

## Red Tides

About, about, in reel and rout  
The death fires danced at night  
The water, like a witch's oils,  
Burnt green and blue and white.

Samuel Taylor Coleridge, *The Rime of the Ancient Mariner*

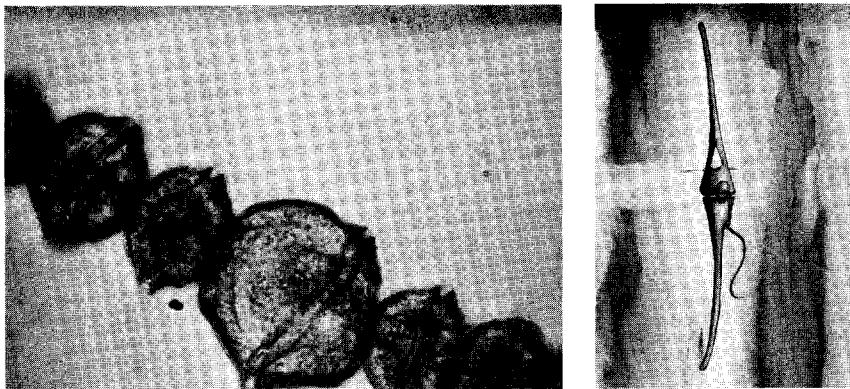
Perhaps the manifestations of plankton best known to Puget Sound residents are phenomena called “colored water”—red, brown, and luminescent—collectively known as “red tide.” Red tides occur anytime from spring through fall, though they are most common during late summer. They form impressive displays in bays, along shorelines, and in boat wakes. Most red tides are caused by one of several genera of pigmented dinoflagellates, and most are nontoxic. *Gonyaulax*, *Gymnodinium*, *Ceratium*, and *Prorocentrum* appear to be toxic; but *Peridinium*, the animal *Noctiluca*, and the unique symbiotic protozoan *Mesodinium* are nontoxic. Many of these organisms are also bioluminescent, as are some crustaceans, ctenophores, medusae, larvaceans, annelid worms, and fishes.

Any of these organisms can form a “bloom” dense enough to discolor water at the surface, particularly when acted on by physical concentrating forces. They are often seen in windrows or discrete patches, where they accumulate like flotsam. *Gymnodinium* colors the water a deep pink or chocolate brown, *Noctiluca* a tomato-soup red, and *Mesodinium* brick red to purple. The colors come from accessory pigments to the ever present chlorophyll, which are related to the pigments we see unmasked in autumn leaves.

However pleasing to the eye, these incidences can sometimes have sinister effects, resulting in morbidity and mortality of both marine animals and humans. The two most prominent effects are paralytic shellfish poisoning and oyster larvae mortality.

### Paralytic Shellfish Poisoning (PSP)

In June 1793, Captain George Vancouver and his crew were reconnoitering the area around the central coast of British Columbia when one party of four men pried some mussels from the rocks of a small cove for their breakfast, as they had done on many previous mornings. On this unfortunate day, however, all four of the men, within a few minutes after breakfasting, were beset by a numbness of the lips and fingertips. This was followed by paralysis of the arms and legs, a feeling of dizziness, and nausea. For one man, John Carter, it meant death. The



**Figure 8.1** *Gonyaulax (Protogonyaulax) catenella* (above left), the chain-forming dinoflagellate responsible for paralytic shellfish poisoning in Puget Sound. The enlarged cell (center) has been infected by the parasitic dinoflagellate *Amoeobophrya ceratii*, and will soon burst and die. Actual size approximately 30 micrometers per cell. (Photo courtesy Louisa Nishitani). *Ceratium fusus* (above right), a spiny dinoflagellate linked to oyster larvae mortality in the southern Sound. Actual length approximately 100 micrometers. (After Cardwell et al., 1977)

other three men, acting on the advice of a fellow crewman who had experienced a similar malady in England, exercised vigorously and, coincidentally, survived. They named the location Poison Cove. This was the first recorded incidence of paralytic shellfish poisoning (PSP) on the Pacific coast of North America.

Paralytic shellfish poisoning is found on coasts throughout the world, including Northern Europe, Southern Africa, Japan, and both coasts of North America. God is alleged to have slain Egyptians by this means on Moses' behalf: "All the water changed into blood. The fish died and the river stank" (Exodus 7:20-21). It was not until an outbreak of shellfish poisoning in California in 1927 killed several persons and sickened over one hundred more that the poison was connected to red tides. One scientist, thinking that it might have come from the food of the offending mussels, managed to isolate a species of phytoplankton that produced a toxin matching that in the shellfish. This was the first instance in which plankton was found to be an enemy, albeit an unwitting one, of humans.

Although there have been repeated outbreaks in the Puget Sound area, notably with several deaths in 1942 and 1957 in Canada and Washington, it was not until an outbreak in the northern Strait of Georgia in 1965 that the local planktonic culprit was first identified. It is now thought to be *Gonyaulax* (or *Protogonyaulax*) *catenella*, an armored dinoflagellate that ranges from 15 to 55 microns in diameter, and which unlike most dinoflagellates occurs in chains of from two to eight cells (Figure 8.1). It has been grown in culture and its life habits studied. *G. catenella* is ten times more toxic in Washington than in Califor-

nia, but only a tenth as toxic as a sibling species (variously called *G. tamarensis* or *G. excavata*) that has been responsible for poisoning and death from Long Island Sound to Nova Scotia.

Although sparse *G. catenella* populations had been detected before, the first PSP related health problems in the inner waters of Puget Sound appeared in September of 1978, during warm "Indian Summer" weather following heavy rains in August and September. They occurred on Saratoga Passage along the eastern shore of Whidbey Island, and gained public notice when nine people became sick, four of them seriously enough to be hospitalized. PSP spread southward as far as Vashon Island over the course of three weeks, necessitating closure of beaches to shellfish gathering. Toxin levels of 30,000 micrograms per 100 grams of tissue (80 is sufficient to close a beach) were found in shellfish meat. The PSP did not reach south of The Narrows, nor into Hood Canal, and by the end of the month some beaches were reopened in Puget Sound. Beaches on Whidbey Island and the San Juans never reopened, however, and additional closures began again the following April. By July 1979, all beaches north of Tacoma were again closed. (A fatality occurred in the northern Strait of Georgia in May 1980.) It is still a mystery why PSP-related illnesses were never reported from within Puget Sound proper until 1978.

Of all the animals in Puget Sound that feed on phytoplankton, primarily only bivalves acquire PSP and are eaten by humans: the mussels *Mytilus edulis* and *M. californianus*, the oysters *Crassostrea* and *Ostrea*; the butter clam *Saxidomus*, the soft-shell clam *Mya*, the Manila clam *Venerupis*, the littleneck clam *Protothaca*, the cockle *Cardium*, and some others. All of these bivalves obtain their food by pumping water into their shells and over their gills, where plant cells are trapped and directed toward the mouth. The mussels and oysters, which live on rocks and atop the sediment, simply open their shells to obtain water. The clams, living below the sediment, have siphons that extend into the overlying water. All of these bivalves live in the intertidal zone near the water's surface, where phytoplankton is most abundant. Mussels can become poisonous within a few days of an outbreak of *Gonyaulax*, making them an excellent organism for monitoring the onset of toxicity. Mussels also rid themselves of toxin soon after a bloom. In contrast, the butter clam, which concentrates the toxin in its siphon, can retain it there for as long as two years after the initial outbreak.

The effects of PSP are of course worst when eaten on an empty stomach. There is no antidote; treatment is to induce vomiting as soon as possible, and to administer a fast-acting laxative to minimize the absorption of the toxins. In the most serious cases, death occurs by respiratory paralysis within 2 to 12 hours. The principal (but not only) toxin

**Table 8.1** Minimum lethal dose to humans (micrograms of toxin per kilogram of body weight) for selected natural poisons. The 600-microgram dose of saxitoxin needed to kill a 68-kilogram (150-pound) person can be obtained from a single clam.

Toxin	Dose
Botulinus	0.00003
Tetanus	0.001
Diphtheria	0.3
Cobra Venom	0.3
*Saxitoxin	9.0
Curare	500
Strychnine	500
Muscarin, from <i>Amanita</i> mushroom	1100
Sodium Cyanide	10,000

produced by *Gonyaulax*, saxitoxin, has been isolated and synthesized artificially. Saxitoxin is an alkaloid nerve poison (neurotoxin) that acts by blocking transmission of impulses from nerve to muscle, and is one of the more potent natural poisons (Table 8.1). Pure samples of it are kept on hand by the Army at Fort Dietrich, Maryland, in case the Russians land looking for clams.

There is no truth to beliefs that garlic will neutralize PSP toxins, or that they can be detected by the discoloration of silver in cooking water. High-temperature frying can reduce the toxicity slightly, and a portion of it can also be discarded with steaming liquor. Nevertheless, enough toxicity can remain to sicken or kill humans. A dangerous old-wive's tale claimed that shellfish were safe to eat in the months of the year which contained the letter "R"—that is, that they were unsafe from May through August. Blooms of *Gonyaulax* can occur from April to November, however, and shellfish can be toxic all year. The only assurance of safety is the method used by the Health Department for assaying the toxins in shellfish tissues. A standardized amount of meat is ground up and injected into a white mouse. If nothing happens, the stuff is safe to eat. If the mouse suddenly stiffens, begins wildly leaping about its quarters, gasps for breath and dies, so might you. The length of time it takes for the mouse to die is a measure of the strength of the toxins.

PSP toxins do not seem to harm most shellfish in which they are concentrated, despite their toxicity to humans and other, mostly warm-blooded animals. Cats in particular are extremely vulnerable. The reasons for these sensitivity differences are still not well understood, but the toxins are apparently harmless unless acted upon by acid, as occurs during digestion by humans but seemingly not by shellfish. When acid-hydrolyzed saxitoxin is injected into many fish and shellfish, they show clear signs of poisoning; but conversely, some shellfish have an apparent ability to break down the toxin. On the Atlantic Coast, large kills of herring have been blamed on their ingestion of zooplankton which had eaten *Gonyaulax*, and further kills have been traced to other red tide organisms. PSP toxins are found in some other animals, but the place of *Gonyaulax* in the food web has not yet been determined.

Several competing theories still have not fully explained the appearances of PSP. *Gonyaulax* seems to like quite warm water, around 14°C (a typical surface temperature in the main basin in summer), and

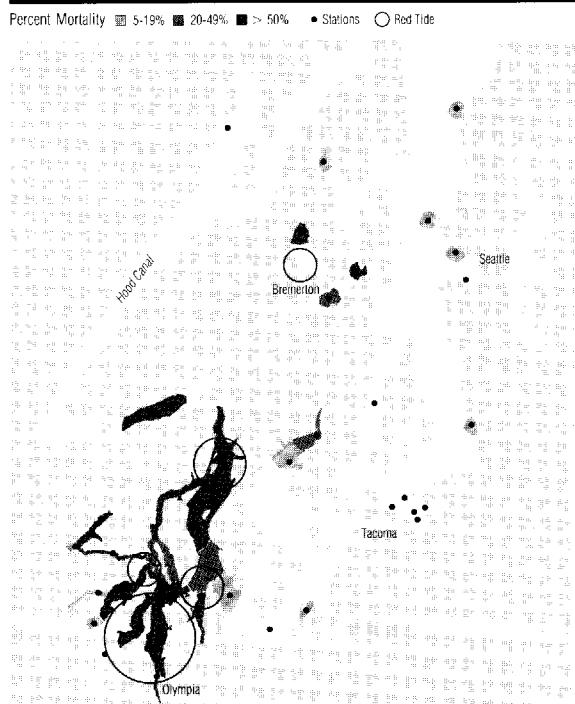
can grow well at any salinity encountered in Puget Sound. *Gonyaulax* seems to appear most frequently in protected inlets during later summer spells of prolonged warm clear weather, when nutrients are depleted from a stratified surface. Its summer abundance is inverse to that of diatoms. Before invading Puget Sound, it was historically most common in Sequim Bay (on the southern shore of the Strait of Juan de Fuca), which is almost completely isolated from the Strait by a narrow mouth and a sandspit, and receives little freshwater runoff. Its abundance there has been correlated with both the intensity of sunshine and the duration of spells of clear weather. Mixing is quite slow here during the summer, and experiments in New England demonstrated that just stirring a flask of different species of *Gonyaulax* (*G. excavata*) stopped its growth.

