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September 1984

THE ECOLOGY OF EELGRASS MEADOWS IN THE PACIFIC NORTHWEST: A Community Profile

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THE ECOLOGY OF EELGRASS MEADOWS IN THE PACIFIC NORTHWEST: A COMMUNITY PROFILE

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PREFACE

Nearly half the population of the United States lives adjacent to coastal waters or to the shores of the Great Lakes. The recreational and economic pressures that accompany this residential pattern are invariably exerted on the nearshore coastal environment and its estuaries. Until recently, we have been accustomed to viewing the oceanic province as being immune to adverse impacts resulting from mild human activity. However, since the large-scale decline of eelgrass (Zostera marina L.) in the North Atlantic in the 1930's, caused by a natural rise in water temperature, we are aware that dramatic and important changes can and do occur in marine ecosystems. Human activity now is increasing so that we may no longer be passive observers of such changes. This community profile has been developed to synthesize information on the structure and function of eelgrass meadows in the Pacific Northwest and their interrelationships with adjacent communities in the estuarine environment. Cowardin et al. (1979) classified this habitat as occurring in the Columbian province, estuarine system, intertidal and subtidal subsystems, aquatic bed class, and rooted vascular subclass. Water regimes vary from irregularly exposed (intertidal) to subtidal. Water chemistry is mesohaline (mixohaline: 5.0 ppt-18.0 ppt; polyhaline: 18.0 ppt-30.0 ppt) and euhaline (30.0 ppt-40.0 ppt).

The text is organized on a taxonomic and functional basis. In Chapter 1 the physiographic setting of the Pacific Northwest eelgrass habitats is presented. Chapter 2 describes the biology of eelgrass in the province. In the next chapters the functional roles (Chapter 3) and components of the eelgrass community (Chapter 4) are described. Chapter 5 describes the interactions of the eelgrass community with adjacent communities. The report concludes with management considerations (Chapter 6).

As with research on specific communities in any area, there are certain gaps in the data on eelgrass of the Pacific Northwest. Research in this region has emphasized the biology, biotic components, trophic relationships, and productivity of the plants. Thus, information on energy flow, nutrient cycling, decomposition, and sediment stabilization roles of eelgrass learned in Alaska and along the Atlantic coast of North America will be applied to the Pacific Northwest for the purpose of filling in the gaps in the research.

This report is not an exhaustive survey of the literature on the eelgrass meadows of the Pacific Northwest. It is intended to characterize the major components and processes that occur and drive the eelgrass community and to form a basis for placing value on this community.

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CONVERSION TABLES

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	Btu
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

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INTRODUCTION

Eelgrass (Zostera marina L.) is 1 of 48 species of seagrasses found in the near-shore coastal environments and estuaries of the world. Seagrasses have horizontal rhizomes and erect leafy shoots extending in the water column (Figure 1). Their roots grow in unconsolidated soft substrate (except for surfgrass, Phyllospadix, in the North Pacific, which attaches to the surface of rocks on exposed coasts).

According to Cowardin et al. (1979), the eelgrass community is classified as the following: SYSTEM: Estuarine; SUBSYSTEM: Subtidal; CLASS: Aquatic Bed; SUBCLASS: Submerged Aquatic; WATER REGIME: Subtidal; and WATER CHEMISTRY: Mixosaline. Inasmuch as the plants are rooted in an unconsolidated substrate, often of uniform relief, and project a "forest" of leaves into the water column, the meadow creates a structured habitat from an otherwise unstructured one. The rooted plants and leaf baffle provide protection and sediment stabilization that result in a much greater diversity of animals within the meadow than in adjacent unvegetated areas.

It is well recognized that estuaries are important in commercial and sport fisheries. Many fishes depend on estuaries for all or part of their life cycle. Since estuaries in the Pacific Northwest have extensive eelgrass meadows, eelgrass beds must have an important role in the life cycles of these fishes.

