes. The topography of different basins influences current speed and direction, as well as mixing and transport by winds and tides. The amount of river runoff alters stratification, residence time, and even water clarity. It is a game of ecological poker, in which each arm of the Sound is dealt a different hand from the same physiographic deck, with its biological behavior determined accordingly.

With a cautious reminder of the variability that characterizes all areas of the Sound, its subdivisions can be distinguished from each other on the basis of their average conditions of mixing and residence time. If these two variables are made the axes of a coordinate system, then basins of the Sound can be placed into quadrants that denote their physical and biological characters (Figure 5.9). There are insufficient data to make this representation strictly quantitative; rather, each subregion of the Sound is placed qualitatively along the spectra from weak to strong mixing, and from short to long residence time.

The two axes express the two measures of phytoplankton fertility. At a given intensity of sunlight (assumed, for simplicity, to affect phytoplankton uniformly over the Sound), mixing governs productivity, and residence time governs standing stock. Intermediate values of both are most favorable for sustained primary production, and thus an area such as the main basin, which on the average lies close to the intersection of the axes, has the greatest productive potential. The farther a basin is placed from the center of the coordinates, whether by increases or decreases in mixing or residence, the lower its potential production.

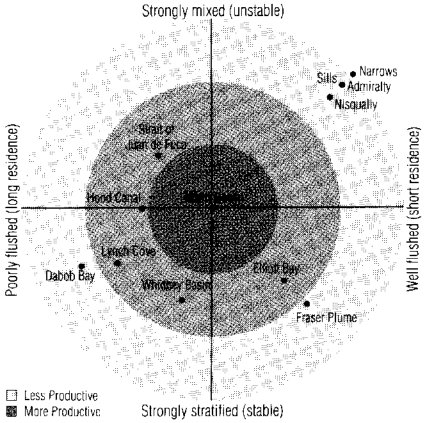


Figure 5.9 Relative productivities of Puget Sound inlets. Compared to the main basin, which seems to have a nearly optimal balance of mixing and flushing for phytoplankton growth, other areas of the Sound are less productive. They may be flushed and mixed too much (as at the sills) or not enough (as in inlets), or another combination of suboptimal conditions.

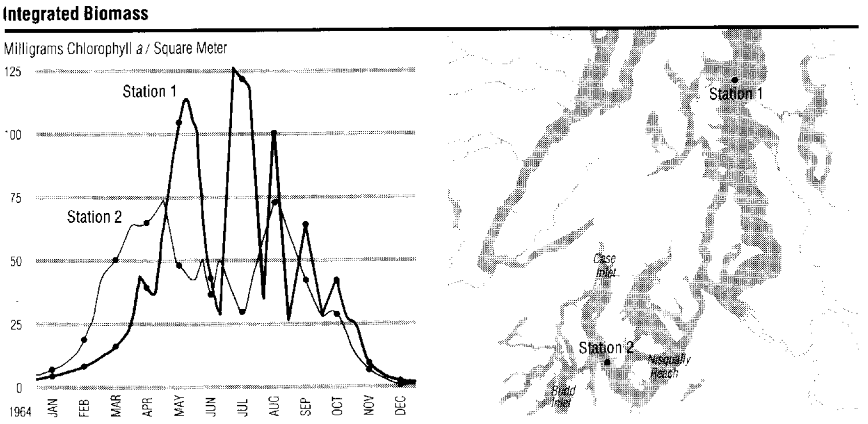


Figure 5.10 In 1964 phytoplankton biomass near a sill in the southern Sound (station 2) showed an earlier spring increase than in the main basin (station 1). During summer, standing stock was lower and less variable at station 2 due to strong vertical mixing in shallow water. (After Anderson, unpublished data)

Sills and Passages

Sills, such as those beneath The Narrows and Admiralty Inlet, are locations of strong mixing and short residence time, past which water is rapidly transported by tidal currents. There is little seasonal variation in the stability or the nutrient content of the waters over sills. Some of the best data on Puget Sound sill areas (Figure 5.10) come from a passage at the mouth of Case Inlet in the southern Sound. Compared to the main basin, stability and phytoplankton biomass change little at this location, on either the long time scale of the seasons or the shorter scale of blooms. Production here begins up to two months earlier than in the main basin, apparently because shallow water limits the depth to which mixing can occur even in the absence of stratification. This mixing restrains photosynthesis later in the season, however, and annual production at this location is estimated to be 270 grams of carbon per square meter, less than 60 percent of that in the main basin.

