CHAPTER SIX

The Fish Factory—Zooplankton

> . . . All things are one thing and that one thing is all things—plankton, a shimmering phosphorescence on the sea, and the spinning planets and an expanding universe—all bound together by the elastic string of time.
>
> John Steinbeck, *The Log from the Sea of Cortez*

The term "food chain" has a mechanical ring to it, evoking images of links and sprockets, of steel and grease. Zooplankters are a vital link in this biological machinery, transforming raw vegetable matter into fish food. Yet the zooplankton community is also something of a missing link in our knowledge of Puget Sound, for less is known about it than about either the phytoplankton or the fishes. Someday it should be possible to trace the flow of trophic energy through the links of Puget Sound's pelagic food chain, but for now a general outline must suffice.

The starting point is the importance of zooplankton size in determining predator-prey relationships. Put simply, animals are larger than the organisms they eat. Predictably, the larger an animal, the larger its food. Each zooplankter actually feeds only within a characteristic range of food sizes, because it cannot capture items which are either too large or too small for its feeding apparatus to handle. The same is true of nekton. This relationship is depicted schematically in Figure 6.1.

Many idiosyncrasies are overlooked in this simplified picture. An animal may select only certain prey from the wide selection available in the appropriate size range, may discriminate between meat and vegetable food, or may occasionally violate the rule of size altogether. Furthermore, predators as disparate in size as juvenile salmon and adult baleen whales may compete for the same prey, in this case euphausiids. Nevertheless, the trend of size dependence is consistent enough to furnish valuable insights into Puget Sound's food chain.

The size of an organism—be it animal, plant, or bacterium—is also directly related to metabolism, its generation of energy from stored carbon. The metabolic rate is the fraction of body mass burned and replaced per unit of time. Again discounting slight species differences, a larger organism generally has a slower metabolism than a small one. An adult salmon, for example, eats, respires, and egests a mass of food equal to its own weight only over a span of days or weeks, while a small copepod may consume as much, proportionately, in as little as a day.

The metabolic rate in turn is related to the life span or generation time of a species. Turnover of biomass is paralleled by turnover of individuals; a slower rate of food utilization is accompanied by slower maturation and aging. Larger organisms consume less food to support each

kilogram of biomass, reproduce later in life, and live longer than small organisms. This trend is portrayed schematically in Figure 6.2, which strongly resembles the previously illustrated dependence of food size on animal size.

Based on these relationships of size to diet and to life schedule, a simple mechanical analog of Puget Sound's pelagic food chain emerges. It resembles a set of sprockets for speed reduction and energy transmission, connected by chains, such as those found on a bicycle. The sprockets represent organisms, the chains represent trophic linkages, and the rotations of the machinery represent the life cycles of the organisms.

The smallest sprocket, representing the phytoplankton, is driven by solar energy through the photochemical conversion process of photosynthesis. The sun's energy arrives in daily increments, and the generation times of phytoplankters, ranging from a few hours to a few days, are tuned to this rhythm. These time periods represent the approximate rate of rotation of the first sprocket. Each successive sprocket is larger, as the body sizes of the animals it represents are larger, and the rates of rotation are correspondingly slower. Zooplankton generation times range from days to months; fish life cycles from months to a few years; and those of birds and mammals upwards to many years.

The analogy of sprockets and chains also reflects how the strategies animals must adopt to deal with prey, predators, and the vagaries of the environment are related to their life cycles. Smaller zooplankters have tremendous reproductive powers, but also have tremendous appetites. Larger zooplankters, which demand proportionately less food and are thus better able to withstand unfavorable conditions, must also take care to preserve their numbers, since their powers of repopulation are more limited. All animals must adapt to the seasonal feasts and famines of Puget Sound waters; but the strategy of a creature such as a euphausiid, which can live to see all the seasons at least once, must be very different from that of a protozoan, which may pass through several generations over the course of a single spring bloom.

A spectrum of life strategies—from steady persistence to rapid fluctuation of population—characterizes organisms in all types of ecosystems. Organisms that maintain relatively constant populations in stable environments and that have consistent, predictable life cycles are called "K-selected" (K is the symbol for the population carrying capacity of an ecosystem). In contrast, "r-selected" organisms have evolved the potential for a high population growth rate (abbreviated as r), with less attention to constancy of population numbers. The latter organisms are characterized as opportunists that can multiply rapidly to fill an ecological void; they may appear on short notice when a system becomes perturbed or unbalanced. Smaller organisms tend to be more r-

selected, and larger more K-selected, although a typical species combines both strategies to its own best advantage.

The relationships of size and diet to life cycle that combine to produce our mechanical analogy also reflect two principal properties of any machine. The predators and prey of the zooplankton assemble in a characteristic way, which at any instant of time forms the structure of the food chain. The ways in which these parts interact, however, change with time as populations of various species wax and wane. Like any machine with moving parts, pelagic ecosystems must therefore be timed and tuned if they are to achieve maximum performance—there must be synchronization as well as structure, a dynamic as well as a static aspect. This synchrony is represented by the meshing life cycles of predator and prey.

Below, we will examine in more detail the zooplankters that dominate the pelagic food chain of Puget Sound, and the ways in which their life cycles interact to transmit trophic energy, not just from organism to organism, but also through space and time. Just as there is a frictional loss of energy along the drive train of a machine, there is a loss of energy along the links of the food chain. In contrast to the increasing sizes of higher animals (and of the "sprockets" used to represent them), the amount of trophic energy transmitted decreases at each successive link of the food chain, so a large output of prey is required to sustain a small production of predators. We will thus conclude by examining Puget Sound with respect to a final fundamental property of machines, the efficiency with which matter and energy are transformed and transmitted, and the ways in which efficiency is affected by changes in structure and synchronization.

Food Chain Structure

The zooplankton community is a multitude of rare and common species, temporary and permanent inhabitants, and life cycle stages from egg to corpse. Its full complexity is beyond our ability to contemplate, much less to describe, and our studies of it have the quality of random peeks through a keyhole into a crowded stadium. Animals select from a broad smorgasbord of possible foods. For simplicity we must focus on the rough structural backbone, which is built around the most common animals in Puget Sound's pelagic zone and is believed to be the principal pathway of trophic energy flow up the food chain.

Feeding on the diatoms, which dominate spring blooms, are the dominant zooplankters—the suspension-feeding crustaceans. Copepods form the largest segment of zooplankton standing stock in the main basin of Puget Sound at all times of the year. Numerically dominant are small copepods such as *Acartia*, which eats phytoflagellates and small diatoms. Dominating the biomass is the larger copepod genus

Calanus, in the main basin thought to be mostly of the species *C. pacificus*. *Calanus* mainly eats phytoplankton of intermediate size, although it sometimes captures a stray larva or protozoan.

Secondary to the copepods in importance are micronekton organisms, particularly the euphausiids, amphipods, and mysids. Euphausiids are also suspension feeders, in Puget Sound consuming mostly the largest chains of diatoms and some microzooplankton. Mysids are believed to be omnivorous, while amphipods are carnivores feeding on microzooplankton.