*Gonyaulax* also appears during periods in which rainfall (particularly a large amount of rainfall without heavy winds to cause mixing) is followed by prolonged clear weather. This may produce necessary stratification. Laboratory cultures of *Gonyaulax* can be stimulated by extracts of terrestrial soil, however; an essential nutrient may thus be provided by the runoff from rainfall, or the organic chemicals in soil may chelate toxic trace metals. More speculative yet is the hypothesis that in some parts of the world PSP may be getting worse due to the chelating effect of sewage dumped into the sea.

The appearances of PSP, like those of phytoplankton in general, are determined in part by localized circulation patterns in coastal and estuarine areas. Although the results have not yet been applied to Puget Sound, examples from England, Florida, and Maine show that dinoflagellates (including *Gonyaulax*) accumulate where highly stratified waters meet mixed waters. Invisible blooms can occur below the surface in stratified, nutrient depleted areas, and blooms also can be highly patchy. This historically has been a problem in observing shellfish toxicity on the long, sparsely populated shoreline of British Columbia where a toxic bloom could appear, last a few days, and depart before scientists could even know it existed—much less study it—and where shellfish taken only a mile apart could vary twentyfold in toxicity.

Finding PSP outbreaks in time to warn the public is complicated by two more problems. Shellfish can acquire toxicity even when *Gonyaulax* is too dilute to color the water. Furthermore, *Gonyaulax*, like other neritic phytoplankters, forms resting cysts under certain conditions, which are yet to be determined. These cysts can be more toxic than the swimming cells, and can contaminate shellfish throughout the year. Once cysts are dropped to the bottom of a body of water, there apparently is no way to eliminate them, although they eventually will die if they do not germinate. The cysts may be spread to uncontaminated areas by dredging and by transportation of shellfish that contain

### Extent of Oyster Larvae Mortality 1977



**Figure 8.2** Oyster larvae mortalities in the central and southern Sound, as determined by surface water bioassays during 1977. Visible red tides are noted.  
(After Cardwell et al., 1979)

them. Low levels of PSP that appeared in the southern Sound in 1981 may have originated in this manner.

A couple of promising developments make the story of *Gonyaulax* not an entirely negative one, however. Saxitoxin shows some promise as an insecticide. Research at the University of Washington has also uncovered a dinoflagellate, *Amoebophyra ceratii*, that can parasitize several other dinoflagellates—including *Gonyaulax*—in the wild, and may in fact exert some control on outbreaks of PSP. This discovery suggests the possibility that *Gonyaulax catenella* might be controlled in confined bays by growing *Amoebophyra* on a nontoxic host such as *Peridinium* in the laboratory, and releasing it in those bays.

## Other Toxic Red Tides

Although southern Puget Sound may (so far) have fewer problems with paralytic shellfish poisoning than the northern Sound, recent research has disclosed a red tide-related problem of a different sort. Very high levels of oyster larvae mortality—over 50 percent of the larvae tested in bioassays—have frequently been observed in shallow inlets of the southern, central, and northern Sound, and Hood Canal (Figure 8.2). In some cases these have been correlated with pulp mill effluent (e.g., Port Gardner, Bellingham Bay), but in the southern Sound some peculiar traits emerge. Well-mixed areas, even those very close to areas

of high mortality, are free of the problem. The toxicity is often most severe at a depth of roughly three meters. Larvae are not sickened by small amounts of the harmful water (as they might be if a chemical pollutant were responsible), but rather are either totally unaffected or are killed.

Oyster larvae mortality correlates best, it turns out, with abundances of the dinoflagellates *Ceratium fusus* (Figure 8.1) and *Gymnodinium splendens*, and sometimes *Prorocentrum gracile*. They seem not to be poisonous, as *Gonyaulax* is; the water by itself is nontoxic, either without cells or with ground-up cells. Instead, *Ceratium* at least may impale the larvae on its long spines.

Similar effects are observed when larvae are exposed to sharp-edged particles from dredge spoils. A kill at a commercial oyster hatchery on Liberty Bay in 1975, first thought to have been caused by mercury from a nearby Navy installation, was later attributed to a red tide. Larval bioassay results also correspond closely with observed mortality of adult oysters in the southern Sound. *Ceratium* blooms were observed years ago in such places as Hood Canal and San Juan channel, before they were linked to mortalities.

Toxins have recently been isolated from related phytoplankton species, including *Gymnodinium breve*, which causes fish kills in Florida, and *Prorocentrum minimum* from the Strait of Georgia. There also appears to be a link between the phytoplankton *Olisthodiscus luteus* and fish mortality in northern Puget Sound and elsewhere, seemingly due to bacterial stimulation by carbon excreted from the alga. The dinoflagellate *Gyrodinium* has been linked to kills of shoreline fish, snails, and limpets in Ireland, and large kills of shellfish have been caused off New York City by oxygen depletion from decay of red tide blooms of another species of *Ceratium* (*C. tripos*).

Are all these harmful red tides really increasing in frequency and severity, as seems to be the case, and if so, why? That question cannot yet be positively answered. The increases in red tides recorded within the last few decades do appear to be real, but they may stem from increased surveillance and reporting, due to higher population density and better scientific knowledge. There may be long-term fluctuations in red tide incidence related to natural causes such as climatic cycles, of which we are seeing only a small segment. The possible link between human activities and red tides is still a speculative one. Every theory of the effect of pollution on red tides has its counter-theory, and as yet none has been reliably confirmed. Certainly toxic red tides have occurred and still cause problems where they could not have been aggravated by civilization nor scrutinized by science. At worst, humans have perhaps only exacerbated an entirely normal process of nature.

## CHAPTER NINE

# Marine Pastures

There, said he, pointing to the sea, is a green pasture where our children's grandchildren will go for bread.

Obed Macy, *A History of Nantucket*

Perhaps the most persistent belief about life in the sea is that one day food from the sea will eliminate world hunger. This myth has been perpetuated by people with more idealism than knowledge, for the realization of this worthy and far-sighted goal is at best years or decades away. There are substantial obstacles to developing the ocean's food supply—obstacles for which there would seem to be no easy solutions.

The first problem is in finding any more food to harvest. Certain of the world's fish stocks appear already to be badly overfished, and the area within which to pursue new fisheries is limited to the more productive coastal and polar regions. Although global phytoplankton production exceeds the global harvest of cultivated crops by a factor of five, most of the world's plankton production takes place in the open seas, where it is so widely dispersed that it is impractical either to harvest it directly, or even to harvest the fishes it supports. The higher rates of plankton and fish productivity, the technology of harvesting, and even issues of international law all favor a concentration of effort in the areas already exploited.

The strong stratification responsible for this low productivity in mid-ocean also restricts the potential for artificially enhancing the productivity of the sea at large. Some means would be needed to stir the ocean to depths of as much as 100 meters over a wide area, in order to bring up enough nutrients to start the food chain going, and even then it is not clear what sorts of organisms would grow. Perhaps the energy for this pumping can someday be derived from projects on the drawing boards today, such as Ocean Thermal Energy Conversion (a sort of floating reverse heat pump, which would generate electricity by pumping deep water to the surface), or from wave or tide power. Clearly, global cultivation of the ocean would require forces not yet even imagined.

The barren condition of the open ocean makes coastal areas such as Puget Sound very important to the future harvest of the sea. Here, many technical difficulties are reduced—the area is easily accessible, well-mixed, and already quite productive. Schemes for extracting more seafood from coastal areas fall into the same categories as food-providing schemes on land: hunting, ranching, and farming. All have applications to the role of plankton in the harvest of food from Puget Sound.

## Hunting

Marine hunters, the commercial and sport fishermen, harvest seafood without participating in its rearing. At the present time, increasing the hunting effort is the quickest and cheapest method of increasing the yield from the sea. New fishing equipment is more efficient at catching those fishes and shellfish that are already being harvested, and with the advent of the 200-mile offshore fishing limit there are new possibilities for exploiting previously underutilized species.

The ceiling on natural fish catch is imposed ultimately by the production of plankton. The types of plankton that grow also determine (and are determined by) the species of fish, shellfish, and other animals that grow. Coastal waters are believed to be most productive because they are well-mixed and because they have large plankters and short food chains with a minimum of trophic inefficiency. When harvesting fish populations, both the natural limits on production and the complex interactions that account for production must be considered.

Peru is a classic example of how attempts to hunt more food from the sea can go awry. Coastal upwelling enriches the coast of Peru and supports a vigorous growth of large diatoms, fed upon by anchovies—a highly-efficient, two-link food chain. At one time, one in every five pounds of fish caught in the world was caught off Peru. But in the waters off South America, as in Puget Sound, biological productivity is intimately tied to the physics of the ocean, and to the weather. Periodically, upwelling ceases, nutrients become scarce, and the planktonic food supply for the anchovies is cut drastically, apparently because of large-scale weather patterns over the South Pacific. The large diatoms are frequently replaced by flagellates, or even by red tides.

Such an event is called an *El Niño* (Spanish for “The Christ Child,” since it appears most frequently around Christmas), and has apparently always been a normal feature of the region’s oceanography. The anchovies dependent on the diatom production simply die back during an *El Niño*, then rebuild themselves when favorable conditions return. In the early 1970s, however, unregulated numbers of fishermen were already taking almost as much fish tonnage as the system would sustain (or perhaps more), when a sequence of *El Niños* decimated the stock. Desperate fishermen worked all the harder to catch what they could. The unfortunate result was that the anchovy population dropped to a level from which it may never recover.

A similar fate may also be overtaking North Pacific and Puget Sound fisheries. The potential harvest of the sea is limited both by the area of the sea from which we can expect to harvest fish, and by a ceiling on the harvestable fish within that area. Both of these limits are set by the plankton and by the meteorological and physical processes that govern plankton production.

One proposed escape from catch limitations is to harvest organisms lower on the food chain; that is, to harvest plankton directly. Although the idea is not totally new—jellyfishes are a traditional food in Asia—its magnitude is new. Already, the richest crop of plankton in the world, the large herbivorous antarctic krill, *Euphausia superba*, is the subject of trial harvests by the Russians and Japanese, and many more countries are contemplating joining them. Antarctic krill grows rapidly and has a standing crop of 40 to 1,000 million metric tons (44 to 1,100 million long tons), compared to the annual world fish harvest of about 60 metric million tons (66 million long tons). Krill has the flavor and nutritional value of its larger cousin, the shrimp, although it is said to resemble cooked maggots in appearance. Antarctic waters are currently unregulated and are open to international exploitation. Additionally, because of the overharvesting of one of the krill's principal predators, the blue whale, there may be an uneaten "surplus" of many millions of tons of krill.

There has been speculation about harvesting copepods, although these smaller crustaceans are more difficult to collect and contain a higher proportion of indigestible chitin exoskeleton. Zooplankton could be used both for animal and human food, as either a dish unto itself or ground into meal as a protein supplement.

There are problems with this potential harvest, however. It is not clear, first of all, that a surplus of antarctic krill really exists, and it is difficult to determine what effect removal of large quantities of krill could have on the remaining whale populations, or on seals and birds. Some preliminary euphausiid harvests have been conducted in the Strait of Georgia for a number of years, but an extensive zooplankton fishery in Puget Sound and the North Pacific would almost certainly conflict with the fishery supported by a major zooplankton predator—the popular, tasty, high-priced Pacific salmon.