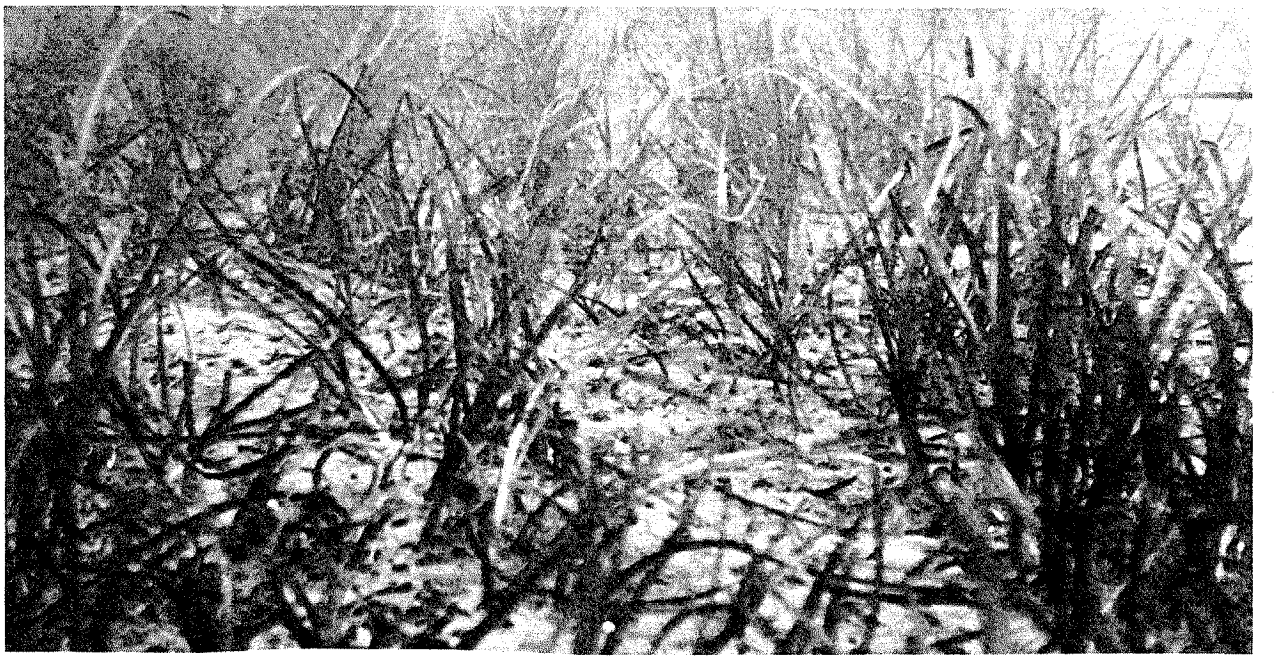

Figure 1. Eelgrass meadow in Puget Sound (Courtesy National Oceanic & Atmospheric Administration, Mar. Fish. Rev. 39:18-22).

Because eelgrass is a rooted plant, it performs a vital function of stabilizing coastal sediment, thus preventing erosion. Studies done in England (Wilson 1949), Denmark (Rasmussen 1977), the Chesapeake Bay (Orth 1977a), and in Puget Sound, Washington (Phillips 1972) have documented the ability of eelgrass to stabilize bottom sediments (Figure 2). The eelgrass meadow provides direct and indirect food sources for marine food chains; it also provides habitat and protection and acts as a nursery for many marine species. Following the die-off of 90% to 100% of the eelgrass in the North Atlantic in 1931-33, many animals associated with eelgrass disappeared. Impacts to the human economy were severe. Scallops, fish, clams, and crabs declined or disappeared, and the brant geese changed their migration patterns and went inland to feed. In Europe, brant geese numbers declined severely (Einarsen 1965) following the "wasting disease." In the Netherlands the overwintering population of brant declined from more than 10,000 birds to at most 100 by 1953.

The Pacific Northwest region extends from southern British Columbia, Canada, to Humboldt Bay in northwestern California (Figure 3), a distance of about 900 km (560 mi) (Proctor et al. 1980a). In