Although many carnivorous zooplankters reside at the third trophic level—including predatory copepods, micronekton, and gelatinous zooplankters such as chaetognaths, ctenophores, and medusae—the carnivore community appears to be dominated by the nekton. Many Puget Sound fishes—from nearshore sculpins and rockfishes to ocean-going basking sharks—derive at least part of their nutrition from zooplankton; so do some birds and the smaller baleen whales that occasionally visit. The data available indicate that the principal predators on zooplankton are pelagic fishes from roughly 50 to 200 millimeters in length. This size class includes juvenile and adult herring, smelt, sticklebacks, and sand lances, and mostly juveniles of such larger animals as salmon, cod, hake, pollock, lingcod, sablefish (black cod), and dogfish. The size class also includes juvenile and adult shrimps.

On a finer level of detail, animals select progressively larger prey as they age and increase in size. Copepod nauplii, for example, begin feeding on the smallest phytoplankton, graduating later to larger diatoms. Furthermore, most planktivorous fishes feed as larvae and juveniles, and to some extent as adults, on small epibenthic organisms that live on the sediment surface near shore. This group includes harpacticoid copepods, mysids, gammarid amphipods, shrimps, cumaceans, and polychaete worms, which are of the same size classes as the zooplankton. These prey, in turn, have consumed benthic algae, bacteria, and some dead matter amongst the silt and mud. Thus, an early root of the food chain, and an especially important one near shore and in the spring, is detritus-based rather than phytoplankton-based.

As these fishes mature they take an increasing proportion of plankton. Small juvenile fish such as herring, smelt, and pink and chum salmon eat principally copepods and crustacean larvae. Large juveniles, including coho and chinook salmon, eat both micronekton and the larvae of the smaller fishes. Swarms of micronekton, visible at the surface and called "red feed," are cues to fishermen seeking to net adult chum, pink, and sockeye salmon, which are mostly planktivorous, in contrast to the adult piscivorous (fish-eating) coho and chinook salmon, which pursue baitfishes such as herring and smelt and are more commonly caught on hook-and-line.

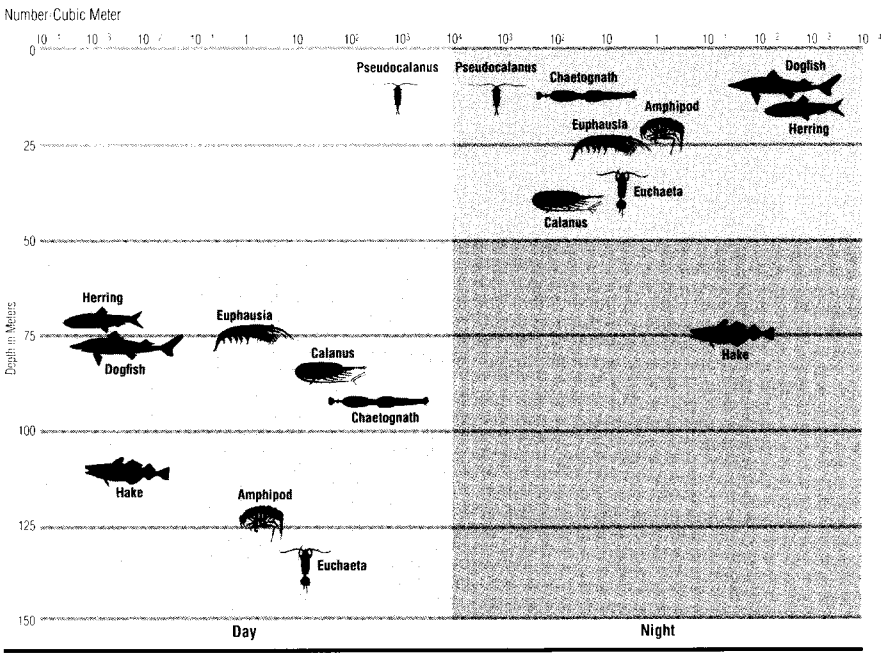

Figure 6.3 Representative standing stocks of pelagic animals (on a logarithmic scale) at their preferred day and night depths. Most animals (the small copepod *Pseudocalanus* is an exception) move to deeper water during the day. Carnivores generally are deeper and fewer, although distributions and abundances vary with time, location, and species.

This complex web can be distilled down to a simple food chain based primarily on size. The dominant diatoms of the phytoplankton feed the dominant crustacean zooplankton—copepods, euphausiids, and larvae—and these in turn feed the young and, to some extent, the adults of commercially important nekton such as herring, smelt, cod, and salmon, as well as many other non-commercial species. Of all Puget Sound's pelagic organisms, these appear to stand out and comprise what may be termed the primary food chain.

Spatial Structure

An essential detail of food chain structure in Puget Sound is the arrangement of organisms in space. Plants and animals are not distributed homogeneously in the Sound in either the vertical or horizontal dimensions, and for an animal to survive, its habitat must overlap at least partially with that of its food. Zooplankton distributions differ significantly from those of the phytoplankton, however, and seem to be determined by their physical dimensions and those of the environment.

Dominating the vertical distribution of zooplankton in the Sound is the phenomenon of vertical migration, on both daily and seasonal cycles (Figure 6.3). Migratory habits of zooplankters are correlated with

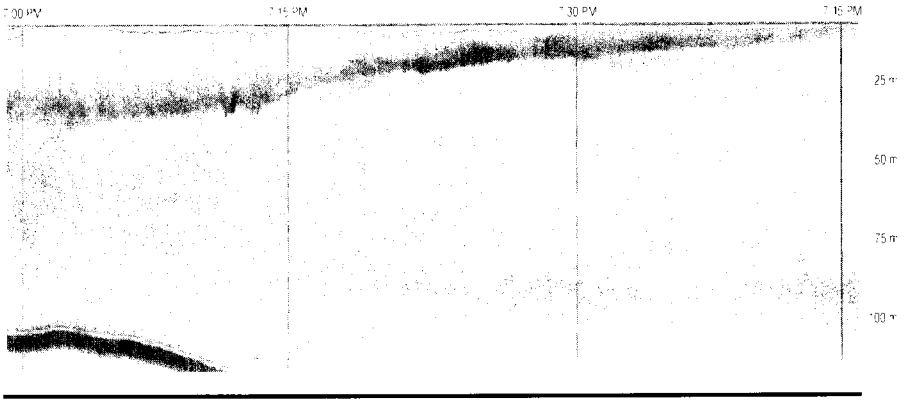

Figure 6.4 High-frequency scattering layer detected in Possession Sound near sunset in the spring. Surfaceward migration occurs over a few minutes; return to depth occurs rapidly near sunrise. (Courtesy T. S. English)

their sizes and swimming abilities. Although phytoplankton is most abundant at or near the water surface, among zooplankton the same is true only of the weakest swimmers, the microzooplankton and larvae. The rest of the zooplankton community spends much of its time below the surface—deeper during the day than at night, and deeper in the winter than in the summer. (Seasonal cycles are considered below under "Food Chain Synchronization.") The herbivorous animals feed only during their intervals near the surface.