The main obstacles to the exploitation of plankton as a food source are technical and economical. Put simply, the question is whether enough plankton can be caught, using state-of-the-art plankton nets, to pay for the effort of pursuing it. Although seafoods in general require less energy than terrestrial foods to bring to market, the plankton resource is so dilute, and the organisms so tiny, that it seems more economical in most cases to allow specialized animals to harvest for us and to accept the loss of efficiency in the food chain than to try to beat nekton at its own game. Imagine, for comparison, humans gathering nectar to make honey, instead of allowing bees to do it for them. The prospects for harvesting zooplankton are supported only because it is found in dense swarms—patches—detectable with echo sounders. Ultimately, the feasibility of zooplankton fisheries will depend on the price it will bring at the grocery store.

One of the most successful and biologically efficient methods of obtaining a harvest from the plankton has been to gather naturally occurring planktivorous shellfish, such as clams, oysters, and mussels. These animals are efficient and powerful at extracting plankton and suspended matter from moving water, and have few predators that compete with humans. Potential shellfish harvest in the wild is even more limited than that of finfishes, however, since the area of suitably productive shallow water habitat is less than the area of open coastal waters. Furthermore, natural growth of some shellfish species is hampered by sporadic failures in larval production and high mortality due to cold water, predators, and pollution. New mechanical shellfish harvesting technologies, such as water jets, conveyor belts, and suction dredges, promise increased supplies and reduced costs for this mode of marine hunting, but are running afoul of political and environmental complications. To increase the harvest of seafood, therefore, scientists and growers are turning to ranching and farming techniques.

## **Ranching**

Marine ranchers, like their terrestrial counterparts, breed their stock, rear them as young, then turn them loose to feed and mature on open rangeland before finally rounding them up for sale or slaughter. Puget Sound ranchers raise fish and shellfish in hatcheries, which reduce reproductive mortality by providing suitable spawning and rearing habitat. It is a form of ranching because the animals are released from human control and allowed to graze freely in their marine pastures, then are harvested upon their return, and because there is a degree of selective breeding.

Ranching techniques have achieved their greatest successes with bivalve molluscs. For years clam and oyster larvae have been reared under controlled laboratory conditions, using a phytoplankton diet, until they could be transplanted to a beach as spat. The rancher may thus breed the shellfish stocks selectively, feed the larvae an optimal food at an optimal temperature and salinity, add antibiotics and vitamins, and control the time and place at which the spat are introduced into the wild, selecting favorable environmental conditions and reducing competition for food and space. Washington growers once imported most of their spat for the Pacific oyster from Japan, since natural sets in Puget Sound are not sufficiently reliable or predictable for commercial operations. Local hatcheries now produce most of the spat planted in Puget Sound oyster beds, however. In addition, the Washington Department of Fisheries has recently begun raising razor clams (*Siliqua patula*) for planting on outer coast beaches, and experiments are underway elsewhere for the raising of Dungeness crab (*Cancer magister*), geoducks (*Panope generosa*), and abalone (*Haliotis* sp.).

Hatcheries have also been successful in maintaining the salmon harvest. In terms of yield per unit of area required and feed consumed, and therefore per dollar spent, such hatcheries are the best investment available for increasing the current yield of the sea. This method cannot increase the capacity of marine ecosystems for producing animals, but in places like the Pacific Northwest, where unexploited plankton food may be available because of declining of salmon stocks, and where many natural spawning grounds have been destroyed, hatcheries can help maintain viable fish populations. Still, the potential benefits of hatcheries are constrained by other limits on salmon populations, including overharvest and loss of genetic diversity. Hatchery rearing of salmon has been carried out in the Puget Sound area for decades, and expansion of salmon-rearing efforts remains one of the best hopes for maintaining the yield of protein from Northwest inland waters.

## Farming

Marine farming, more popularly known as aquaculture or mariculture, entails the husbandry of marine animals (and some plants) from birth to death. Aquaculture is amazingly undeveloped in the United States considering (or perhaps because of) our technological advancement. Americans obtain less than 10 percent of their protein from aquatic animals, eating only 5.5 kilograms (12 pounds) of fish per capita per year, compared to 32 kilograms (70 pounds) in Japan. American aquaculture production is minimal compared to that of the Orient and satisfies but a small portion of our seafood appetite. Research on marine farming falls into two categories: raising planktivorous animals on or in a confined structure within a natural body of water, and growing plankton and planktivores artificially in completely enclosed systems.

One form of mariculture emerging on Puget Sound is net-pen rearing of salmon and cutthroat trout. The fish are kept in large pens immersed in Puget Sound from the time they leave the hatchery as juveniles until they reach a marketable weight of about one pound, called "pan-size." The advantages of this approach are that animals are not lost to either migration or predation, and that they live in very nearly their natural environment, saving growers the trouble and expense of duplicating those conditions artificially. Similar experiments aimed at raising prawns have met with more difficulty, owing to a more complex life cycle.

The disadvantage of net-pen farming is that although natural zooplankton is available, fish populations are so dense that their diet must be augmented with costly feed. Fish cultivation in general is ecologically more efficient than red meat production, but supplementing salmon diets amounts simply to converting one expensive food into another, with a net loss of energy. Also, as in hatcheries, crowding and

genetic uniformity resulting from controlled breeding make fish more susceptible to oxygen depletion and disease. Finally, some forms of plankton can even be hazardous to the penned fish; dense phytoplankton blooms of spiny *Chaetoceros* and *Ceratium* have been known to puncture the sensitive gills of young fish and cause heavy mortality because the animals are not free to swim away from the algal masses as they would in the wild. Nevertheless, because of the attractive prices and demand for salmon, net-pen farming is achieving commercial success on Puget Sound.

Currently the most successful form of marine farming worldwide—second only to hatcheries in efficient use of energy and space, and second only to seaweeds in global tonnage of cultivated harvest—is the raising of bivalves using suspension culture. Oysters and mussels, in particular, are allowed to attach to ropes or are placed in cages as spat, then hung from posts, buoys, or rafts in waters that offer both suitable protection from storms and healthy flushing by currents, tides, and winds. Suspending bivalves off the bottom tremendously increases the volume of water from which these animals can filter their phytoplankton food by extending their habitat both vertically and offshore. Suspension culture maintains more animals in the productive surface layer and eliminates exposure during low tides. Shellfish in suspension culture reach market size twice as fast as those in bottom culture and produce a higher quality of meat since less bottom sediment is ingested.

One advantage of using shellfish as a means of extracting more plankton protein from the sea is that the shellfish are extremely efficient filterers and are able to capture very small plant prey such as flagellates. This is a simple, two-link food chain, with a minimum of the trophic inefficiency that accompanies longer food chains, and the crop is sessile and relatively easy to harvest. The yield of raft cultures of mussels approaches the phenomenal figure of 30,000 metric tons (33,000 long tons, fresh weight) of meat per square kilometer of raft area per year. That compares to yields of a few hundred to a few thousand metric tons for bottom culture of oysters; less than a hundred metric tons for coastal finfisheries such as those of Puget Sound, Georges Bank, and the North Sea; and at most 50 metric tons of beef or pork on a feedlot. These figures further demonstrate that the potential productivity of water is much higher than that of land—if the limitations of fluidity can be overcome—because marine bivalves do not have to expend as much energy as terrestrial animals in supporting themselves, moving about, or maintaining their body temperatures, and so can devote proportionally more energy to protein production.

Suspension culture of oysters is beginning in Washington State, and there is potential for mussel culture as well. Some problems still must be dealt with in raft culture: red tides, bacteria, viruses, and pollu-

tants can contaminate entire crops. Labor is expensive, and on Puget Sound there is an aesthetic consideration as well: it can be difficult to convince citizens to accept rafts, buoys, and posts along their expensive waterfronts and in their favorite boating spots.

The ultimate marine farm would not depend on natural plankton production. Artificial stimulation of phytoplankton production in a natural setting to enhance the yield of shellfish farming has been successful in ponds in Alaska and in the Virgin Islands. These experiments involved pumping deep, nutrient-rich water to the surface, in an enclosed area where enrichment effects would not be dissipated, and where raft or net-pen cultures could be maintained. Such a project might be useful in those Puget Sound embayments where surface stratification limits primary production, such as in Dabob Bay. First, however, the problems of conflicting shoreline uses, impact on the indigenous food chain, and pumping technology and costs would have to be solved.

The economic prospects of smaller scale, completely enclosed marine farms may be bright, especially when used to treat sewage and pulp effluent before it is discharged to the environment. Considerable research, in fact, has gone into the possibility of turning sewage into food via phytoplankton and shellfish in artificial ponds. There are problems with ingestion of sewage pollutants, bacteria, and viruses by the shellfish, and it remains to be demonstrated whether the products—clean water and food—will repay the cost of pumps, land, labor, and fuel, particularly in well-watered and productive regions like Puget Sound. Nevertheless, such self-contained ecosystems are ranked among the brightest of aquaculture prospects nationwide.

There may also be prospects for farming phytoplankton for direct human consumption. Natives in Africa have for hundreds of years eaten filamentous microalgae from Lake Chad. Formal research on cultivation of plankton as human food began in the 1950s, and at one point algal cultures were proposed as a food and oxygen source for space travelers. Research efforts today are leading to enclosed farming of such freshwater organisms as the cyanobacterium *Spirulina* and the green algae *Chlorella* and *Scenedesmus*, which are filtered, dried, and eaten as a food supplement in powdered form. These genera grow rapidly under harsh conditions, and can have a higher protein content and a higher per acre yield than such terrestrial crops as soybeans, but require bright sunlight and must also repay the additional costs of containers, pumps, and processing.

Algal cultures appear to be economical in arid climates where water itself is precious. They may be useful for sewage treatment in Israel, and for supplementing protein intake of both people and animals in underdeveloped countries, such as Peru, Thailand, and India. There

seems little prospect for their application to the Puget Sound region. Perhaps their presence here will remain limited to the newly-developing market for *Spirulina* as a health-food supplement. Popular in Japan, the alga is cultured in Mexico, and in 1981 sold in Seattle for \$30 per pound.

From all of this mixture of encouraging and discouraging news, what then is the consensus about the potential for plankton in increasing the harvest from Puget Sound and the rest of the world's oceans? The greatest potential for enhancing the harvest of food from Puget Sound seems to be in controlling the high reproductive mortality of already popular species of planktivorous animals, particularly salmon and shellfish. In addition, for the sedentary and highly efficient shellfish, there seems to be bright prospect in the creation of additional habitat for adult growth if political problems can be overcome. But these resources, even if developed to the fullest extent, will likely boost only slightly the supply of what will always be luxury foods. The great popular hope for feeding the world's starving masses remains, if not totally spurious, at least far beyond our present technological, economic, or political capabilities.

Civilization is altering its relationship with the sea and its organisms in the same way that it has changed the face of the land. We have domesticated wild animals from the dog to the chicken, and plants from the geranium to the Douglas fir. In so doing we have transformed the landscape from a wilderness into a patchwork of farms. Even more drastically, we have altered the course of evolution for entire species, intervening to perpetuate those breeds which were of value to us and neglecting or even exterminating others.

We stand today, perhaps, at the threshold of doing the same in the sea, this time with more scientific maturity and awareness of the possible consequences. Although it may seem impossible to ever change the face of the open ocean, human activities are already having an impact on coastal areas such as Puget Sound, and many difficult choices are ahead. Coastal areas can be maintained in their natural states, or developed for industry or food. Wild marine creatures can be allowed to exist in their natural habitats, or domesticated and made forever dependent on people. We may be trading in the ethic of the hunter for that of the farmer, and turning the marine wilderness into marine pastures.