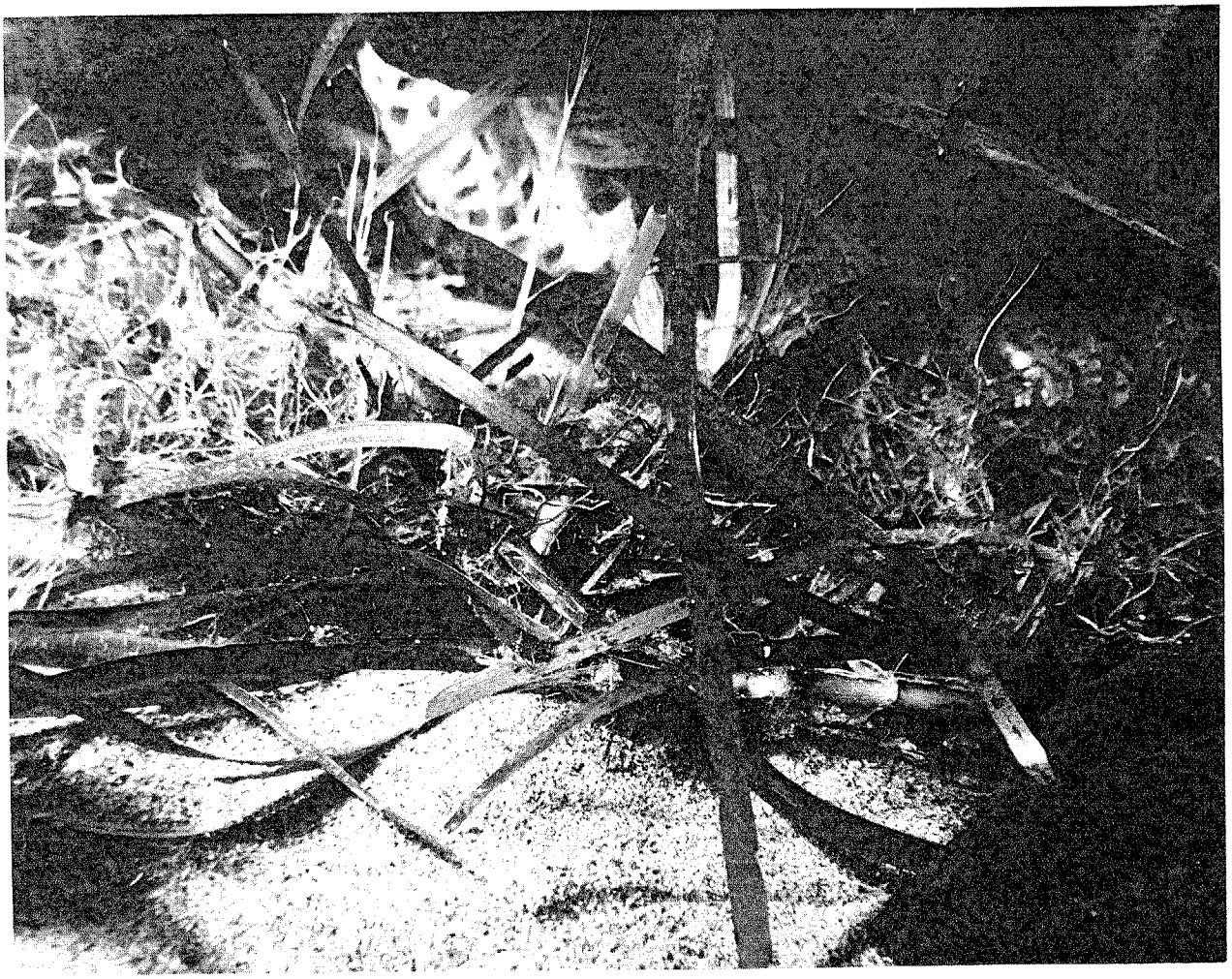

Figure 2. Effect of wave shock on rhizome mat of eelgrass, 22 February 1964. West side of Whidbey Island, Washington (shows persistence of eelgrass).