This pattern is typical of most species of micronekton, and of roughly half of the species of mesozooplankton. Larger species, and larger (older) individuals of a given species are more likely to be migratory. Vertical migration patterns are difficult to detect in microzooplankton, small copepods (such as *Acartia*), and the juvenile stages of larger copepods (such as *Calanus*) that migrate as adults. Larger and older migrators make excursions that are greater in amplitude and deeper in the water. Larvae that first orient toward the surface foray progressively deeper and for longer periods of time as they mature. The result is a segregation of animals, according to age and size, with depth.

Migratory zooplankters congregate in narrow, discrete depth strata called sonic scattering layers that are detectable with high-frequency sonar. The layers are observed near the surface at night, and at depths approaching 200 meters during the day (Figure 6.4). Seasonal migrations can also be observed. Net tows within these scattering layers capture euphausiids, amphipods, and large copepods, animals of just the size detectable by 105 kHz sonar. Whales feeding on krill (euphausiids) use sonar of a similar frequency to locate their prey. Although sonar can sense targets as small as individual fishes, equipment to sense the small-scale distributions of zooplankters within a scattering layer is still experimental. Observed from a submersible in Saanich Inlet, how-

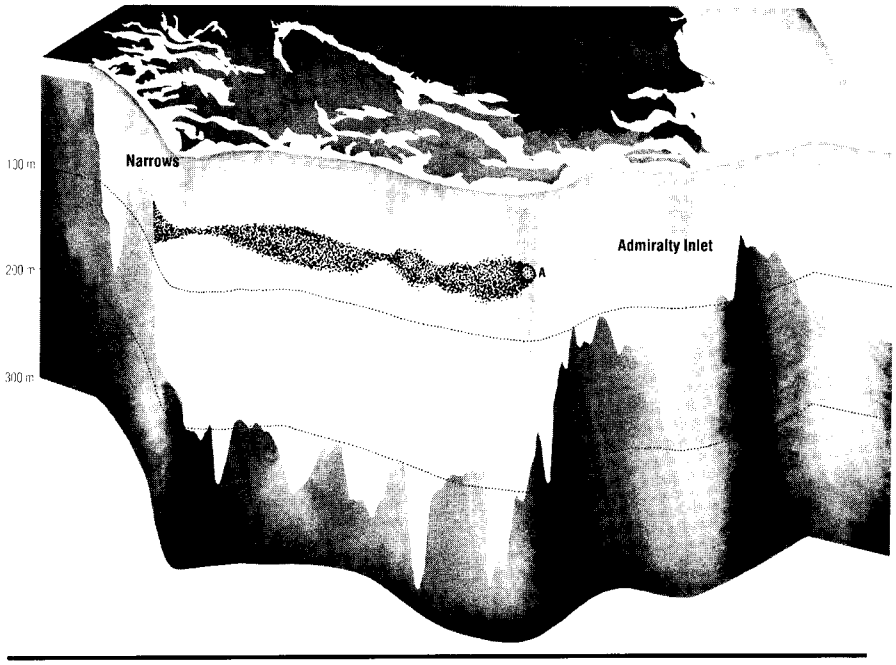

Figure 6.5 A high-frequency scattering layer is found throughout the deep waters of Puget Sound during the summer, and is absent only from shallow turbulent areas such as The Narrows and Admiralty Inlet. The layer disappears from open waters during winter (probably also due to turbulence), remaining only in protected deep inlets. "A" indicates where the scattering layer passes out of the main basin into the Whidbey basin. (After Cooney, 1971)

ever, copepods appear to be aggregated in very dense strata just a few meters thick.

Sonic scattering also yields information on horizontal zooplankton distributions. Scattering and the associated zooplankters are characteristic of deeper, quieter waters. Scattering layers are not observed at shallow locations of high turbulence, such as The Narrows (Figure 6.5). Large, migratory zooplankters may avoid these places either because of the turbulence, or because the water is too shallow to permit migration. Near shore smaller nonmigratory mesozooplankton and microzooplankton assume a more important role, due to the exclusion of the larger migrators. An extreme example is the large copepod *Neocalanus*, which spends the winter at depths exceeding 300 meters in the Strait of Georgia, cannot complete its life cycle in shallower Puget Sound, and so is found here only occasionally when it accidentally washes in.

There are more subtle differences, too, in the zooplankton fauna of various areas. More oceanic species such as the large copepods *Metridia* and *Calanus marshallae* are found in the deeper and more stratified waters of Dabob Bay and the Strait of Juan de Fuca. Certain truly

offshore species are carried into the western Strait of Juan de Fuca during oceanic intrusions, the most visible of which is the floating oceanic jellyfish *Velella,* which bears a triangular sail to carry it before the wind, and which appeared in unusual quantities along the Washington coast during the spring and summer of 1981 and in the Strait of Juan de Fuca in April 1983.

The spatial arrangement of planktivorous fishes and their predators in Puget Sound closely parallels that of the zooplankton. Many fishes form tight layers detectable by sonic scattering. There is also a correspondence between fish size, depth, and distance from shore. Fish usually spawn close to—or even landward of—the edges of the Sound. Fish larvae and juveniles congregate near shore and close to the water surface. As animals age, grow, and seek larger prey, they are also found farther offshore and deeper. Herring, dogfish, sablefish, and salmon undergo daily and seasonal vertical migrations, which tend to be proportional in amplitude to age and size, and which appear to be synchronized with those of their planktonic prey. Farthest from shore and migrating most extensively are the largest animals, including such relatively rare planktivores as the gray whale.

Emerging from these data is a spatial gradient in the sizes of Puget Sound pelagic animals, in which larger species and older individuals are found farther from the shore and the surface. Thus the links and sprockets of the food chain extend from the land and the surface of Puget Sound toward the bottom and the Pacific, because energy travels bottomward and seaward from its source, the sunlight striking the Sound. It is transported by three mechanisms. The first is the passive transport of plankton and detritus by sinking to the bottom, and by currents out to sea. The second is a "bucket brigade" effect, whereby each organism is eaten by a larger one whose habitat extends deeper and farther from shore. The bucket brigade is reinforced by the third mechanism, active migrations of animals into deeper and more offshore waters as they mature, carrying inshore trophic energy with them as they go. While it thus appears that Puget Sound is a net source of energy for more offshore waters, there has been little research on the subject. Furthermore, the amount of energy transported and the times at which it is transported cannot be determined without considering the element of synchronization.