Similar conditions can be inferred at other sill locations. Data from the area surrounding the San Juan Islands, for example, demonstrate vertical homogeneity in the waters that seesaw through the shallows between the Straits of Georgia and Juan de Fuca.

River Mouths and Fronts

River mouths are areas of short residence time and of strong stratification and weak mixing. This is particularly true where a large river enters a sheltered inlet in which mixing forces are reduced.

There are additional reasons why river mouths can be less productive. Many rivers entering the Sound—particularly the large pristine rivers, which carry mostly snow melt rather than lowland drainage—are quite low in nutrients, further diminishing the productive capacity

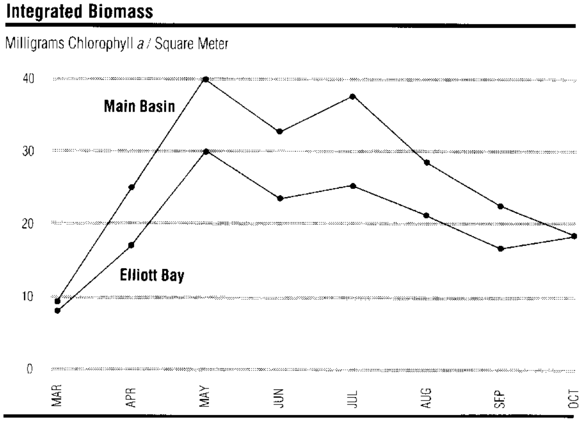


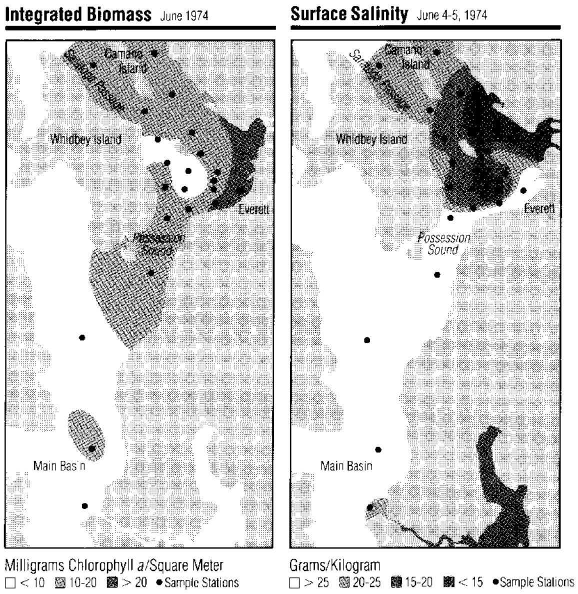
Figure 5.11 Average monthly phytoplankton biomass is consistently lower in Elliott Bay than in the main basin, despite high nutrient concentrations and strong stratification, due to turbidity and rapid flushing. (After Ebbesmeyer and Helseth, 1977)

of a stable runoff layer. Furthermore, these rivers can carry various sorts of turbid suspended matter (from natural glacial flour to urban waste), which absorb sunlight otherwise available to phytoplankton.