Pacific Northwest Coastal Region

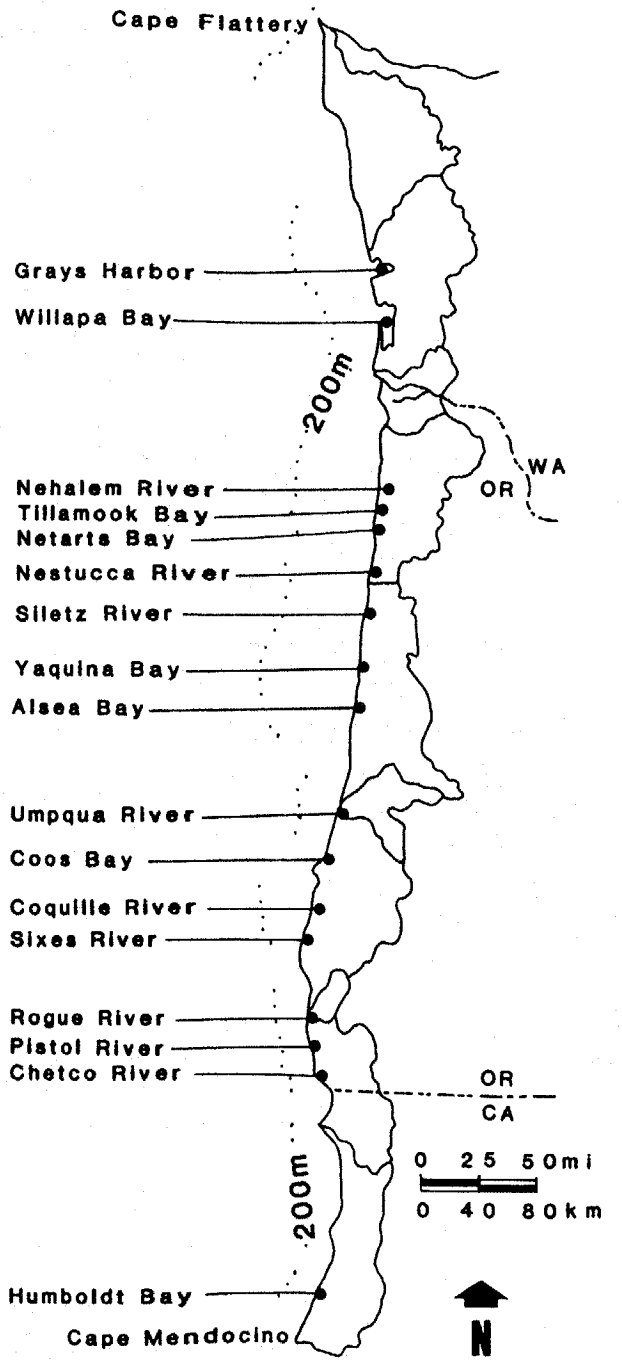

Figure 3. Map of the Pacific Northwest coastline showing the locations of the estuaries and river systems containing eelgrass (after Proctor et al. 1980b).

contrast to southern California, the coastline of this region is sparsely populated. It has not been without modification, however. In southern British Columbia, Moody (1978) reported that the sand and mud flats of the Fraser River foreshore, which supports extensive meadows of eelgrass, were threatened by an increasing number of residential, industrial, and recreational developments.

The largest meadows of eelgrass in the Pacific Northwest occur in protected estuarine areas away from the open coast; i.e., Padilla and Willapa Bays in Washington State, and Humboldt Bay in northern California. The largest stand in northern Oregon occurs in Netarts Bay, while small stands are confined to several narrow river valleys (Figure 3). This report also includes Z. japonica Aschers. & Graebn., since the species is heavily used as food by black brant geese.

CHAPTER 1
THE PHYSIOGRAPHIC SETTING

1.1 GEOLOGICAL HISTORY OF REGION

Bedrock of the Pacific Northwest was bent, folded, fractured, and uplifted by the collision of the Juan de Fuca and Gorda Plates with the North American Plate (Figure 4). Weathering has modified the uplifted formation, with riverborne sediments deposited in estuaries and beaches (Proctor et al. 1980b). In many places there are long stretches of sand beaches, broken by steep, resistant sea cliffs, rock headlands, and the mouths of bays and small streams (Jefferson 1975).

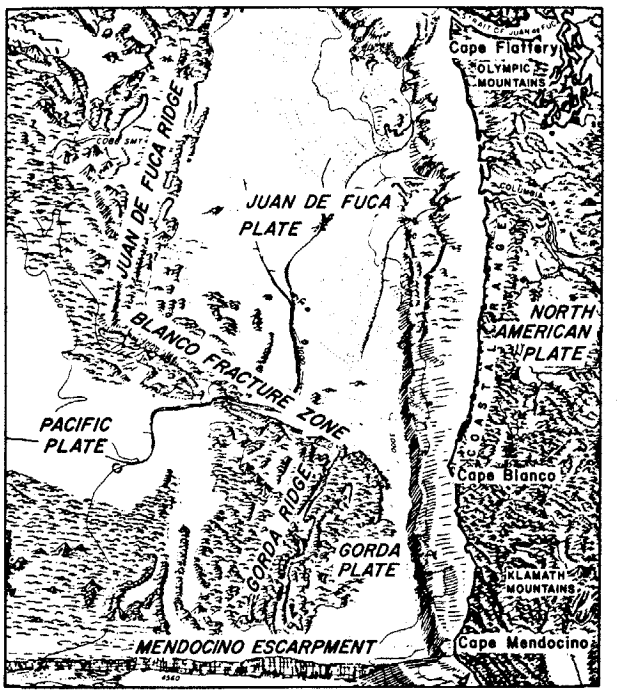

Figure 4. Topographic and bathymetric features of the northeast Pacific (after Proctor et al. 1980b).