Food Chain Synchronization

The transmission of trophic energy from lower to higher organisms depends on the coupling between trophic levels. To be coupled, an animal and its food must be in the same place at the same time. The complexities of life cycles, seasonal migrations, and population variability, however, can separate predator and prey in space and time. Because

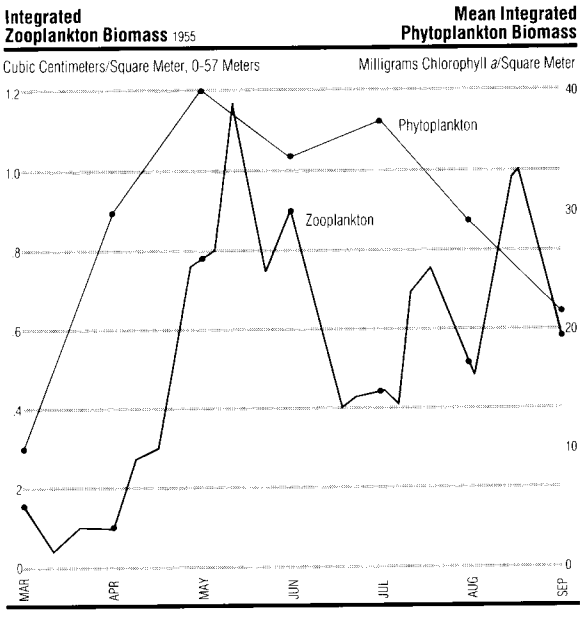

Figure 6.6 Monthly average phytoplankton abundance (Figure 5.7) compared to 1955 weekly zooplankton volume in the upper 57 meters of the main basin during daytime. The seasonal pattern must be interpreted with caution, because protozoa, micronekton, and most vertical migrators probably escaped the net (mesh size 239 micrometers), and volume could vary fourfold in 24 hours. The most abundant animals were *Pseudocalanus*, *Corycaeus*, *Calanus*, and amphipods. (After Hebard, 1956)

animal and plant sprockets are so dynamic, the food chain may frequently become uncoupled. When it does, no trophic energy is transmitted; a link is missing from the biological machinery. Food chain synchronization therefore involves the orchestration of life cycles and migrations to arrange for the maximum extent of coupling.

Life Cycles

When coupled, biomass and trophic energy are transferred from the eaten to the eater. The biomass of the organism being eaten declines (or increases at a slower rate), and that of the animal doing the eating increases. The result should resemble that depicted in Figure 6.6, which presents some of the only seasonal zooplankton biomass data available from the main basin. Peaks in zooplankton abundance appear to just follow peaks in phytoplankton, as would be expected from a coupled transfer of biomass.

This particular pretty picture, however, is likely to be almost completely fortuitous. The composite of mixed species of plants and animals hides both methodological problems and significant differences in feeding and reproductive behaviors of different zooplankters. Nevertheless, the data of Figure 6.6 suggest the adaptation of zooplankton life cycles to the long-term probabilities of food supply. These adaptations involve the timing and the frequency of reproduction.

The simplistic notion of correlated peaks in food supply and animal abundance is most easily observed in the zooplankters not represented in Figure 6.6, those with the shortest and simplest life cycles, the protozoans. An increase in food supply, which will stimulate a rise in biomass in any animal, will also soon boost the population numbers

of a short-lived animal such as a protozoan. Likewise, a decline in food supply will trigger a rapid decline in population. Microzooplankton population changes can be more easily observed (as they have been in such places as Saanich Inlet and the Strait of Juan de Fuca) because they are not confounded by stages of immaturity, migratory patterns, or changes in food preference. These quick population adjustments indicate tight coupling between two trophic levels.

Uncoupling is best illustrated using salmon, at the opposite end of the pelagic size spectrum from the protozoans. When a juvenile salmon eats its zooplankton prey, its increased biomass will not be converted into new offspring until spawning, two to five years later (if the animal lives that long). During that time the fish may migrate as far as the Aleutian Islands and back, and consume other prey from benthic worms to adult herring. On this journey, the link between salmon and Puget Sound zooplankton is uncoupled, and another is forged in the open Pacific. This new link may also, at any stage, become uncoupled if, say, the salmon migrates to an unproductive area barren of prey. The difference between the salmon and the protozoan, however, is that being relatively large and mobile, the salmon can store food, and can migrate when food is scarce. The fish adjusts its behavior, more than its numbers. Populations of such animals do not fluctuate as rapidly as those of the microzooplankton; the turning of the food chain gears is smoother and steadier at this upper end of the machine.

In keeping with their sizes, microzooplankters are more r-selected, and salmon are more K-selected. The life cycles of larger animals are longer, more complex, and more rigid than those of the microzooplankton. Although salmon can maintain steady populations through temporary food shortages, the inflexibility of their life cycle prevents them from repopulating rapidly after a catastrophe, or from producing young whenever food conditions are favorable, as protozoans can. To be successful over evolutionary time, animals of all sizes must have adapted their life cycles to conform to those of their prey in some optimal fashion. That is, they must have learned to play the long-term odds on when and where to find proper food for each of their stages of maturity. At the same time, the animals must adapt to minimize their own losses to competition and predation, and their prey must do the same.

The copepods and euphausiids, with sizes and life spans intermediate between those of the protozoans and the salmon, dominate the Puget Sound zooplankton. They are adapted to the seasonal rhythms of the dominant phytoplankters. Although the smallest copepods may reproduce continuously all year, there is a general maximization of zooplankton reproductive effort during the spring bloom season. Most zooplankters reach sexual maturity and release eggs when food is most abundant, and continue feeding and reproducing throughout the sum-

mer as long as the food supply lasts. During winter when food is scarce, most zooplankters restrict their activities, conserving energy while they live off stored food, and many enter a physiological resting state (diapause) analogous to hibernation.

Within these generalizations, there is some variability. The large copepod *Neocalanus*, for example, releases its eggs deep in the Strait of Georgia in February of each year regardless of the state of phytoplankton growth. Its nauplii float to the surface, and the young of the year return to the depths by July. Puget Sound's medium-sized *C. pacificus*, in contrast, must swim to the surface and feed on the first spring blooms in order to mature and produce eggs, and continues to reproduce nearer the surface throughout the summer as food permits. *Neocalanus* produces just one generation per year; *C. pacificus*, several. *Euphausia*, while producing just one generation per year (possibly two), does not occur simply as one life stage at a time like *Neocalanus*, but rather as a mixture of stages. During the growing season euphausiids are more or less constantly maturing, producing young, and dying, but there is a dramatic increase in egg production in April and May with the first spring blooms.

Thus the mesozooplankton and the micronekton have adopted strategies of both the r-selected microzooplankton and the K-selected fishes. Their life cycles are programmed to concentrate reproductive effort when it is most likely to succeed, but they have also retained the flexibility to reproduce through most of the growing season. Their life schedules also include a rest period to maintain populations during the winter. A diversity of strategies has evolved to permit different species to coexist.

The meroplankton larvae exhibit a similar synchronization. Planktivorous larval and juvenile fishes inundate the surface of Puget Sound from roughly March, when larval herring begin feeding, through August, when most young salmon have left the Strait of Juan de Fuca. The reproductive timetables of benthic animals are not as well studied, and appear to be adapted to several factors in addition to the abundance of pelagic food, competitors, and predators. Some animals seek an optimal temperature: the Pacific Oyster, *Crassostrea gigas*, waits to spawn until the surface water reaches 21°C (70°F). Others seem to seek dispersal of their larvae: the polychaete worm *Nereis vexillosa* swims to the surface and releases its gametes in a brilliantly luminescent mating ritual at high tide on summer nights near the full moon, when tidal currents will be strongest. The limited and scattered data indicate, however, that the appearances of all planktonic larvae are strongly influenced by food availability, and allow for some adaptability to variable conditions.