Elliott Bay, for example, is only about two-thirds as productive as the open main basin throughout the year (Figure 5.11). Despite its enrichment by nutrients in sewage effluent from a treatment plant in Renton, productivity at the mouth of the Duwamish River is inhibited by turbidity and by the low residence time of the outflow. During most of the year, the few kilometers of river upstream of the mouth have a low biomass of mostly freshwater phytoplankton. At the times of lowest runoff (and therefore longest residence time), usually in August, there can be intense blooms of marine diatoms as far as 10 kilometers upstream. Similar conclusions might be applied to Commencement Bay and the Puyallup estuary, which have received little study.

The same principles, plus some others, operate on a grander scale in the Whidbey basin. Saratoga Passage, between Whidbey and Camano Islands, receives the prodigious runoff from the Skagit River, which is glacial, turbid, and nutrient-poor. Substantial additional runoff from the Snohomish River enters Port Gardner near the basin mouth. The basin waters are strongly stratified, rapidly flushed, and poorly productive. The stratification is reinforced by the shelter of the island and by the lack of a shallow sill at the basin mouth. Tidal currents, furthermore, are weakened by a hairpin turn through narrow Possession Sound at the basin entrance, and by subsequent dissipation in its broader upper reaches.

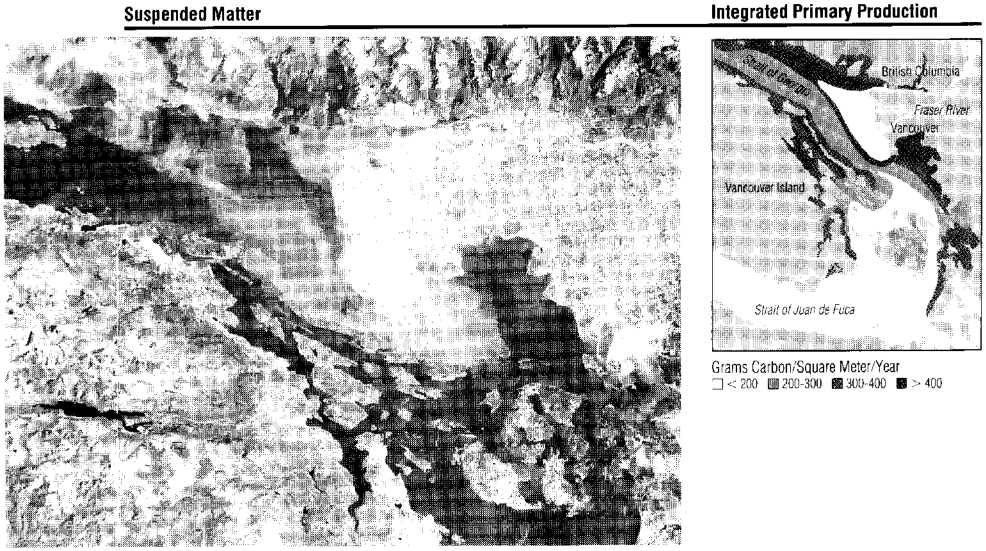
Certain unique features combine, however, to make Possession Sound itself a very productive spot. Here, the spring outflow from the Whidbey basin tends to collide with that from the main basin. Reinforced by tidal intrusions and by southerly winds, this collision between waters produces a definite boundary zone or stripe called a hydrographic front, something like a weather front in the atmosphere. Phytoplankton standing stock along this front is consistently higher than that of either the main or Whidbey basins (Figure 5.12), due in part



Integrated Biomass June 1974

Surface Salinity June 4-5, 1974

Figure 5.12 Phytoplankton abundance along a river-mouth front. Chlorophyll *a* concentrations are consistently higher in Possession Sound than in the Whidbey basin or the main basin. The highest chlorophyll concentrations in this snapshot (data from June 4–5, 1974) are found along the edge of the Snohomish River plume, where the surface salinity gradient is extremely sharp (river salinity is near zero; normal surface salinity in the main basin is 25 to 29 parts per thousand) (After English, 1979, and unpublished data).