The long, narrow coastal strip of the Pacific Northwest slopes steeply from east to west (Proctor et al. 1980a). The coast has experienced geologically recent orogenic activity with resulting coastal subsidence (Proctor et al. 1980b). In the region the continental shelf extends from 16 km (10 mi) off Cape Mendocino in northern California to 65 km (40 mi) in central Oregon to 48 km (30 mi) off northern Washington (Proctor et al. 1980b). Offshore subduction is or was until recently occurring along a line coinciding with the coast of North America between Vancouver Island and Cape Mendocino (the area of concern in this profile).

The geology of the coast south of the Salmon River in Oregon differs from that to the north (Proctor et al. 1980b). In the southern coast ranges, formations of metamorphic rocks are Pre-Tertiary (Wiedemann et al. 1974). Geologic history began during early Eocene with the deposition of pillow basalts near Alsea, Oregon. Later in the Eocene vast sedimentary beds (Tyee formation) were deposited along most of the southern end of the coast during coastal subsidence. This subsidence was due to a geosyncline from the Klamath Mountains (southern Oregon) north to Vancouver Island (Wiedemann et al. 1974). Scattered igneous intrusions occurred during the Oligocene. In the Miocene localized deposits of sedimentary and volcanic rocks occurred near Newport and Coos Bay, Oregon. No new deposits were made in the Pliocene, but rapid erosion of the thick beds of sediments occurred as coastal uplift occurred (Wiedemann et al. 1974; Proctor et al. 1980b). In the Pleistocene new sandy deposits were made throughout

the area during a period of rising sea level.

North of the Salmon River all rock formations are Tertiary. Eocene formations are widespread and include volcanic (basalts with tuffs and breccias) and sedimentary rocks (siltstones and sandstones)(Proctor et al. 1980b). In the Oligocene limited sedimentary formations developed (siltstones, shales, sandstones). In the Miocene extensive basalt flows occurred in northern Oregon and southwestern Washington. During the Pleistocene, extensive erosion occurred during coastal uplifting.

It appears that the late Pliocene and Pleistocene were characterized by alternating coastal submergence and uplift, with resulting deposition and erosion, respectively. The Puget Sound Basin-Willamette Trough was formed in the late Pliocene (ca. 3 million years ago) when a general north-south uplift, forming the Olympic and Cascade Mountains, was accompanied by a downwarp between the two ranges (Yoshinaka and Ellifrit 1974). Present coastal configurations and sediments in estuaries to the north are the result of the melting of lobes of the Vashon glacier of the Wisconsin period (17,000 to 9,000 years ago) (Wiedemann et al. 1974; Yoshinaka and Ellifrit 1974; Jefferson 1975). As the glaciers melted, erosion occurred with bay deposits forming beds, filling in all river mouths (Jefferson 1975). Coastal submergence occurred again, creating the general features of the present coastline. Even though the glaciers did not extend south of the Olympic Mountains (Kumler 1969), the glacial melting did result in a general rise in sea level 120 to 150 m (400-500 ft) above its recent level (Jefferson 1975).

1.2 CLIMATE OF REGION

The climate of the Pacific Northwest coastal region is marine (Proctor et al. 1980b). It is characterized as a mid-latitude, west-coast-marine type, with wet winters and dry summers. The region is located in the center of the prevailing westerlies, with local winds ranging from northwest to southwest throughout most of the year. The winds exchange heat with the ocean and become nearly saturated with moisture from evaporation. The air rises as it reaches land, cools, and gives up considerable moisture. Thus the climate is moderated by the Pacific ocean and characterized by high rainfall and a moderate temperature range. There is little north-to-south variation in temperature and only a slight increase in precipitation to the north in the region.

Two semipermanent pressure patterns, the Aleutian Low and the North Pacific high, control the climate. The Aleutian Low, consisting of a series of low pressure centers, lies over southwest Alaska and the Aleutian Islands. Winds blow counterclockwise around the low, bringing a series of wet onshore frontal storms which are often characterized by strong winds. This pressure system dominates the winter weather from October to March. The low shifts southward during winter, resulting in an increased frequency of frontal storms reaching the coast. Eighty percent of the annual precipitation falls during this period (Table 1).

The North Pacific High dominates the summer weather of the region. As summer approaches, the high expands over the eastern Pacific north of 29° N almost to Alaska and westward to 169° E. Storms are veered northward from the region by the high. Only 5% of the annual precipitation falls in July and August. Winds flow clockwise and bring predominantly fair weather. During this time coastal winds are from the northwest and north. Seasonal shifts in wind direction influence nearshore ocean currents, resulting in upwelling which brings cooler water to the surface near shore in summer. This produces fog, reduced insolation, and lower air temperatures.