Migrations

An additional dimension is added to the problem of synchronization by the bottomward and seaward movement of animals as they grow. Predators must program into their life cycles the location of each stage of maturity, as well as its timing, to couple itself to its prospective food. Some migrations are also dictated by the hydrographic conditions of Puget Sound.

During the fall and winter, for example, zooplankton populations decline both in surface waters and in the deep waters of certain poorly sheltered areas. The prominent sonic scattering layer disappears from the main basin and, slightly later, from Elliott Bay. There may be a population decline due to predation and hunger, but this disappearance seems more strongly linked to increased winter turbulence and flushing, like that found year round at The Narrows. Scattering layers persist through the winter in more sheltered locations such as Carr Inlet and the Whidbey basin. This raises the possibility that larger zooplankters undergo horizontal seasonal migrations, overwintering in the depths of protected inlets to seek shelter from turbulence and seaward currents, and thereby to conserve energy and population. This needn't tax their limited swimming powers; the landward currents in subsurface waters help carry them to shelter if they don't surface and reverse their progress. In the spring, likewise, larvae floating to the surface get a free ride back out into the main basin aboard seaward currents.

Animals overwintering in inlets are also close to waters that warm and bloom earlier in the season, making a more favorable environment for larval growth. (There may be less of an advantage in the Whidbey basin, with its heavy springtime runoff and turbidity, than in the southern Sound.) Assuming that production in inlets begins to decline by June, when production in the main basin is near its seasonal peak, riding surface currents seaward at that time would not only increase the foraging area, but would also deliver larvae to more productive waters and thus increase their rates of growth and survival. Such predictable behavior might also make them more vulnerable to predators, however.

The seasonal migrations of planktivorous fishes and their predators are better documented and parallel the apparent movements of the zooplankton. From the variability in life span and migratory locations within and between species of pelagic fishes, the trend emerges of seaward migration from the spring through the summer. Herring, for instance, begin their lives in January and February as eggs attached to eelgrass and other objects along the shores of protected inlets in the southern Sound and Port Orchard, around Vashon, Marrowstone, and the San Juan Islands, and along the southern Strait of Georgia. They spend their first summer close to the shore, then move farther offshore

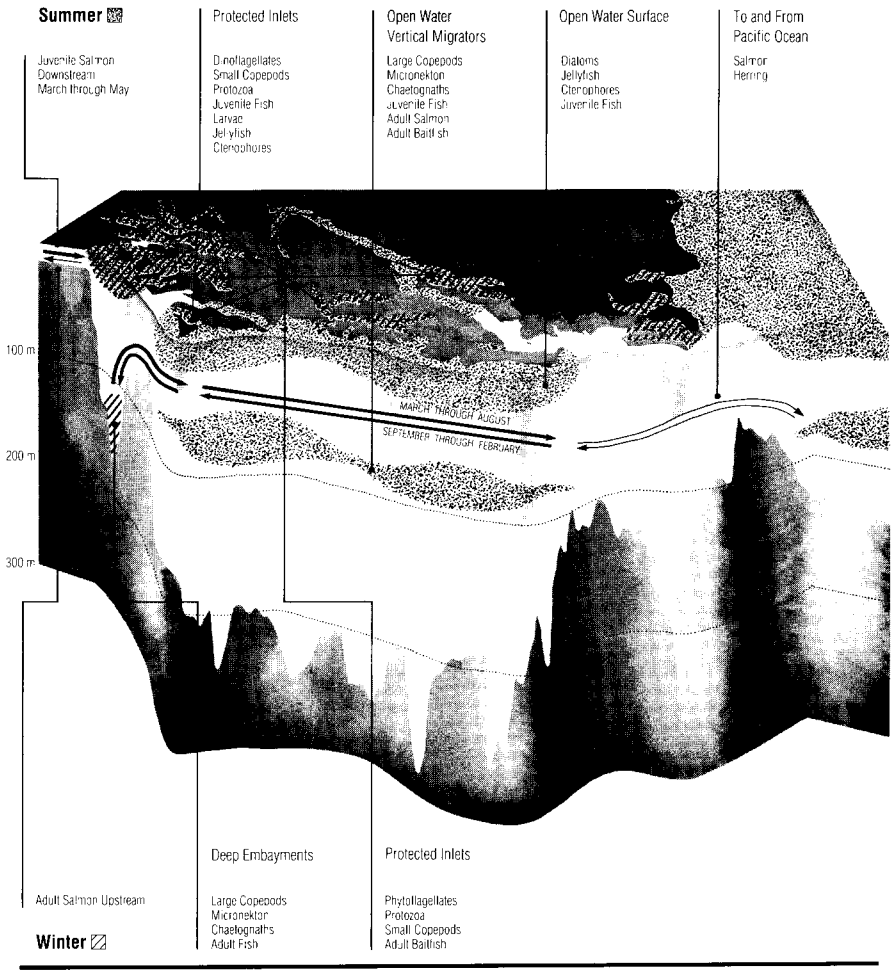

Figure 6.7 Seasonal life cycles and migrations of dominant pelagic organisms of inlets and the main basin. This caricature depicts idealized seasonal contrasts and overlooks minor organisms and variability between years. Protected inlets are sites of earlier phytoplankton blooms and are refuges for animals in the winter and spring. As deeper open waters stabilize and bloom in the late spring and summer, animals follow. The migrations reverse in the fall, completing the cycle. (After Dexter et al., 1981)

and increase in size as the season progresses. After migrating as far as the open Pacific, they return to spawn each winter and early spring near the beaches where they were hatched.

Smaller planktivorous fishes, such as the sand lance, remain closer to shore. The larger members of the cod family, while not known to migrate to the Pacific, are seen to congregate in the Whidbey basin and Case and Carr Inlets during the winter. Members of the salmon family emerge from freshwater streams as juveniles between April and June, and as they increase in size feed progressively farther from shore and

deeper in the water, exiting the Strait of Juan de Fuca by late July of the summer in which they enter salt water. Resident populations of coho and chinook salmon spend their entire lives within the Sound. They are suspected of originating mostly from streams farthest from the Pacific and from the populations of juveniles which are last to reach salt water.

The life cycles and migrations of zooplankton and nekton in Puget Sound can be combined with the knowledge of phytoplankton to produce a proposed grand scheme of pelagic synchronization, depicted in Figure 6.7. It shows a coordination between the seasonal cycles of production, reproduction, and migration at all levels of the food chain. Phytoplankton production begins to increase in shallow and protected waters in the early spring, is in full swing throughout the Sound in the summer, declines in the autumn, and is virtually dormant in the winter. Phytoflagellates are present all year, but may be most important in the winter and the earliest stages of spring when other types of phytoplankton are sparse. The microzooplankton and small copepods that consume them reproduce all year near the surface and the shore. Large diatoms dominate the spring and summer blooms, and dinoflagellates perhaps make regular appearances in the late summer and fall. Diatom feeders, the large copepods, and later the euphausiids, rise from deep water to begin feeding and release their larvae in March and April. This is also the time when the zooplanktivorous larvae of herring, smelt, sand lance, codfishes, and salmon begin to arrive. Both zooplankters and their predators, like the phytoplankton blooms, increase in abundance and appear to move from inlets to the open Sound through May and June. These animals, in addition, begin to take up residence deeper in the water by day, migrating to the surface by night. By the fall, fishes that migrate to the Pacific will have already left.