# Glossary

**alga** (plural **algae**) Plant having simple internal organization without fluid-transporting structures; unicellular or multicellular

**anoxic** Containing little or no oxygen

**aphotic** The deeper pelagic zone where sunlight is insufficient for plant growth

**autotroph** Organism (usually a plant) that manufactures its own food from raw materials and energy (usually sunlight)

**bacterioplankton** Bacteria suspended in the sea, or attached to other suspended matter

**benthic** Associated with the sea bottom

**benthos** Benthic plants and animals

**binary fission** Reproduction of a cell by duplication of its parts and separation into identical daughter cells

**bioaccumulation** Retention of pollutants in organisms at concentrations higher than in ambient water

**bioassay** Estimation of pollutant concentration by toxic effects on a standard test organism

**biomagnification** Higher body content of pollutants in animals at higher trophic levels

**biomass** Standing stock of organisms as measured by their collective weight

**bloom** Rapid, enormous increase in phytoplankton standing stock during favorable environmental conditions

**B.O.D. (biological oxygen demand)** Consumption of dissolved oxygen in water after addition of chemicals or organic matter

**calorie** Amount of energy required to heat one gram of pure water one degree Celsius

**carnivore** Animal that eats only other animals

**Celsius (or Centigrade)** Temperature scale having 0° at freezing point and 100° at boiling point of pure water

**centimeter** One-hundredth of a meter; 0.4 inches (**square centimeter** equals 0.16 square inch, **cubic centimeter** equals 0.06 cubic inch)

**CEPEX (Controlled Ecosystem Pollution Experiment)** Plankton growth experiment series performed in large cylindrical plastic bags deployed in Saanich Inlet, Vancouver Island, during the mid-1970s

**chelation** Binding of metallic ions to a complex organic molecule, affecting their solubility and activity in seawater

**chelator** Organic molecule causing chelation

**chlorophyll a** Principal green plant pigment, used as a measure of phytoplankton biomass

**cilia** Short bristly hairs that move in unison in cellular feeding or propulsion

**ciliate** Protozoan having distinct ciliary structure

**Coelenterate** Phylum of animals with stinging cells and an ancestral two-stage sedentary (hydroid) and mobile (medusoid) life cycle

**colony** Aggregation of organisms that could survive individually

**Competitive Exclusion Principle** Theory that in a constant homogenous environment, a single superior species should drive all competitors to extinction

**continental shelf** Shallow sea bottom fringing the continents to a depth of roughly 200 meters

**copepod** Small torpedo-shaped crustacean with antennae, probably the dominant metazoan in the sea

**copepodite** Later juvenile stage of a copepod

**cyst** Hard pellet formed by many neritic plants and some animals for overwintering or other long-term refuge

**cytoplasm** Mixture of fluid and structures in the interior of a cell exclusive of the nucleus

**detritus** Nonliving particles, suspended or on the bottom

**diapause** Period of inactivity in winter among crustaceans, analogous to hibernation in vertebrates

**dinoflagellates** Unicellular plants and animals possessing two characteristic flagella, and frequently outer cellulose plates

**direct uptake** Uptake of pollutants from water directly into organisms

**El Niño** Short for *El Niño de Navidad* (Child of Christmas), Peruvian term for occasional catastrophic mortalities of fish and birds, usually during December, caused by decreased upwelling

**embryology** Study of development of the egg from conception to mature organism

**estuary** Area in which fresh water meets salt water, usually in an inlet

**euphotic** Upper hundred meters or less of the pelagic zone, where sunlight is sufficient for plant growth

**eutrophication** Overenrichment of a water body by nutrients, causing nuisance phytoplankton overgrowth

**fjord** A long, narrow, steep-sided marine inlet, carved by a glacier, usually with a sill at its mouth

**flagellum (plural flagella)** Long whiplike cellular hair used for propulsion

**fluorometer** Instrument that measures chemical concentrations from how they re-emit incident fluorescent light

**flushing** Turnover of water in a basin by the outflow and inflow of runoff and tides

**flushing time** Same as **residence time**

**food chain** Simple model of a community having organisms assigned in a linear sequence of numbered trophic levels

**food web** Complex community model in which interlocking feeding patterns create a multidimensional trophic mesh without discrete levels

**Foraminifera (forams)** Class of protozoa having a spiral outer shell of calcium carbonate

**frustule** The two halves of the silica outer shell of diatoms

**gram** 0.035 ounce

**herbivore** Animal that eats only plants

**hermaphrodite** Animal with both sets of sexual organs

**heterotroph** Organism dependent for food on other organisms or their organic products

**holoplankton** Organisms that spend their entire lives as plankton

**holotrich** Group of ciliate protozoa

**hydra (hydroid)** The sedentary phase of the coelenterate life cycle

**ichthyoplankton** Planktonic fish larvae

**intertidal** Benthic zone between the highest and lowest tide levels

**ion** Chemically reactive atom or molecule having an electrical charge

**kilocalorie** Amount of energy required to heat one kilogram of pure water one degree Celsius; one thousand calories

**kilogram** One thousand grams; 2.2 pounds

**kilometer** One thousand meters; 0.62 miles. (**square kilometer** equals 0.4 square miles or 247 acres)

**K-selected** Evolved to maintain a constant population despite environmental fluctuations

**Langley** Radiation delivering an energy flux of one calorie per square centimeter

**Langmuir cells** Small-scale current spirals visible as slicks and bands paralleling the wind

**larva** (plural **larvae**) Earliest stage of maturity, after hatching from the egg

**Limiting Nutrient Concept** Theory derived from agriculture that a single nutrient, in scarcest supply relative to requirements, limits yield of a plant crop

**lipid** Fat or oil molecule

**liter** One thousand cubic centimeters; 1.06 quarts

**littoral** Shallowest benthic zone, often used synonymously with “intertidal”

**lorica** Outer sheath of a tintinnid ciliate, frequently adorned with cemented sediment

**medusa** (plural **medusae**) Free-floating jellyfish stage of the coelenterate life cycle, named for the resemblance of its tentacles to the snake-haired woman of mythology

**meroplankton** Planktonic (usually larval) stages of animals that are nekton or benthos the rest of their life cycle

**meso-zooplankton** Intermediate-sized zooplankton (about 0.25 to 10 millimeters) reliably sampled with a net

**metazoa** multicellular animals

**meter** 3.28 feet; 1.09 yards (**square meter** equals 10.7 square feet; **cubic meter** equals 35.3 cubic feet, 1.3 cubic yards)

**metric ton** One thousand kilograms; 2,200 pounds; 1.1 English tons

**microalga** Alga having only one or a few cells per organism

**microgram** One millionth of a gram

**micrometer (micron)** One millionth of a meter, one thousandth of a millimeter

**micronekton** Larger zooplankton (more than about one centimeter) with significant net-avoiding swimming ability

**micro-zooplankton** Smaller zooplankton (less than about 250 micrometers) poorly sampled by nets

**milligram** One-thousandth of a gram

**millimeter** One-thousandth of a meter, one-tenth of a centimeter

**mitosis** Duplication of a cell's genetic material prior to binary fission

**morphology** Internal and external structures of organisms, and their functions

**nanoplankton** Organisms too small (less than 20 micrometers) to be sampled even by a fine-meshed phytoplankton net

**nauplius** (plural **nauplii**) Earliest larval stages of copepods and many other crustaceans

**neap tides** Biweekly periods of weaker tidal currents and narrower tidal ranges associated with the quarter moons

**nekton** Pelagic animals swimming strongly enough to oppose ocean currents

**neritic** Shallow pelagic waters overlying the continental shelf

**net plankton** All plankton large enough to be caught with a fine-meshed phytoplankton net (above about 20 micrometers)

**neuston** Organisms associated with the very thin water-air interface

**nutrient** Dissolved chemical essential for plant growth

**oceanic** Deep pelagic waters beyond the edge of the continental shelf

**oligotrich** Ciliate protozoan with weak or absent sheath

## The Fertile Fjord/Strickland

**omnivore** Animal that eats both plants and animals

**organic** Pertaining to or derived from organisms; a chemical containing a carbon-hydrogen complex

**organism** A living entity: plant, animal, or otherwise

**Paradox of the Plankton** Apparent violation of the Competitive Exclusion Principle by the observed diversity of coexisting plankton species

**pelagic** Contained within a body of water, off the bottom

**periphyton** Organisms living on rooted aquatic plants

**phylum** (plural **phyla**) The coarsest division (after kingdom) into which organisms are categorized by their morphological and evolutionary similarities

**physiology** Study of metabolic systems and processes in organisms

**phytoplankton** Small flagellate microalgae from several phyla, including chlorophytes, chrysophytes, and cryptophytes

**phytoplankton** Planktonic microalgae

**plankton** Aquatic organisms living unattached to the bottom and having swimming powers insufficient to resist water currents

**population** Standing stock of organisms as measured by their collective numbers

**ppb (parts per billion)** One part in  $10^9$  by weight, or one milligram per metric ton

**ppm (parts per million)** One part in  $10^6$  by weight, or one gram per metric ton, one milligram per kilogram

**ppt (parts per trillion)** One part in  $10^{12}$ , or one microgram per metric ton

**predator** A carnivore, especially a mobile one

**prey** An animal eaten by a carnivore

**primary productivity** Productivity by autotrophs that supports the remainder of the community

**productivity** Rate of generation of new living matter by organisms

**protozoa** Unicellular animals

**PSP (paralytic shellfish poisoning)** Nerve poisoning due to eating shellfish containing toxin ingested from the dinoflagellate *Gonyaulax*

**radiolarians** Class of protozoa with a star-shaped silica outer skeleton

**red tide** Discoloration of surface water by a dense plankton bloom, including but not limited to those associated with toxicity and luminescence

**residence time** Average time spent by a water molecule in a basin before being flushed to sea; estimated as ratio of basin volume to inflow or outflow

**r-selected** Evolved for rapid population changes in response to environmental fluctuations

**saxitoxin** The principal neurotoxin generated by *Gonyaulax catenella* that causes paralytic shellfish poisoning

**seta** (plural **setae**) Small immobile bristle; its branches are “setules”

**sill** Shallow submerged pile of debris left across a basin by a retreating glacier; called a moraine on land

**spectrophotometer** Instrument that measures chemical concentrations from their absorption of known colors of light

**spores** Small, thinly covered bodies shed by plants for vegetative asexual reproduction or short-term refuge

**spring tides** Biweekly periods of stronger tidal currents and wider tidal ranges associated with the full and new moons

**standing stock** Quantity of organisms at a given time and place, expressed per unit area or volume

**synergism** Interaction of controlling factors (e.g., pollutant concentrations) in which the effect of one is enhanced by the presence of the other

**taxonomy** Categorizing organisms by their structural and evolutionary similarities

**tintinnid** Ciliate protozoan with a sturdy vase-shaped outer sheath (lorica) with cemented sediment grains

**ton** see **metric ton**

**trophic** Pertaining to the feeding relationships among organisms

**trophic energy** Energy fixed during primary production and available to animals as organic matter

**trophic level** Theoretical numerical ranking that expresses how many organisms trophic energy must pass through from its source to reach a given organism