Suspended Matter

Integrated Primary Production

Figure 5.13 Mean annual primary productivity in the Fraser River plume (right) is highest along the freshwater-saltwater boundary. Within the plume, salinity and nutrients are low and turbidity is high, while beyond it stratification is weak. Fraser River runoff is three to five times greater than all Puget Sound rivers combined, peaking in June due to snowmelt. High productivity also occurs in shallow, protected, nearshore waters. (After Stockner et al., 1979)

LANDSAT photo (left) taken during ebb tide, July 20, 1974, of the 600–700 nanometer wavelength band revealing suspended matter and chlorophyll. Plumes of suspended sediment are visible off the Fraser, Nooksack, and Skagit rivers. Also visible are tidal fronts or "stripes."

to the longer residence time where the two opposing flows are stalemated. It also results from the overlapping of stable and nutrient-rich waters, each contributing half of what is needed for a bloom. Such a front may also foster the blooms in the Duwamish River. Such fronts are probably better-defined and more persistent than the smaller-scale stripes in the main basin.

An even larger and more pronounced front has been studied in the Strait of Georgia, surrounding the mouth of the Fraser River. The runoff from the Fraser exceeds that from all of Puget Sound, and spreads far across the open strait. The surface front where it contacts the surrounding seawater forms a large green ring (Figure 5.13), which oscillates with the tides and the wind.

Until enough measurements were made to reveal its existence, the green ring confused early research on waters of both the Strait of Georgia and the San Juan Islands. Phytoplankton standing stock changed radically at some locations within the few hours of a tidal change. Under a sustained northerly wind the ring could be blown amidst the islands, producing an apparent sudden bloom.

The interior of the green ring is believed to be turbid, nutrient-poor and unproductive, although some researchers suggest that it recently has been fertilized by sewage from the city of Vancouver (see Chapter Seven). That this conclusion has been disputed by other researchers highlights again the problem of drawing conclusions from limited sampling of a highly patchy environment: with the movements of the ring, only an extensive survey can place single measurements in their proper context.

Although recognized for years, such fronts have begun to receive more careful attention with the advent of rapid survey techniques. Research off England and elsewhere indicates that fronts may be highly favorable sites for the growth of dinoflagellates. Such knowledge may prove important in understanding species compositon and patchiness in Puget Sound, and may even provide clues to the outbreaks of red tides.

The Strait of Juan de Fuca also exhibits a boundary between different water masses. Estuarine water from the Sound and the Strait of Georgia flows seaward at its surface and raw deep Pacific water flows landward along its bottom, both oscillating with the tides. In addition, surface water from the Pacific can intrude into the Strait of Juan de Fuca as far east as Port Angeles, forming a front where it contacts inland surface water (Figure 5.13). These intrusions seem to be caused by the wind—not just by westerly winds in the Strait itself, but by larger-scale wind patterns over the ocean, causing currents which drive ocean water eastward into the Strait. Intrusions have been documented both by measurements of surface currents, and by the capture of species of