The entire cycle begins to reverse itself in the fall. Phytoplankton production drops, although it can be temporarily stimulated in inlets by the renewed stirring of stratified waters, and continues longest in the shallows. Congregations of zooplankters disperse in the main basin and remain only in protected waters. Fewer larvae are around, and there is a general trend among the larger zooplankters to remain deep in the water rather than visiting the surface. Salmon return from the sea and begin heading upstream; herring and codfishes also withdraw to more sheltered waters. Herring deposit their eggs on protected beaches in January, and the cycle begins again.

This synchronized cycle is, of course, highly idealized. Many organisms do not conform exactly to it, and many other details have been left out or are still unknown. We began, however, wanting to know how trophic energy is transmitted, and we have seen that the important element is the degree of food chain coupling created by structure and syn-

chronization in the pelagic zone. When the synchrony outlined above works according to plan the coupling is tight, and trophic energy is transferred efficiently.

The life cycle programming of pelagic animals cannot, however, always accommodate the weather-related temporal patchiness that characterizes primary production. There is a high degree of randomness to the timing and placement of phytoplankton blooms, which seldom coincide with their long-term average. What happens when animals are waiting and no bloom occurs? Or when a bloom happens prematurely, with no animals around to exploit it? Zooplankton and fishes with fortunes keyed to a semi-strict calendar can depend on the weather of a given year no more than humans can when planning their vacations.

The result of the unpredictability of nature is frequent and inevitable uncoupling of the food chain. When this occurs, links are missing from the works, and energy may be lost from the pelagic zone. Uncoupling affects another mechanical property of the pelagic food chain—its efficiency. Like the gas mileage of a car, the efficiency of an ecosystem is the yield of animals generated from the energy consumed. The tighter the coupling, the higher the efficiency; energy lost due to uncoupling reduces the efficiency.

Efficiency and the Secondary Food Chain

The efficiency of a food chain is the fraction of the original sunlight remaining when the raw materials of carbon dioxide and water are converted to their final animal product. Whatever the degree of coupling, significant energy losses occur at each stage of transformation. Calculated values of food chain efficiency, though imprecise, never exceed a mere fraction of a percent. The greatest loss occurs before the biological processes are triggered, in the transit from the sun to the phytoplankton. Both incoming solar energy, and the trophic energy it becomes when stored in biomass, can be measured in kilocalories, the same unit of energy used to measure dietary requirements. Of the roughly twenty kilocalories of sunlight entering each square meter of the atmosphere during each minute of daylight, at most one-third reaches Puget Sound. Figure 6.8 shows that less than one percent of the energy reaching the upper atmosphere is actually absorbed by phytoplankton to serve as the starting point for the pelagic food chain.

Once metabolic processes begin, there is a different set of losses: plants and animals use some of their biomass as fuel simply to keep their metabolic furnaces burning, and expend additional to energy for locomotion, reproduction, etc. Of the light energy absorbed by phytoplankton, less than two percent is stored more than temporarily in plant matter. The rest is expended to power the photosynthetic appara-

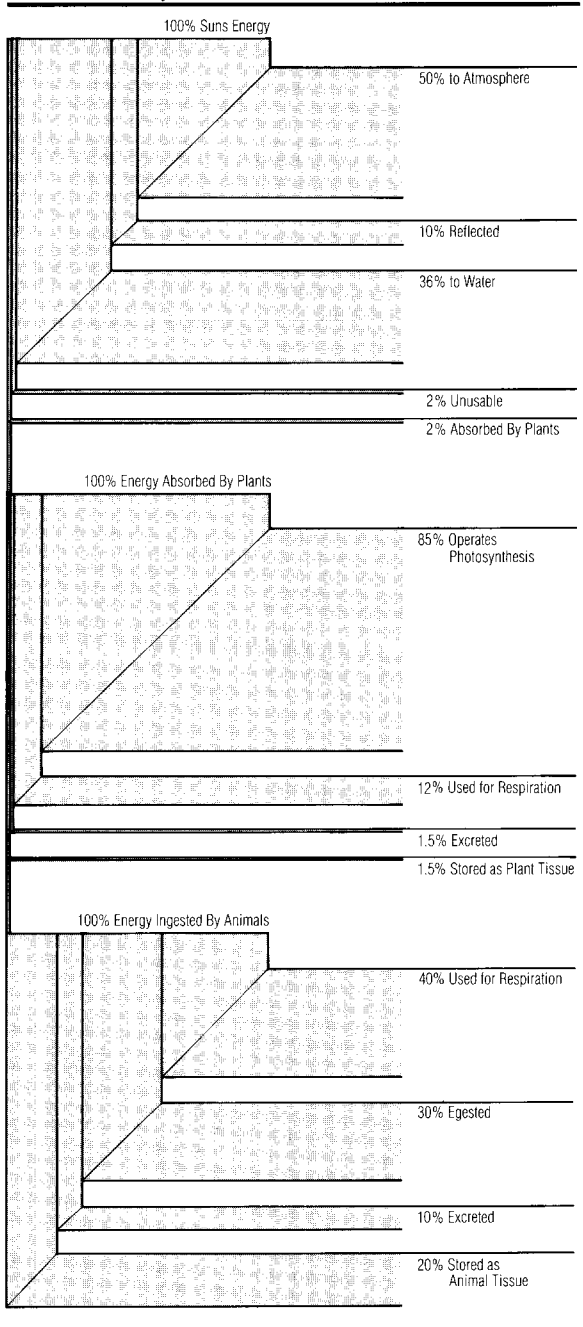

Figure 6.8 Only a tiny fraction of the solar energy reaching the earth enters the pelagic food chain. Night hours exclude one to two-thirds of sunlight (depending on season); nearly one-third is removed by scattering and absorption by air and clouds; and some is reflected off water. Of the solar energy that penetrates Puget Sound, half is of the wrong wavelength to stimulate photosynthesis, and most of the rest is absorbed by water or detritus instead of by plants.

Of the solar energy that is absorbed by phytoplankton, about 85 percent drives photosynthetic reactions and 12 percent powers other metabolic activities. Less than two percent remains as plant tissue to be eaten by animals.

Of the solar energy stored in plants that are eaten by herbivores, roughly 40 percent is voided as feces and urine, and another 40 percent is metabolized. About 20 percent is left to be eaten by carnivores. Similar losses apply at successive trophic levels.

tus, to acquire the nutrients and vitamins necessary for building tissue, to operate the hereditary works in the nucleus, to excrete, or to move. Of the matter eaten by an animal, a major portion is egested as feces rather than assimilated; most of the rest is respired or excreted, and only a fraction is added permanently as animal tissue.