**trophic uptake** Uptake of a pollutant via food

**unicellular** Having only one cell per organism

**upwelling** Upward water motion that stimulates phytoplankton growth by nutrient supply, caused by winds and currents

**vacuole** Hollow space in a cell for storage or buoyancy

**vortex** (plural **vortices**) Spiral motion

**zooplankton** Planktonic animals, including meroplankton

**zygote** Original cell of any organism, a fertilized egg

# Guide to Pronunciation

Acartia uh-CAR-sha  
Aequorea eve-QUOR-ee-uh  
Amoebophyra ceratii uh-mee-boy-FY-ruh sir-AY-she-eye  
aphotic ay-FO-tick  
Brachionus brack-ee-OH-nuss  
Burien BYOO-ree-un  
Calanus KAL-un-us  
CEPEX SEE-pecks  
Ceratium sir-AY-shum  
Chaetoceros kee-TAH-sir-us  
Chaetognath KEE-tog-nath  
chelation kee-LAY-shun  
Chlorella klor-ELL-uh  
chordates KORE-dates  
cilia SILL-ee-uh  
Clione kly-OH-nee  
Coelenterates suh-LEN-ter-ates  
copepod KOH-puh-pods  
Corycaeus koh-RIH-see-us  
Coscinodiscus kah-sin-oh-DISS-kuss  
Ctenophore TEEN-oh-for  
detritus dee-TRITE-us  
diatoms DYE-uh-toms  
dinoflagellates dye-noh-FLAJ-uh-lates  
El Niño El-NEEN-yoh  
Euchaeta you-KEET-uh  
Euphausiid you-FOW-zid  
euphotic you-FOH-tick  
fjord fyord  
geoduck GOO-ee-duck  
Gonyaulax gonn-ee-AWL-ax  
halocline HAY-loh-kline  
ichthyoplankton ICK-thee-oh-plank-tunn  
larvaceans lar-VAY-shuns  
medusae muh-DOO-see  
Mytilus MIH-tih-luss  
Navicula nuh-VICK-you-luh  
Neocalanus nee-oh-KAL-uh-nuss  
Nereis NEAR-ee-us  
neritic nuh-RIT-ick  
neuston NEW-stun  
Nitzschia NITCH-ee-uh  
Noctiluca nock-tih-LOO-kuh  
Oikopleura oy-koh-PLOO-ruh  
Olisthodiscus oh-liss-thoh-DISS-kuss  
Pasiphaea pass-ih-FEE-uh  
phytoflagellates fy-toh-FLAJ-uh-lates  
Pleurobrachia ploo-roh-BREAK-ee-uh

polychaetes PAHL-ee-keets  
*Polyorchis* pahl-ee-OAR-kiss  
*Pseudocalanus* soo-doh-KAL-uh-nuss  
pycnocline PICK-noh-kline  
Puyallup pyoo-AL-up  
*Pyramimonas* puh-ram-ih-MOAN-us  
Saanich SAN-itch  
Sequim skwim  
*Skeletonema* skeleton-EE-muh  
*Spirulina* spy-roo-LEAN-uh  
*Synchaeta* sin-KEET-uh  
*Thalassiosira* thuh-lass-ee-oh-SIGH-ruh  
Tintinnids tin-TIN-idz  
trophic TROH-fick

# BIBLIOGRAPHIC NOTES

The extensive collection of references consulted in preparing this book has been compiled and will be available as a Washington Sea Grant Technical Report (The Fertile Fjord: Annotated Bibliography) in late 1983. Much of the same literature has also been reviewed and discussed in Dexter et al., 1981 (see Chapter 6). Below are the sources of quotes and illustrations, along with selected references to further interesting reading.

## Chapter 1 Plankton Primer

Hardy, A.C. 1965. *The Open Sea: Its Natural History*. Boston: Houghton Mifflin. Vol. 1, 335 pp.

Porter, K.G. and E.I. Robbins. 1981. Zooplankton fecal pellets link fossil fuel and phosphate deposits. *Science* 212:931–933.

Rand McNally. 1977. *The Rand McNally Atlas of the Oceans*. Chicago: Rand McNally. 208 pp.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. *Science* 166:72–76.

\_\_\_\_\_. 1970. Is the world's oxygen supply threatened? *Nature* 227:374–375.

Steinbeck, J. 1951. *The Log from the Sea of Cortez*. New York: Viking Press. 282 pp.

Tunnicliffe, V. 1981. High species diversity and abundance of the epibenthic community in an oxygen-deficient basin. *Nature* 294:354–356.

Whittaker, R.H. 1975. *Communities and Ecosystems*. Second Edition. New York: MacMillan. 385 pp.

## Chapter 2 Studying Plankton

Agassiz, A. 1865. North American Acalephae. *Mem. Mus. Compar. Zool. Harvard College* 1:1–234.

Barham, E.G. 1979. Giant larvacean houses: Observations from deep submersibles. *Science* 205:1129–1131.

Cousteau, J.-Y., with J. Dugan. 1963. *The Living Sea*. New York: Harper and Row. 239 pp.

Harbison, G.R. and L.P. Madin. 1979. Diving—a new view of plankton biology. *Oceanus* 22:18–27.

Orr, M.H. 1981. Remote acoustic detection of zooplankton response to fluid processes, oceanographic instrumentation, and predators. *Can. J. Fish. Aqua. Sci.* 38:1096–1105.

Thompson, T.G. and L.D. Phifer. 1936. The plankton and the properties of the surface waters of the Puget Sound region. *Univ. Wash. Publ. Ocean.* 1:111–134.

## Chapter 3 Plankton Hall of Fame

Arai, M.N. and A. Brinckmann-Voss. 1980. Hydromedusae of British Columbia and Puget Sound. *Can. Bull. Fish. Aqua. Sci.* 204. 192 pp.

Cupp, E.E. 1943. Marine plankton diatoms of the West Coast of North America. *Scripps Inst. Ocean. Bull.* 5:1–237.

Gardner, G.A. and I. Szabo. 1982. British Columbia pelagic marine Copepoda: Identification Manual and annotated bibliography. *Can. Spec. Publ. Fish. Aqua. Sci.* 62. 536 pp.

Gran, H.H. and E.C. Angst. 1931. Planktonic diatoms of Puget Sound. *Publ. Puget Sound Mar. Biol. Sta.* 7:417–456.

Smith, D.L. 1977. *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae*. Dubuque, Iowa: Kendall-Hunt Publishing Company. 161 pp.

Vinyard, W.C. 1975. *A Key to the Genera of Marine Planktonic Diatoms of the Pacific Coast of North America*. Eureka, Calif.: Mad River Press. 27 pp.

#### **Chapter 4 Seascapes**

Bienfang, P.K., P.J. Harrison, and L.M. Quarmby. 1982. Sinking rate response to depletion of nitrate, phosphate, and silicate in four marine diatoms. *Mar. Biol.* 67:295–302.

Evans, G.T. and F.J.R. Taylor. 1980. Phytoplankton accumulation in Langmuir cells. *Limnol. Oceanogr.* 25:840–845.

Silver, M.W., A.D. Shanks, and J.D. Trent. 1978. Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations. *Science* 201:371–373.

Strickler, J.R. 1982. Calanoid copepods, feeding currents, and the role of gravity. *Science* 218:158–160.

#### **Chapter 5 The Green Machine**

Barlow, J. 1958. Spring changes in phytoplankton abundance in a deep estuary, Hood Canal, Washington. *J. Mar. Res.* 17:53–67.

Booth, B.C. 1969. Species differences between two consecutive phytoplankton blooms in Puget Sound during May, 1967. Unpubl. M.S. Thesis, Univ. Wash., Seattle. 28 pp.

Campbell, S.A., W.K. Peterson, and J.R. Postel. 1977. Phytoplankton production and standing stock in the Main Basin of Puget Sound. Final Report to the Municipality of Metropolitan Seattle, Puget Sound Interim Studies. 132 pp.

Christensen, J.P. and T.T. Packard. 1976. Oxygen utilization and plankton metabolism in a Washington fjord. *Estuar. Coast. Mar. Sci.* 4:339–347.

Coomes, C.A., C.C. Ebbesmeyer, J.M. Cox, J.M. Helseth, L.R. Hinckley, G.A. Cannon, and C.A. Barnes. (in press) Synthesis of current measurements in Puget Sound Washington. Volume 2. Indices of mass and energy inputs into Puget Sound: Runoff, air temperature, wind, and sea level. NOAA Tech. Memo.

Ebbesmeyer, C.C. and C.A. Barnes. 1980. Control of a fjord basin's dynamics by tidal mixing in embracing sill zones. *Estuar. Coast. Mar. Sci.* 11:311–330.

Ebbesmeyer, C.C. and J.M. Helseth. 1977. An analysis of primary production observed during 1966–1975 in central Puget Sound, Washington. Final Report to the Municipality of Metropolitan Seattle, Puget Sound Interim Studies. 68 pp.

English, T.S. 1979. Biological systems acoustical assessments in Port Gardner and adjacent waters. Contract report to Wash. Dept. Ecol., Olympia. 137 pp.

Feely, R.A. and M.F. Lamb. 1979. A study of the dispersal of suspended sediment from the Fraser and Skagit rivers into northern Puget Sound using LANDSAT imagery. Interagency Energy/Environment Research and Development Program Report EPA-600/7-79-165. 46 pp.

Frisch, A.S., J. Holbrook, and A.B. Ages. 1981. Observations of a summertime reversal in circulation in the Strait of Juan de Fuca. *J. Geophys. Res.* 86:2044–2048.

Harris, D.L., 1981. Tides and tidal datums in the United States. U.S. Army Corps of Engineers Coastal Engineering Research Center Special Report 7. Fort Belvoir, VA.

## The Fertile Fjord/Strickland

Harrison, P.J., J.D. Fulton, F.J.R. Taylor, and T.R. Parsons. 1983. A review of the biological oceanography of the Strait of Georgia: Pelagic environment. *Can. J. Fish. Aqua. Sci.* 40:1064-1094.

Munson, R.E. 1970. The horizontal distribution of phytoplankton in a bloom in Puget Sound during May, 1969. Unpubl. M.S. Thesis, Univ. Wash., Seattle. 13 pp.

Parsons, T.R., J. Stronach, G.A. Borstad, G. Louttit, and R.I. Perry. 1981. Biological fronts in the Strait of Georgia, British Columbia, and their relation to recent measurements of primary productivity. *Mar. Ecol. Prog. Ser.* 6:237-242.

Parsons, T.R., R.I. Perry, E.D. Nutbrown, W. Hsieh, and C.M. Lalli. 1983. Frontal zone analysis at the mouth of Saanich Inlet, British Columbia, Canada. *Marine Biology* 73:1-5.

Stockner, J.G., D.D. Cliff, and K.R.S. Shortreed. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. *J. Fish. Res. Bd. Can.* 36:657-666.

Takahashi, M., J.E. Barwell-Clarke, F. Whitney, and P.A. Koeller. 1978. Winter condition of marine plankton populations in Saanich Inlet, B.C., Canada. I. Phytoplankton and its surrounding environment. *J. Exp. Mar. Biol. Ecol.* 31:283-301.

Thomson, R.E. 1981. Oceanography of the British Columbia Coast. *Can. Spec. Publ. Fish. Aqua. Sci.* 56. 291 pp.

U.S. Environmental Data Service. Climatological Data for Washington. National Weather Service, Seattle.

Winter, D., K. Banse, and G. Anderson. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. *Mar. Biol.* 29:139-176.

### Chapter 6 The Fish Factory

Banse, K. 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. *Mar. Ecol. Progr. Ser.* 9:281-297.

Chester, A.J., D.M. Damkaer, D.B. Dey, G.A. Heron, and J.D. Larrance. 1980. Plankton of the Strait of Juan de Fuca, 1976-1977. Interagency Energy/Environment Research and Development Program Report EPA-600/7-80-032. 64 pp.

Cooney, R.T. 1971. Zooplankton and micronekton associated with a diffuse sound-scattering layer in Puget Sound, Washington. Ph.D. Thesis, Univ. Wash., Seattle. 208 pp.

Copping, A.E. and C.J. Lorenzen. 1980. Carbon budget of a marine phytoplankton-herbivore system with a carbon-14 as a tracer. *Limnol. Oceanogr.* 25:873-882.

Corkett, C.J. and I.A. McLaren. 1978. The biology of *Pseudocalanus*. *Adv. Mar. Biol.* 15:1-231.