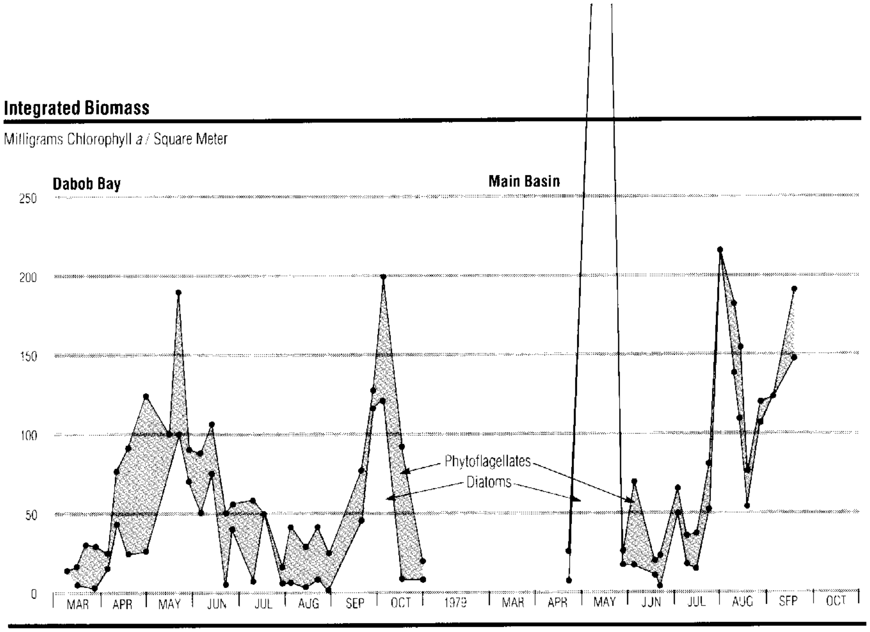


Figure 5.14 Biomass of phytoplankton smaller than five micrometers (mostly phytoflagellates) and larger phytoplankton (mostly diatoms) in Dabob Bay and the main basin in 1979. Dabob Bay began to bloom at least six weeks before the main basin, but was less productive after May, and did not bloom again until nearly October when stratification lessened. The standing stock of phytoflagellates is consistently higher in Dabob Bay, reflecting weaker mixing. (After Runge, 1981)

plankton found almost exclusively in Pacific waters. Thus the biological character of the Strait is that of a buffer zone: at its western end it is mostly oceanic, and at its eastern end it is mostly estuarine.

Deep Inlets

Three large, deep inlets in Puget Sound—Case and Carr Inlets in the southern Sound, and Dabob Bay off Hood Canal—all face south. Like the Whidbey basin, therefore, they are cul-de-sacs for surface outflow; they have weak estuarine and tidal currents, and they retain water on a southerly wind and are flushed by a northerly wind. Unlike the Whidbey basin, however, they receive little river runoff.

Such inlets thus have long residence times, and despite weak stratification are poorly mixed. While all have shallow areas at their mouths, the water motions and resultant mixing are much weaker than those of the main basin. Water is blocked from moving through the inlet—as parcels do in the main basin—by the dead-end nature of the circulation. The resulting biological pattern is one of high potential both for blooms and for subsequent surface nutrient depletion.

Such inlets tend to be productive early in the season because of their weak mixing. Later in the summer, however, and for the year as a whole, they tend to be quite unproductive due to nutrient exhaustion (Figure 5.14). In such instances, phytoplankton may be unable to grow in the upper ten meters, and the community is likely to be dominated