The numbers in Figure 6.8 are crude averages, which vary greatly among different organisms and conditions, and are difficult to measure reliably. A rule of thumb in terrestrial ecosystems has been that when one organism is eaten by another, about 90 percent of the material is metabolized or eliminated. The productivity of an herbivore, for example, is thought to be only a tenth that of the plant on which it feeds. The "transfer" efficiency—the fraction of energy transmitted from one trophic level to the next—is therefore traditionally reckoned at 10 percent. The transmission of energy to a third trophic level, then, is only one percent, and to a fourth only a tenth of a percent.

Steele has argued that in the ocean, the transfer efficiency may approach 20 percent rather than 10 percent. In reality, its value is probably quite variable, and the lesson remains that the food chain is an inherently costly and inefficient machine. The difference between 10 and 20 percent, however, is highly significant when the multiple links in the food chain are considered. The productivity of a carnivore on the third trophic level, for example, would differ by a factor of four, on the fourth trophic level, by a factor of eight, and so on.

Furthermore, regardless of precise values of efficiency, another factor governs the overall efficiency of an ecosystem, the length of the food chain between primary producers and human harvest. The more links in the food chain between raw material and product—for example, between plant and fish—the lower will be the cumulative efficiency, and the lower the yield. Ryther has hypothesized, for example, that coastal upwelling areas, such as that off Peru, are the richest fish-producing areas of the world partly because there are fewer trophic levels. A shorter food chain, the theory says, minimizes metabolic losses and maximizes harvest. If Puget Sound salmon could feed one link lower on the food chain, by this reasoning, they could expand their potential food supply, populations, and yield to humans, by a factor of five or ten.

The Secondary Food Chain: Hypothesis

Greve and Parsons have expanded on Ryther's theory in studying the relationship between efficiency and food chain coupling. They suggest that paralleling the primary diatom-crustacean-nekton food chain in temperate coastal waters, such as those of the Puget Sound area, is a secondary food chain that supplants it under certain conditions, and which is less efficient at producing commercially important fishes.

Populating this other side of the ecological tracks are some of the smallest plankters—the phytoflagellates, protozoans and small copepods, and some of the largest—the carnivorous ctenophores and medusae. When diatom populations dwindle under unfavorable environmental conditions, such as strong stratification (or possibly pollution), the primary food chain is uncoupled, and trophic energy is theorized to be diverted instead to this secondary food chain.

Because this secondary food chain originates with smaller phytoplankton, three trophic levels rather than two are required to produce zooplankters of the sizes preferred by larval and juvenile fishes. Ryther's theory, therefore, would predict a five-to-tenfold decrease in the fish yield from this lengthening of the food chain.

Greve and Parsons, however, further argue that fishes eat few ctenophores and medusae, making the secondary food chain a dead end that shunts trophic energy away from fish production altogether. There is some persuasive evidence to support these contentions, but the complexity of the pelagic realm presents alternative explanations as well, which merit a closer and more detailed examination.

The plankters of the secondary food chain are highly r-selected, with short life spans and the potential for rapid growth under favorable conditions. Their abrupt appearances and disappearances have been characterized as a boom-or-bust pattern of abundance. The gelatinous ctenophores and medusae, or "jellies," have a much higher body-water content than do the crustaceans, and do not fall neatly into the pattern of life span versus length (Figure 6.1). They can reproduce rapidly when food is abundant, and are much shorter-lived than other zooplankters of similar dimension. This discrepancy is rectified if animals are compared on the basis of the dry masses, which among the gelatinous carnivores are similar to those of microzooplankton. Other zooplankters potentially classed on the secondary food chain are the larvaceans and the chaetognaths, which possess the dimensions of micronekton but the mass of a small copepod.

The carnivores of the secondary food chain also capture prey differently than those of the primary food chain. Ctenophores and medusae sweep their prey from the water passively using sticky cells and stinging cells, respectively. Neither of these are raptorial predators, which select their prey individually, as carnivorous crustaceans and vertebrates are thought to do. When food is abundant, gelatinous carnivores can process large volumes of water and gather more prey than a raptor; but when prey are sparse, selective hunting requires less energy and raptors have an advantage. The result of this combination of vigorous reproduction and feeding is that gelatinous zooplankters can appear suddenly, devour huge quantities of small prey, then just as suddenly disappear. They are reported to accumulate, almost like red

tides, into dense windrows at certain times and places in the summer, but are virtually absent during the winter.

A major consequence of this r-selected ecological niche is a higher metabolic rate for a given-sized animal. More of the calories ingested by these animals are expended in respiration, and thus the transfer efficiency among such animals may be at the lower end of the assumed 10 to 20 percent range.

Although it is difficult to verify because their remains are more difficult to identify in fish stomachs than those of crustaceans, there is also justification for the belief that gelatinous zooplankton are an inferior food source for fishes of all ages. Being mostly water, they yield little nutrition for their size, or for the energy expended to capture them. The sticky or stinging cells may also discourage predators.

Thus there are three theoretical reasons why, if a distinct secondary food chain does exist, it should be less productive: it is longer, making for more metabolic loss; it incurs greater metabolic losses at each link; and it produces a food of poor quality for commercially important fishes. What this theory does not take into account, however, is the fate of biomass and energy when the food chain is uncoupled. It overlooks the fundamental problem of the fluid world: that food which cannot be stored in living organisms sinks to the bottom and is lost to the pelagic zone almost entirely.

The Secondary Food Chain: Field Evidence

The theory of Greve and Parsons attempts to explain the results of the CEPEX experiments in Saanich Inlet (see Chapter Seven), in which water and plankton were captured in enormous flexible plastic cylinders (9.5 meters in diameter and 23.5 meters deep) suspended from the surface. The reduction of water motion in the cylinders apparently caused diatoms to sink out, and flagellates to replace them. (Greve and Parsons proposed that this replacement can also be triggered by pollution.) In such instances, large copepods were observed to die off, and to be replaced by jellies; juvenile salmon placed in the enclosures appeared to be slowly starving, and trophic energy was apparently shunted into a dead end.

What happens to this energy when the primary food chain is uncoupled? Its fate is dictated in part by the physiological differences between the zooplankters of the primary and secondary food chains. The urine and feces of both types of animals contain high concentrations of the nutrients (especially nitrogen) that were originally mixed upward from deep water to be taken up by phytoplankton. As long as these waste products remain near the surface, they can help replenish the nutrient supply through biochemical decomposition and recycling by bacteria, and so help sustain phytoplankton growth. Much of the ex-

creta sinks out of the surface, however, and comes to rest permanently on the bottom, where it sustains the benthic community. Only a small amount of this "lost" matter and energy, yet to be measured, returns to the pelagic zone through vertical mixing, and via surface-seeking meroplankton larvae.