Dexter, R.N., D.E. Anderson, E.A. Quinlan, L.S. Goldstein, R.M. Strickland, S.P. Pavlou, J.R. Clayton, Jr., R.M. Kocan, and M. Landolt. 1981. A summary of knowledge of Puget Sound related to chemical contaminants. NOAA Tech. Memo. OMPA-13. 435 pp.

English, T.S. and R.E. Thorne. 1977. Acoustic and net surveys of fishes and zooplankton. Final Report to the Municipality of Metropolitan Seattle, Puget Sound Interim Studies. 64 pp.

Greve, W. and T.R. Parsons. 1977. Photosynthesis and fish production: Hypothetical effects of climatic change and pollution. *Helg. Wissenschaft. Meeresunt.* 30:666-672.

Grice, G.D., R.P. Harris, M.R. Reeve, J.F. Heinbokel, and C.O. Davis. 1980.

Large-scale enclosed water-column ecosystems. An overview of Foodweb I, the final CEPEX experiment. *J. Mar. Biol. Assoc. U.K.* 60:401–414.

Grice, G.D. and M.R. Reeve, Eds. 1982. *Marine Mesocosms*. New York: Springer-Verlag. 430 pp.

Hebard, J.F. 1956. The seasonal variation of zooplankton in Puget Sound. M.S. Thesis, Univ. Wash., Seattle. 64 pp.

Huntley, M.E. and L.A. Hobson. 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *J. Fish. Res. Bd. Can.* 35:257–261.

King, K.R. 1979. The life history and vertical distribution of the chaetognath, *Sagitta elegans*, in Dabob Bay, Washington. *J. Plankton Res.* 1:153–167.

\_\_\_\_\_. 1981. The quantitative natural history of *Oikopleura dioica* (Urochordata: Larvacea) in the laboratory and in enclosed water columns. Ph.D. Thesis, Univ. Wash., Seattle. 152 pp.

Koeller, P.A., J.E. Barwell-Clarke, F. Whitney, and M. Takahashi. 1979. Winter condition of marine plankton populations in Saanich Inlet, B.C., Canada. III. Mesozooplankton. *J. Exp. Mar. Biol. Ecol.* 37:161–174.

Landry, M.R. 1981. Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Mar. Biol.* 65:77–82.

Mackas, D.L., G.C. Louttit, and M.J. Austin. 1980. Spatial distribution of zooplankton and phytoplankton in British Columbia coastal waters. *Can. J. Fish. Aquat. Sci.* 37:1476–1487.

Mauchline, J. 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.* 18:1–682.

Maynard, S. 1972. A study of the stomach contents of five fish species collected in Carr Inlet, Puget Sound. Unpubl. M.S. Thesis, Univ. Wash. 96 pp.

Ross, R.M., K.L. Daly, and T.S. English. 1982. Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. *Limnol. Oceanogr.* 27:304–314.

Runge, J.A. 1981. Egg production of *Calanus pacificus* Brodsky and its relationship to seasonal changes in phytoplankton availability. Ph.D. Thesis, Univ. Wash., Seattle. 116 pp.

Shuman, F. 1978. The fate of phytoplankton chlorophyll in the euphotic zone—Washington coastal waters. Ph.D. Thesis, Univ. Wash., Seattle. 243 pp.

Simenstad, C.A., B.S. Miller, C.F. Nyblade, K. Thornburgh, and L.J. Bledsoe. 1979. Food web relationships of northern Puget Sound and the Strait of Juan de Fuca. Interagency Energy/Environment Research and Development Program Report EPA 600/7-79-259. 335 pp.

Steele, J.H. 1974. *The Structure of Marine Ecosystems*. Cambridge, Mass.: Harvard University Press. 128 pp.

Takahashi M. and K.D. Hoskins. 1978. Winter conditions of marine plankton populations in Saanich Inlet, British Columbia, Canada. II. Micro-zooplankton. *J. Exp. Mar. Biol. Ecol.* 32:27–37.

Welschmeyer, N.A. 1982. The dynamics of phytoplankton pigments: Implications for zooplankton grazing and phytoplankton growth. Ph.D. Thesis, Univ. Wash., Seattle. 176 pp.

Yen, J. 1982. Predatory feeding ecology of *Euchaeta elongata* Esterly, a marine planktonic copepod. Ph.D. Thesis, Univ. Wash., Seattle. 130 pp.

### Chapter 7 Plankton and Pollution

American Petroleum Institute. 1979. 1979 Oil Spill Conference. Washington, D.C.: API. 728 pp.

Berrick, R.C. 1982. Flux of aliphatic and polycyclic aromatic hydrocarbons to central Puget Sound from Seattle (Westpoint) primary sewage effluent. *Environ. Sci. Tech.* 16:682-692.

Beak Consultants. 1975. Oil pollution and the significant biological resources of Puget Sound. Final Report to Wash. Dept. Ecol., Olympia. 3 volumes.

Brown, L.R. 1980. Fate and effect of oil in the aquatic environment—Gulf Coast region. EPA Rep. 600/3-80-058a. 101 pp.

Brown, D.A. and T.R. Parsons. 1978. Relationships between cytoplasmic distribution of mercury and toxic effects to zooplankton and chum salmon (*Oncorhynchus keta*) exposed to mercury in a controlled ecosystem. *J. Fish. Res. Bd. Can.* 35:880-884.

Cardwell, R.D., C.E. Woelke, M.I. Carr, and E.W. Sanborn. 1979. Toxic substance and water quality effects on larval marine organisms. Wash. Dept. Fish. Tech. Rep. 45, 71 pp.

Carpenter, R., M.L. Peterson, and R.A. Jahnke. 1978. Sources, sinks, and cycling of arsenic in the Puget Sound region. In M.L. Wiley, Ed., *Estuarine Interactions*. New York: Academic Press. Pp. 459-480.

Corner, E.D.S. 1978. Pollution studies with marine plankton. Part I. Petroleum hydrocarbons and related compounds. *Adv. Mar. Biol.* 15:289-380.

Davies, A.G. 1978. Pollution studies with marine plankton. Part 2. Heavy Metals. *Adv. Mar. Biol.* 15:381-508.

Edmonson, W.T. and J.T. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. *Limnol. Oceanogr.* 26:1-29.

GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Pollution). 1977. Impact of Oil on the Marine Environment. Reports and Studies #6, Food and Agriculture Organization of the United Nations, 250 pp.

Geyer, R.A., Ed. 1980. *Marine Environmental Pollution*. 1. Hydrocarbons. Amsterdam: Elsevier Scientific Publishing Co. 591 pp.

Goldberg, E.D., V.T. Bowen, J.W. Farrington, G. Harvey, J.H. Martin, P.L. Parker, R.W. Risebrough, W. Robertson, E. Schneider, and E. Gamble. 1978. The mussel watch. *Environ. Conserv.* 5:101-125.

Grice, G.D. and D.W. Menzel. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. VIII. Summary of results. *Mar. Sci. Comm.* 4:23-31.

Jernelov, A. and O. Linden. 1981. IXTOC I: A case study of the world's largest oil spill. *Ambio* 10:299-306.

Kineman, J.J., R. Elmgren, and S. Hansson, Eds. 1980. *The Tsesis Oil Spill*. NOAA Office of Marine Pollution Assessment, Boulder, CO.

Krebs, C.T. and K.A. Burns. 1977. Long-term effects of an oil spill on populations of the salt-marsh crab *Uca pugnax*. *Science* 197:484-487.

Lannergren, C. 1978. Net- and nanoplankton: Effects of an oil spill in the North Sea. *Botanica Marina* 21:353-356.

Mackie, P.R., R. Hardy, and K.J. Whittle. 1978. Preliminary assessment of the presence of oil in the ecosystem at Ekofisk after the blowout, April 22-30, 1977. *J. Fish. Res. Bd. Can.* 35:544-551.

Malins, D.C., Ed. 1977. *Effects of Petroleum on Arctic and Subarctic Marine Environments and Organisms*. Volume 1: Nature and Fate of Petroleum. 321 pp. Volume 2: Biological Effects. 500 pp. New York: Academic Press.

Malins, D.C., B.B. McCain, D.W. Brown, A.K. Sparks, H.O. Hodgins, and S.-L. Chan. 1982. Chemical Contaminants and Abnormalities in Fish and Invertebrates from Puget Sound. NOAA Tech. Memo. OMPA-19. 168 pp.

Menzel, D.W. 1977. Summary of experimental results: Controlled ecosystem pollution experiment. *Bull. Mar. Sci.* 27:142-145.

Middleditch, B.S., Ed. 1981. *Environmental Effects of Offshore Oil Production*. New York: Plenum Press. 446 pp.

O'Connors, H.B., Jr., C.F. Wurster, C.D. Powers, D.C. Biggs, and R.G. Rowland. 1978. Polychlorinated biphenyls may alter marine trophic pathways by reducing photoplankton size and production. *Science* 201:737-739.

Officer, C.B. and J.H. Ryther. 1977. Secondary sewage treatment versus ocean outfalls: An assessment. *Science* 197:1056-1060.

Parsons, T.R., L.J. Albright, and J. Parslow. 1980. Is the Strait of Georgia becoming more eutrophic? *Can. J. Fish. Aquat. Sci.* 37:1043-1047.

Phillips, D.J.H. 1978. Use of biological indicator organisms to quantitate organochlorine pollutants in aquatic environments—a review. *Environ. Poll.* 16:167-229.

Rasmussen, L.F. and D.C. Williams. 1975. The occurrence and distribution of mercury in marine organisms in Bellingham Bay. *Northwest Sci.* 49:87-94.

Shea, G.G., C.C. Ebbesmeyer, Q.J. Stober, K. Pazera, J.M. Cox, S. Hemingway, J.M. Helseth, and L.R. Hinckey. 1981. History and Effect of Pulp Mill Effluent Discharges, Bellingham, Washington. Report to U.S. Department of Justice and Environmental Protection Agency by Northwest Environmental Consultants, Inc. 491 pp.

Spooner, M.F. 1978. Editorial introduction (to special issue on Amoco Cadiz). *Mar. Poll. Bull.* 9:281-284.

Stockner, J.G., D.D. Cliff, and D.B. Buchanan. 1977. Phytoplankton production and distribution in Howe Sound, British Columbia: A coastal marine embayment-fjord under stress. *J. Fish. Res. Bd. Can.* 34:907-917.

Welch, E.B., R.M. Emery, R.I. Matsuda, and W.A. Dawson. 1972. The relation of periphytic and planktonic algal growth in an estuary to hydrographic factors. *Limnol. Oceanogr.* 17:731-737.

### Chapter 8 Red Tides

Cardwell, R.D., C.E. Woelke, M.I. Carr, and E. Sanborn. 1977. Evaluation of water quality of Puget Sound and Hood Canal in 1976. NOAA Tech. Memo. ERL/MESA-21, 36 pp.

Cardwell, R.D., S. Olson, M.I. Carr, and E.W. Sanborn. 1979. Causes of oyster larvae mortality in South Puget Sound. NOAA Tech. Memo. ERL/MESA-39, 73 pp.

MacDonald, E.M. 1970. The occurrence of paralytic shellfish poison in various species of shore animals along the Strait of Juan de Fuca in the state of Washington. M.S. Thesis, Univ. Wash., Seattle. 65 pp.

Norris, L. and K.K. Chew. 1975. Effect of environmental factors on growth of *Gonyaulax catenella*. In R. LoCicero, Ed. *Toxic Dinoflagellate Blooms*. Wakefield, Mass.: Massachusetts Science and Technology Foundation, pp. 143-152.

Quayle, D. 1969. Paralytic Shellfish Poisoning in British Columbia. *Fish. Res. Bd. Can. Bull.* 168. 68 pp.

Steidinger, K.A. and K. Haddad. 1981. Biologic and hydrographic aspects of red tides. *Bioscience* 31:814-819.