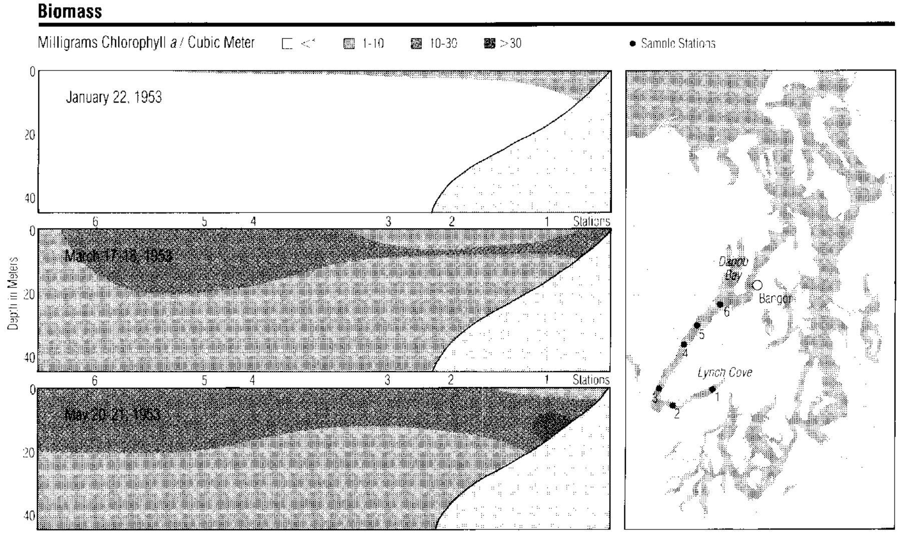


Figure 5.15 The 1953 spring bloom in Hood Canal began near the surface in the shallow waters of Lynch Cove, where vertical mixing is restricted. The bloom spread deeper and farther from shore as runoff and solar warming stratified the surface waters. As the season progressed, persistent stratification in the shallow waters caused nutrient depletion near the surface. (After Barlow, 1958)

by flagellates. The annual primary production of Dabob Bay, for instance, is only 340 grams of carbon per square meter. Unlike sill areas of comparable annual production, growth in these areas is highly intermittent; blooms are even more pronounced than those in the main basin. The weak mixing in these inlets permits a bloom to erupt during a sunny spell at any time of year, or during summer when a northerly wind flushes the stagnant surface water and leaves nutrient-rich deeper water in its place. Thus averages are even less representative of instants of time in these inlets than they are in the main basin.

Shallow Inlets

Scattered about the perimeter of the Sound are several other smaller shallow inlets: Henderson, Budd, Eld, Totten and Hammersley in the southern Sound, Lynch Cove at the head of Hood Canal, Quartermaster Harbor on Vashon Island, Sinclair and Dyes Inlets and Liberty Bay off Port Orchard, Sequim and Discovery Bays off the Strait of Juan de Fuca, and East Sound in the San Juan Islands. Most of these waters have received little study. They appear to be poorly flushed because of the baffling effect of all the passages through which water must travel to reach them, and therefore have a long residence time. Although the tidal ranges at the heads of these inlets can be larger than those elsewhere in the Sound, nevertheless the volume of water and the current speeds that accompany them are generally lower.

As observed over the sill in the southern Sound, shallow spots where the extent of vertical mixing is limited will begin to bloom early in the spring. With increased sunlight and stabilization, increased productivity spreads progressively farther from shore, as observed in Hood Canal (Figure 5.15). The open stretch of the Canal somewhat resembles the main basin in its size and orientation, but it has been studied little and is probably less productive annually because it receives half the amount of runoff of the main basin and is not enriched by an upstream sill.

Evidence suggests that many such inlets in addition to having a long residence time are also poorly mixed like their deeper neighbors. Similar results have been observed in inlets off the Strait of Georgia, including Vancouver Harbor. The most reliable indicator of late-season stratification and nutrient depletion in these areas is the appearance of harmful dinoflagellates (see Chapter Eight). Sometimes dense enough to form red tides, these dinoflagellates seem to be associated only with highly stratified waters and are scarce over sills. Additional studies have found low nutrient concentrations at the surface and low oxygen concentrations near the bottom, both signs of weak mixing and flushing.

East Sound, a shallow bay enclosed by the two arms of Orcas Island, may be an exception to the rule of low annual productivity in inlets. Blooms have been observed here in March, whereas beyond its mouth in San Juan Channel productivity was suppressed and standing stocks ten times lower until May. Productivity here may be sustained through the summer by the tidal intrusion of well-mixed water from the Channel.

Substantial gaps exist in our knowledge of phytoplankton on the Sound. Many areas have not been studied, there is little continuity in the time sequence of studies, and scales of patchiness are still poorly understood. The largest gap, however, is in the knowledge of how phytoplankton and zooplankton interact. Clearly each must have a large and vital impact on the other, yet in all the data on phytoplankton abundance there is almost no evidence of the presence of zooplankton. Apparently such effects are camouflaged by physical forces, by patchiness, and by the limitations of field research. The state of our knowledge improves only slightly when examining the influence of plants on the food chain.