Protozoans and gelatinous zooplankters release their feces in amorphous form, as marine "snow," which sinks slowly and fragments as it goes. Crustaceans release larger, compacted, membrane-enclosed fecal pellets, which sink at rates of tens of meters per day. Larger animals also live deeper in the water, so their excretion is of less value to surface-living phytoplankton, especially if it occurs under conditions of high stability and poor vertical mixing. As a result, the larger the zooplankton, the more rapidly matter is transported bottomward—because of faster sinking of feces, and because of vertical migration—and so the greater the fraction of trophic energy that escapes from the pelagic zone and reaches the benthos.

These differences have been measured in Dabob Bay. Sinking suspended matter was collected in sediment traps, cylinders several centimeters in diameter, hung vertically on a cable at several depths below the surface, and open at the top until retrieval. Most phytoplankton growth in Dabob Bay occurs in the spring and early summer. Most of the grazing was also observed at this time, as reflected by the appearance in the traps of digested chlorophyll voided in fecal pellets. But most of the carbon did not fall to the bottom until autumn, having been carried about in the bodies of zooplankton all summer. Little material reached the traps during phytoflagellate blooms; instead, it apparently was retained in the surface layer where it could refuel phytoplankton growth. Under the tight coupling between phytoflagellates and microzooplankters, not only did animal waste sink more slowly, but less of the phytoplankton sank out uneaten. During diatom blooms, however, large quantities of raw or poorly digested plant material sank bottomward. In such cases, diatom growth must have been uncoupled or poorly coupled, since only with minimal grazing could bloom populations have appeared and sunk out. A greater likelihood of uncoupling, in fact, is expected from the less flexible, more K-selected organisms of the primary food chain.

It thus appears that the blooms so characteristic of phytoplankton in Puget Sound (especially of the diatoms of the primary food chain) are in fact evidence of uncoupling—of animal populations insufficient to consume plant matter at the rate it is generated. The magnitude of spring blooms can be attributed in part to the presence of only the few adult herbivores surviving the winter; grazing pressure does not become intense until the first hordes of copepod and euphausiid larvae are produced from the final feeding of their parents. This contrasts with

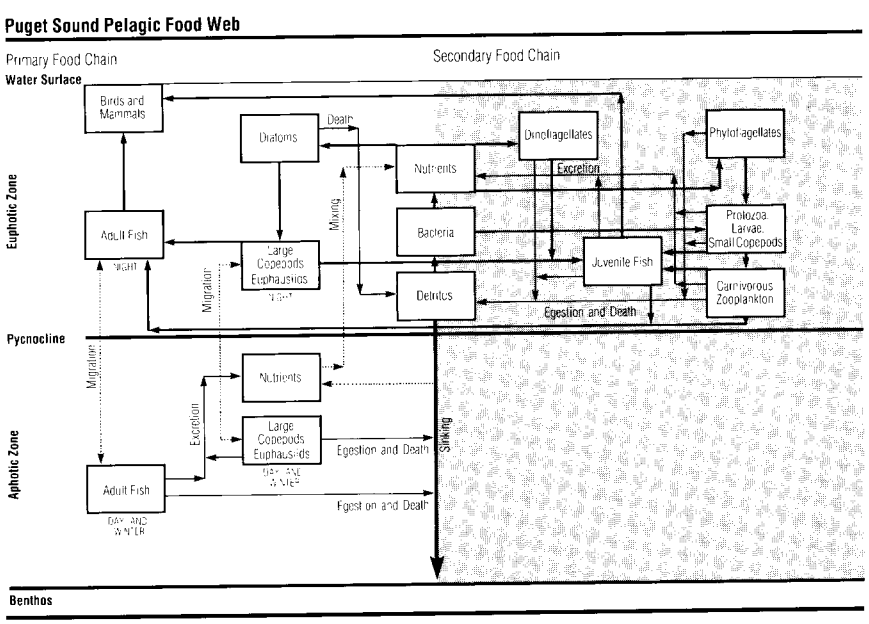

Figure 6.9 Simplified diagram of the pelagic food web of Puget Sound, incorporating the primary and secondary food chains. Many secondary food chain organisms are important foods for animals of the primary food chain. The secondary branch of the food web also is characterized by less sinking and migration into deep water, and by tighter coupling and more surface nutrient recycling, all of which are advantageous when environmental conditions are unfavorable.

conditions in the Gulf of Alaska, where *Neocalanus* nauplii, released surfaceward early in the spring by the unfed adults, begin feeding at the earliest opportunity. The tight coupling in these waters effectively maintains phytoplankton standing stocks at a constant level throughout the year, despite a spring increase in primary productivity.

The paradoxical result of these differences, is that, coupled or uncoupled, the main, diatom-based track of the food chain appears to deliver large quantities of trophic energy to the bottom, as well as to the fishes. The delivery may be direct, by sinking when uncoupled, or indirect, through the bucket brigade of zooplankton, fish, and their waste products. Larger quantities of energy may be transmitted by diatoms than by flagellates, but apparently more of it also is transported into deep water, where it is at least temporarily lost to surface organisms. In a location such as Dabob Bay, which in contrast to the main basin suffers stratification and poor vertical mixing, this can lead to a serious decline in productivity.

The secondary food chain, on the other hand, while seemingly less productive, is more tightly coupled and retains organic and recycled nutrients near the surface. In the few areas of the ocean where such research has been conducted—the Grand Banks, the Gulf of Mexico, the Bering Sea—it appears that areas dominated by flagellates and micro-

zooplankton may actually produce more pelagic fishes, and those populated by diatoms and copepods more bottom fishes. Thus the so-called secondary food chain may be neither less efficient than the primary food chain, nor even distinct from it.

The most realistic, yet still comprehensible, picture of trophic relationships in Puget Sound eliminates the artificial distinction between primary and secondary food chains. They are actually entangled with one another, branches of a more complex food web, as depicted in Figure 6.9.

Bridging the gaps between the two food chains are the changes in size and feeding habits of animals of the primary food web branch, which both pass through and are dependent on the secondary branch. Dinoflagellates and the protozoans, larvae, and small copepods that consume phytoflagellates are themselves prime food sources for larval fishes. Fishes and other animals are very sensitive to the availability of the proper food during their first days and weeks of life, and the health of individual organisms and of fish populations as a whole depends on this synchronization. Thus it may be misguided to view the secondary branch of the Puget Sound pelagic food web as a dead end, especially in the early spring when diatom blooms have yet to begin, and when hungry larval fishes are emerging in search of a first small meal.

Flagellates in Puget Sound exhibit a conservative strategy, growing under hydrographic conditions—low light intensity, chronic stratification, depleted nutrients—that are unfavorable for the production of diatoms. Rather than displacing diatoms through competition, flagellates might be viewed as filling an ecological void left when diatoms cannot grow. Rather than supplanting an efficient food chain with a wasteful one, flagellates may supplement primary production under harsh conditions to which diatoms are poorly adapted. The organisms with the shortest life cycles and the fastest growth rates are well-adapted to respond to the changeability of Puget Sound, where favorable conditions can appear and disappear within matters of hours or days. In the trophic machinery, the secondary branch of the food web seems to take on the role of shock absorber, damping out plunges in productivity and keeping the gears running more smoothly.