Taylor, D.L. and H.H. Seliger, Eds. 1979. *Toxic Dinoflagellate Blooms*. New York: Elsevier/North Holland. 534 pp.

Taylor, F.J.R. 1968. Parasitism of the toxin-producing dinoflagellate *Gonyaulax catenella* by the endoparasitic dinoflagellate *Amoebophyra ceratii*. *J. Fish. Res. Bd. Can.* 25:2241-2245.

Welling, K. 1982. The effects of extracellular products of *Olisthodiscus luteus* Carter on the survival of Pacific oyster larvae (*Crassostrea gigas* Thunberg) and on the growth of larval associated bacteria. M.S. Thesis, Univ. Wash., Seattle. 66 pp.

**Chapter 9 Marine Pastures**

Goldman, J.C. 1979. Outdoor algal mass cultures. I. Applications. *Water Res.* 13:1-19.

Omori, M. 1978. Zooplankton fisheries of the world: A review. *Mar. Biol.* 48:199-205.

Soeder, S.J. and R. Binsack, Eds. 1978. Microalgae for food and feed. *Ergebnisse der Limnol. Archiv fur Hydrobiol. Beiheft 11.* 300 pp.

# Index

Italic page numbers denote illustrations.

abalone 123  
*Acartia* 30, 69  
Admiralty Inlet 42-43, 45, 48, 50, 51, 58, 73; sill, 37, 44, 46, 48-49, 59  
*Aequorea* 25, 25  
Agassiz, Louis and Alexander 9, 10  
Albatross 9, 10  
ammonia 92  
*Amoebophyra ceratii* 113, 117  
amphipods 23, 34, 70, 71, 75  
*Anacortes* 95, 96, 102  
annelids 27, 28, 112  
aphotic zone 37, 37, 87  
aquaculture 123, 125  
arsenic 92, 93, 98, 99, 100, 104, 106, 107  
ASARCO 99  
atmosphere 3, 81, 82, 100  
autotroph 39  
  
bacteria 2, 110, 118, 124, 125  
as food 66, 70  
biodegradation by 93, 94, 97, 103, 106  
nutrient recycling by 34, 85, 87  
size of 30, 66  
Bainbridge Island 45  
barnacle, larva 12  
Bellingham 95, 104  
Bellingham Bay 92, 96, 100, 106, 117  
benthic zone 36, 37  
benthos 2, 77, 85, 87, 94, 100, 107  
bioaccumulation 104-109, 104  
bioassay 97, 117-118  
Biological Oxygen Demand 94  
biomagnification 91, 92, 102-111  
biomass 40, 41, 81, 99  
animal 14, 66, 66-68, 75-76  
plant 13, 32, 53-57, 59, 60-61, 63-65  
birds 68, 70, 87, 89, 102, 108, 109, 121  
bivalves 105, 109, 113, 122, 124  
black cod 70  
Blake Island 46, 47  
blooms 45, 48, 51-58, 63-65, 68, 69, 77-79, 80-81, 86, 88, 94, 110, 116, 124  
bottles, sampling 8, 8-9  
*Brachionus* 24, 24  
British Columbia 57, 61, 96, 109, 116  
Budd Inlet 59, 64, 94  
Burien 95  
  
cadmium 92, 98, 100, 104, 107  
*Calanus* 22, 24, 70, 71, 75, 110  
*Calanus marshallae* 73  
*Calanus pacificus* 70, 77  
Camano Island 60, 61  
  
*Cancer magister* 122  
carbon xviii, 16, 35, 41, 86  
fixation 53, 54-55, 57, 59, 61, 64  
carbon-14 14-15  
carnivores 22, 24, 39, 40, 71, 82, 87, 87, 109  
in primary food chain 70  
in secondary food chain 83, 84  
Carr Inlet 63, 79  
Case Inlet 59, 59, 63, 79  
CEPEX 85, 101, 109-111  
*Ceratium* 30, 112, 113, 118, 124  
*Chaetoceros* 19, 30, 56, 57, 109, 124  
Chaetognaths 25, 26, 33, 70-71, 79, 84  
Challenger, H.M.S. 6  
chelation 94, 96, 101, 106, 110, 116  
Chesapeake Bay 37, 51  
chlorine 92, 93, 95, 100, 102  
chlorophyll 13, 49, 54-55, 57, 59, 61, 63, 64, 65, 75, 86, 112  
chordates (see also vertebrates) 25, 27  
chromium 98, 104  
cilia 21-22, 24, 26  
ciliates 21-22, 24  
circulation, see currents  
clams 5, 114, 122  
*Clinocardium* 114  
*Clione* 25, 27  
coasts xviii, 1, 3, 126  
coast, Pacific 113  
coast, Washington 74, 102, 122  
cod 70, 78, 80  
Coelenterates 23-26  
Columbia River 102  
Colvos Passage 42-43, 47  
Commencement Bay 60, 92, 99  
competition 38, 76-77, 88  
Competitive Exclusion Principle 38  
continental shelf 3, 4, 37  
copepods 7, 28, 30, 33, 66, 79, 88, 106, 107, 121  
CEPEX 110-111  
description 22-23, 24  
harpacticoid 70  
in primary food chain 69-71  
in secondary food chain 84-88  
life cycles and coupling 76-77, 80, 86  
vertical migration 71-73  
copper 92, 98, 100, 101, 104, 105, 107  
CEPEX 109, 110  
*Corycaeus* 22, 75  
*Coscinodiscus* 19, 30  
coupling 74-76, 80-81, 83-87  
Cousteau, Jacques-Yves 9

## The Fertile Fjord/Strickland

crab 28, 99, 122  
*Crassostrea* 77, 114  
crustaceans 22-24, 24, 105, 112, 121  
  in primary food chain 69-71, 83-86  
  larvae 27-28  
*Ctenophores* 25, 26, 79, 112  
  in secondary food chain 70, 84  
*Cumaceans* 70  
currents 4, 48-50, 78, 94, 116  
currents, tidal 42-44, 52, 60, 63-65  
cysts 17-18, 34, 37, 116-117

Dabob Bay 46, 58, 63-64, 64, 73, 86-87, 125  
DDT 5, 89, 102, 106, 109  
Deception Pass 46; sill, 37  
density 44-45, 54-55  
deserts xviii, 3, 40  
detritus 34-35, 82, 94, 105, 109  
  in pelagic food chain 70, 87  
diapause 77  
diatoms 18-20, 19, 30, 33, 66, 105, 106,  
  110, 116, 120  
  and synchronization 79, 80  
  during blooms, 56-57, 57, 63  
  in primary food chain 83, 85-88, 87, 109  
*Dichthyocha* 19  
diffusion 43  
dinoflagellates 19, 20-21, 24, 79, 87, 88,  
  110  
  and fronts 62  
  and patchiness 36  
  environmental preferences of 56-57  
  in inlets and sills 65  
  red tides 112, 116, 117  
Discovery Bay 64  
*Ditylum* 105  
dogfish 66, 70, 71, 74, 108, 109  
*Dunaliella* 109  
Dungeness sill 46  
Dungeness Spit 96  
Duwamish Head 95  
Duwamish River 43, 46, 47, 60-62, 94, 95,  
  102  
Dyes Inlet 64

East Passage 43  
East Sound 64, 65  
Echinoderm larvae 27, 28  
echo scattering 14, 72, 73, 74, 78, 121  
ecosystems 3, 38, 68, 81-83  
Ediz Hook 96  
efficiency, of food chain 69, 81-88, 82, 120,  
  121, 124  
Eld Inlet 64  
Elliott Bay 60, 78, 92, 94, 104  
El Niño 120  
entrainment 43, 50  
Environmental Protection Agency 100, 103  
epibenthic organisms 70

estuary 3, 37, 42-43, 45, 48, 50  
*Euchaeta* 22, 24, 71, 77  
*Euphausia* 23, 24, 71  
*Euphausia superba* 121  
euphausiids 23, 24, 30, 33, 66, 67, 68, 87,  
  96, 106, 121  
  in primary food chain 70-71  
  life cycles and coupling 76-77, 80, 86  
euphotic zone 37, 37, 50, 87  
eutrophication 5, 93  
Everett 61, 95, 96  
excretion 35-36, 82-83, 85, 87, 110, 118

fecal pellets 86, 105, 107  
fishes xviii, 4, 66, 79, 87, 96, 107, 108, 109,  
  112, 118  
  in primary food chain 66, 68, 70-71  
  in secondary food chain 83, 85, 86  
  larvae and juveniles 7, 29, 70, 79, 84, 87,  
  98, 119, 120, 122-124  
  life cycles and synchronization 68, 79  
  vertical migration 74, 77  
  seasonal migration 78-80  
fjord 37  
flagella 18-20, 19, 21, 24  
flagellates (see also dinoflagellates, phyto-  
  flagellates) 18, 21, 57, 63-65, 66, 85, 87,  
  88, 109, 110, 120, 124  
fluorometer 13-14, 49  
flushing (see also residence time) 51, 58,  
  60, 94-96, 100, 102  
food chain 39-40, 108, 119-121, 124, 125  
  pelagic 41, 68-69, 81, 82, 83, 87, 107,  
  109-111  
  primary 71, 83-84, 86, 87, 88, 109  
  secondary 83-88, 110  
  structure 69-74  
  synchronization 75-81  
food web 39, 87-88, 104, 108, 115  
foraminiferans 21  
forests xviii, 1, 3, 32, 40  
Fraser River 58, 61, 62, 94  
Friday Harbor Laboratories, see University  
  of Washington  
fronts (see also stripes) 60, 61, 62  
frustule 18, 19, 20  
Frye, T.C. 10, 11

gelatinous zooplankton 9, 84, 86  
generation time (see also metabolism) 66,  
  67-68  
geoduck 122-123  
*Gonyaulax* 19, 112-118, 113  
Grays Harbor 37  
grazing 86, 99, 122  
Greve, Wulf 83-85  
Gulf of Alaska 87  
*Gymnodinium* 19, 112, 118