Food Versus Size of Pelagic Animals

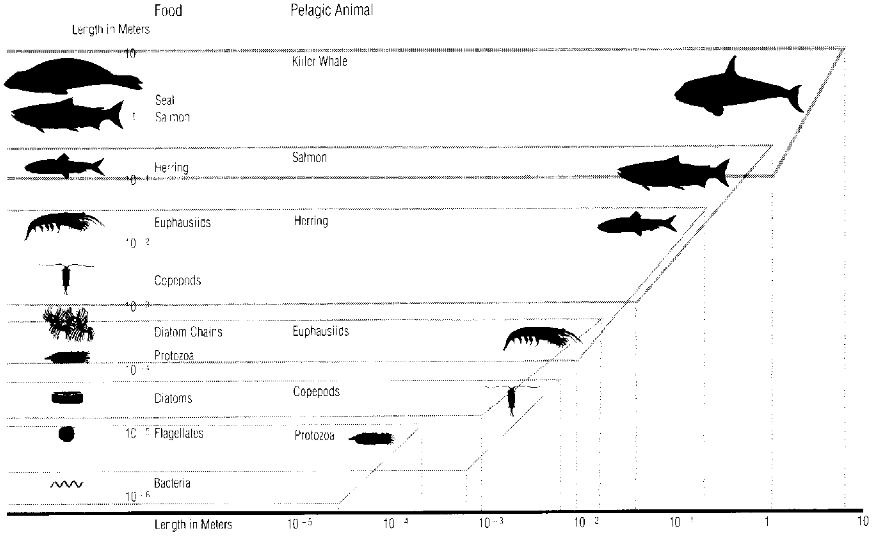


Figure 6.1 Size ranges of pelagic animals from immaturity to adulthood, and of their prey. Sizes are expressed in powers of ten on a logarithmic length scale. Length is a good measure of size in this example because predator-prey relationships often depend on length-related physical properties, such as jaw size or swimming speed. (After Dexter et al., 1981)

Metabolism Versus Size of Pelagic Organisms

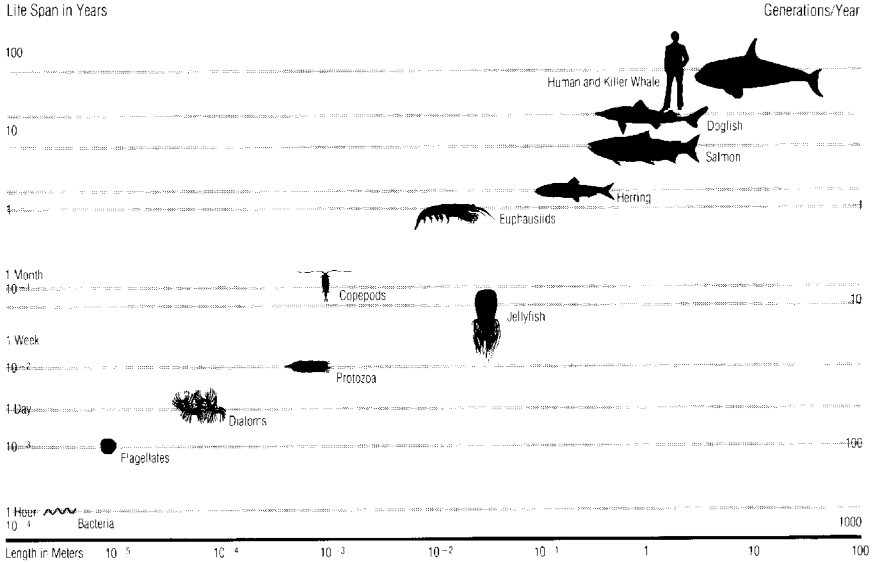


Figure 6.2 Lengths of adult pelagic organisms compared to their approximate life spans and reproductive rates, which are physiologically linked to other metabolic factors such as food intake. Metabolism is actually specified less by length than by biomass of an organism. Jellyfish are atypical in having large size but low biomass. (After Dexter et al., 1981)