hake 70, 71  
*Haliotis* 123  
 halocline 42-43, 45, 49  
 Hammersley Inlet 64  
 Haro Strait 46  
 hatcheries 122-124  
 Henderson Inlet 64  
 herbivores 24, 39, 40, 82, 83, 86  
 herring 30, 66, 70-71, 71, 74, 76, 78-79, 79, 80, 115  
 heterotroph 39  
 holoplankton 2  
 Hood Canal 37, 44, 46, 58, 64-65, 64, 104, 114, 117, 117, 118  
 hydrocarbons (see petroleum, oil) 92  
 ichytoplankton 29  
 inlets 58-65, 73, 78, 79, 80, 116  
 intertidal zone 36, 114  
 intrusions 50, 62-63  
 jellyfish (see also coelenterates, gelatinous zooplankton, medusae) 9, 23, 25, 66, 73, 79, 121  
 kilocalories 81, 82  
 Kincaid, Trevor 10-11, 11  
 King County 95  
 krill 1, 23, 24, 121  
 K-selected 68, 76-77, 86  
 Lake Washington 4, 46, 93, 95, 97  
 LANDSAT 49, 61  
 Langmuir cells 35  
 larvaceans (see also *Oikopleura*) 25, 27, 84, 110, 112  
 larvae (see also meroplankton) 27, 28, 29, 70, 72, 77-78, 79, 80, 87, 88, 98, 99, 110, 122  
 lead 92, 92, 93, 98, 100, 101, 104  
 Liberty Bay 64, 118  
 life cycles 74-76, 79, 80  
 life span, see generation time, metabolism  
 light, see solar energy  
*Limacina* 27  
 lingcod 70  
 littoral zone 37  
 locomotion 2, 18-20, 81  
 Long Island Sound 48, 109, 114  
 lorica 22, 24  
 luminescence 21, 24, 25, 26, 27, 77, 112  
 Lynch Cove 58, 64, 65  
 main basin 42-43, 45, 46, 50, 54-55, 57, 58, 64, 65, 73, 75, 78, 79, 94  
 mammals 66, 68, 87, 89, 104, 107, 109  
 mariculture 123  
 marine snow 34-35, 86, 94  
 medusae 10, 23-26, 25, 70, 83-84, 112  
 mercury 89, 92, 98, 100, 101, 104, 106-110  
 meroplankton 2, 12, 27, 77, 86  
*Mesodinium* 112  
 mesozooplankton 32, 72-73, 77  
 metabolism 82, 91  
 metabolic rate (see also generation time) 66-67, 81, 83-84  
 metallothionein 106  
 metals 95, 98-102, 105, 106, 116  
*Metridium* 73  
 METRO 95  
 micronekton 32, 70, 72-73, 75, 77, 79, 84  
 microzooplankton (see also protozoa) 32, 70, 72, 75-77, 80, 84, 86, 87  
 migration, seasonal 78-81  
 migration, vertical 25, 33-34, 50, 71-74, 75, 79, 86, 87  
 Minamata 89, 100, 106  
 mixing 86-87, 100, 116  
     and primary productivity 42-43, 42-45, 48, 50, 58, 59, 63-65, 94, 119  
 molluscs 25, 26-27, 28, 122  
 morphology 12  
 mussels 5, 103, 105, 112, 113, 122, 124  
 Mya 114  
 mysids 23, 34, 70  
*Mytilus edulis* 105, 114  
*Mytilus californianus* 114  
 nanoplankton 31  
 Nansen bottle 8  
 Narrows, The 37, 42-43, 45, 46, 46, 48, 50, 50, 51, 58, 59, 73, 73, 78, 114  
 nauplii 70, 77, 87, 110  
*Navicula* 19  
 nekton 2, 29, 70-71, 83, 121  
*Neocalanus* 73, 76-77, 86  
*Nereis vexillosa* 77  
 neritic zone 37, 37, 116  
 net-pens 123-125  
 net plankton 31  
 nets 6-9, 7, 72, 121  
 neuston 103  
 Nisqually River 42-43, 47  
 Nisqually sill 46, 58, 59  
*Nitzschia* 30, 109  
*Noctiluca* 21, 24, 112  
 Nooksack River 61  
 nutrients 16-17, 33-36, 81, 87, 88, 90, 99, 105, 106, 116, 119, 120, 125  
     and mixing 43-45, 48, 51, 51, 59, 63-65, 119  
     and recycling 85, 87, 88  
     in rivers 60, 62  
     in sewage 93-94  
 oceanic zone xviii, 1, 3, 3, 37, 126, 119  
*Oikopleura* 25, 27, 99, 104, 110  
 oil (see also petroleum) 4, 89, 97, 105, 106, 107, 109  
*Olisthodiscus* 118

## The Fertile Fjord/Strickland

Olympia 94  
omnivore 39, 70  
Orcas Island 12, 65  
organochlorines 95, 96, 102, 105, 109  
*Ostrea* 114  
oxygen 3-4, 94, 96, 111, 118, 124, 125  
oyster larvae 96-97, 112, 113, 117-118  
oysters 5, 77, 114, 122, 124

Pacific Ocean 38, 50, 62-63, 89, 120, 121  
    migrations to 74, 76, 78, 79, 80  
*Pandalus* 23  
*Panope generosa* 123  
paradox of the plankton 38-39  
paralytic shellfish poisoning 5, 19, 112-118  
Parsons, Timothy 83-85  
*Pasiphaea* 23  
patchiness 35-36, 39, 40, 116, 121  
    and primary production 45, 48-49, 52,  
        56, 62, 80  
PCBs 89, 92, 102-109, 104  
pelagic zone 36, 37, 37, 69, 81, 85, 86  
*Peridinium* 112, 117  
periphyton 103  
Peru 83, 120, 125  
petroleum 4, 92, 95, 97-99, 102, 106, 107,  
    109, 110  
photic zone (see also euphotic) 37  
photosynthesis 3, 14-16, 42-43, 51, 68,  
    81-82, 96, 103  
physiology 12  
phytoflagellates (see also flagellates) 18,  
    19, 20-21, 30, 56-57, 63, 79, 80, 110, 118  
    in secondary food chain 69, 84, 86, 87,  
        88  
*Pleurobrachia* 25, 26  
pollock 70  
polychaetes 28, 70, 77  
*Polyorchis* 10, cover  
population 13, 57, 68, 69, 71, 98  
    and synchronization 75-76, 78  
Port Angeles 62, 95, 96  
Port Gardner 60, 61, 96, 117  
Port Orchard 64, 78-79  
Port Townsend 9-10  
Possession Sound 60, 61, 72  
prawns 123  
predators 38, 76-78, 85, 122  
predator-prey relationship 66, 67, 74, 84,  
    108  
productivity, primary xviii, 1, 3, 14-15, 83,  
    99, 111  
    and food supply 119, 120, 124, 125  
    and secondary food chain 86, 88  
    and zooplankton migration 78, 80  
    of inlets 58-65  
    of main basin 53-56  
*Prorocentrum* 112, 118  
*Protogonyaulax*, see *Gonyaulax*

*Protothaca* 114  
protozoans 21-22, 24, 66, 70, 79, 112  
    in secondary food chain 84, 86-88  
    life cycles and coupling 68, 75-76  
*Pseudocalanus* 22, 71, 75, 110  
PSP. see paralytic shellfish poisoning  
pteropods 25, 27  
pulp and paper 92, 95-97, 101, 117, 125  
pumps, sampling 9  
Puyallup River 42-43, 46, 47, 49, 60  
pycnocline 45, 87  
*Pyramimonas* 19

Quartermaster Harbor 64

radionuclides 14, 15, 101, 105  
radiolarians 21  
recycling 34-35, 85, 87  
red feed 70  
red tides (see also paralytic shellfish poi-  
    soning) 5, 6, 20, 21, 24, 62, 65, 84, 101,  
    112-118, 120, 124  
Renton 60, 94, 95  
reproduction 80, 81, 122, 126  
    phytoplankton 17-18  
    zooplankton 21-27, 75, 77, 84  
residence time 51-52, 58, 59-65  
respiration 81-82, 84  
Richards, Francis 13  
rivers, see runoff  
rockfishes 70  
Rosario Strait 46  
rotifers 23, 24  
r-selected 68, 76-77, 85  
runoff 94, 97, 99, 116  
    and primary production 42-43, 45, 46,  
        47, 48, 51-53, 54-55, 58-65  
Ryther, John 83-84

Saanich Inlet 72, 76, 85, 109  
sablefish 70, 74  
*Sagitta* 25, 26  
salinity 42-43, 48, 60-62, 61  
salmon 30, 38, 109, 110, 121, 123, 124, 126  
    in pelagic food chain 66, 67, 70-71, 83  
    juvenile 67, 80, 85  
    migration 74, 76-78, 79  
sampling 6-9, 53, 56  
sand lance 70, 79, 80  
San Francisco Bay 37, 51  
San Juan Islands 37, 59, 62, 64, 78, 114  
San Juan Channel 65, 118  
Saratoga Passage 60, 61, 114  
*Saxidomus* 114  
saxitoxin 115  
sculpins 70  
Seahurst Park 95  
sea lions 89  
seals 66, 89, 102, 104, 108, 109, 121

Seattle 45, 93, 94, 103, 126  
sediments (see also suspended matter) 4, 101-103, 106-108, 124  
sediment traps 86  
Sequim Bay 64, 116  
sewage 60, 62, 92, 93-97, 100-102, 116, 125  
shark 70  
Shelton 95  
Shilshole Bay 45  
shrimp 7, 23, 70, 104, 108, 121  
*Siliqua patula* 122  
sills 37, 44, 46, 47-53, 58-60, 65, 94  
Sinclair Inlet 64, 94  
sinking 32-34, 51, 87  
size 30-33, 39-40, 66, 67-68  
and synchronization 72, 74, 78, 84  
Skagit River 46, 47, 60, 61, 105  
Skeletonema 19, 56-57, 109  
smelt 70-71, 80  
Smith Island 46  
Snohomish River 46, 47, 60, 61  
solar energy 46, 47, 51, 51, 54-55, 64, 116, 125  
in food chain 41, 68, 74, 81, 82, 88  
solstice, summer 53  
sonic scattering, see echo scattering  
Southern Sound 38, 78, 95, 102, 108  
primary productivity 42-43, 46, 47, 59, 63-65  
red tides 113, 117-118  
spat 122, 124  
species composition 17, 56-57, 95, 99, 101  
spectrophotometer 13  
spring bloom, see blooms  
*Spirulina* 125, 126  
stability (see also stratification) 44-45, 48, 54-55, 59, 79, 86  
standing stock 13-14, 71, 109  
phytoplankton 51, 51, 53, 54-55, 59, 60-61, 61, 94  
Steele, John 83  
Steinbeck, John 1, 67  
sticklebacks 70  
Stillaguamish River 47  
Strait of Georgia 38, 78, 94, 100  
primary productivity 59, 61, 62, 65  
red tides 113, 118  
zooplankton 73, 77, 121  
Strait of Juan de Fuca 12, 38, 116  
migrations to 73, 76, 77, 79  
primary productivity 42-43, 46, 48, 50, 58, 59, 61-64  
stratification (see also stability) 94, 116, 119, 125  
and primary productivity 42-45, 46, 47, 48, 51, 59-60, 61, 63-65  
and secondary food chain 80, 84, 86, 88  
stripes (see also fronts) 48, 49, 56, 60, 61, 62  
submersible 9, 72  
sunlight, see solar energy  
suspended matter 49, 60, 61, 62, 86, 103, 105, 107, 122  
suspension culture 124  
suspension feeding 22, 69, 105, 109  
swimming 7, 18-20, 21-29, 33-34, 66, 72, 78, 116  
swordfish 108  
*Synchaeta* 23  
synchronization 69, 74-81, 79  
synergism 91  
Tacoma 93, 99, 100, 114, 117  
*Thalassiosira* 56-57, 109  
*Thalassiosira pseudonana* 30  
Thompson, J. Vaughn 6, 12  
Thompson, Thomas G. 11, 12-13  
tides 77, 124  
and currents 42-44, 42-43  
and primary productivity 49, 51-53, 54-55, 57, 60, 63, 65  
red, see red tides  
tin 106  
Tintinnids 22, 24  
*Tintinnopsis* 24  
tolerance 91  
Totten Inlet 64  
trawls 7, 7, 8  
trophic energy 41, 69, 74, 75, 80, 81, 84, 85-87  
trophic levels 39, 74, 75, 82, 83, 104, 107, 108  
trout 123  
tuna 108  
turbidity 60, 61, 62  
turbulence 73, 78  
University of Washington 10-12, 13, 117  
upwelling xviii, 1, 83, 120  
Vancouver 62, 65, 94  
Vancouver, Captain 112  
Vashon Island 42, 64, 78, 95, 114  
*Velella* 73  
*Venerupis* 114  
vertebrates 27, 29, 84  
Washington Department of Ecology 95  
Washington Department of Fisheries 122  
weather 41-42, 116, 120  
West Point 94, 100, 104  
whales 1, 23, 30, 31, 40, 66, 67, 70, 72, 74, 89, 108, 121  
Whidbey basin 46, 58, 60, 61, 63, 73, 78, 103  
Whidbey Island 5, 60, 61, 114  
winds 44, 51, 52, 53, 60, 62, 116  
zinc 92, 98, 101, 104, 105

Other Books in this Series

*The Water Link: A History of Puget Sound as a Resource*  
Daniel Jack Chasan

*Governing Puget Sound*  
Robert L. Bish

*Marine Birds and Mammals of Puget Sound*  
Tony Angell and Kenneth C. Balcomb III

*The Coast of Puget Sound: Its Processes and Development*  
John Downing