Precipitation in winter varies from a high of 32 cm (13 inches) at Tatoosh Island in northwestern Washington to 27 cm (11 inches) at North Bend in southwestern Oregon to 18 cm (7 inches) at Eureka in northern California, all in December (Proctor et al. 1980b). In summer, precipitation varies from a low of 5 cm (2 inches) in August at Tatoosh Island, to 2 cm (0.8 inch) in July at North Bend, to 0 at Eureka in July.

Table 1. Precipitation, temperature, and tidal data for selected locations in the Pacific Northwest (from Wiedemann et al. 1974; Jefferson 1975; Moody 1978; Proctor et al. 1980a, 1980b).

Location	Mean annual precipitation cm (inches)	Mean annual air temp. °C (°F)	Range of surface water temp. °C (°F)	Mean tidal ranges m (ft)
Humboldt Bay, California	101 (39.8)	--	8.5 - 11 (47.3 - 51.8)	1.3 (4.3)
North Bend, Oregon	162.5 (64)	11.1 (52)	--	1.5 (4.9)
Astoria, Oregon	192.5 (76)	10.6 (51)	--	2.0 (6.6)
Tatoosh Island, Washington	207.5 (82)	--	--	2.0 (6.6)
So. British Columbia, Canada	--	--	7.5 - 17.5 (45.5 - 63.5)	--

Air and water temperatures are diurnally and seasonally mild and show relatively little variation. At Aberdeen, Washington, normal daily summer air temperatures range from 21° C (70° F) to 10° C (50° F). Winter air temperatures usually range between 7° (45° F) and 1.6° C (35° F) from Astoria, Oregon, in the north and North Bend, Oregon, in the south (Wiedemann et al. 1974). Air temperature extremes are 40° C (104° F) and -14° C (7° F): Army Corps of Engineers, July 1977) for the Aberdeen area in southwest Washington. At Brookings in southern Oregon, the mean low air temperature in January is 4.4° (40° F), while the mean high temperature in August is 19.5° C (67° F; Jefferson 1975).

Coastal water temperatures in northern Washington range from 8° C (46° F) in winter to 14° C (57° F) in summer (Proctor et al. 1980a). In Humboldt Bay, northern California, water temperatures varied from 8.5° C (47.3° F) in January to 11° C (52° F) in May (Proctor et al. 1980b). In an eelgrass meadow at Roberts Bank, southern British Columbia, Moody (1978) recorded a maximum range of surface temperatures of 7.5° C (45.5° F) in January to 17.5° C (63.5° F) in July.

The relative humidity in the region is quite high, owing to low evaporation rates due to low temperatures (Wiedemann et al. 1974). Values range in March from 79% at 4:00 pm to 96% at 4:00 am at Tatoosh Island in northwest Washington (Proctor et al. 1980b). Values were almost identical in Astoria in northern Oregon.

Tides in the region are a mixture of semi-diurnal (twice daily) and diurnal (daily) components, with inequality appearing primarily in the successive low waters (Proctor et al. 1980b). Tidal ranges increase along a gradient from south to north (Table 1).

1.3 EELGRASS DISTRIBUTION IN REGION

Five seagrass species are found in the Pacific Northwest. Three of these are species of surfgrass (*Phyllospadix scouleri*, *P. torreyi*, *P. serrulatus*; cf., Phillips 1979 for an analysis of the distribution and morphology of these species in this region). All three species occur on rocky substrate in exposed waters. The first two species range from the northern end of Vancouver Island, Canada, to the lower end of Baja California. The third, *P. serrulatus*, extends from Cape Arago, Oregon, northward and westward to at least Adak Island in the Aleutians. The other two species are in the genus *Zostera*: eelgrass (*Zostera*

marina; Figure 5) and the diminutive Zostera japonica. Both species are found on a muddy or mixed mud and sand substrate in areas sheltered from turbulent water. Zostera japonica is usually found from +1.2 m (4.0 ft) to +2.4 m (8.0 ft) (Harrison 1979), while eelgrass occurs from +1.8 m (6.0 ft) down to -6.6 m (-22.0 ft) deep (Phillips 1972, 1974). In Canada the two species overlap in the +1.0 m (3.3 ft) to +1.5 m (5 ft) region (Harrison 1979).

A standard key to separate species is unnecessary since only two species are under consideration. Both can be easily distinguished, not only by tidal elevation but also size. Zostera japonica is a very small plant, producing leaves no wider than 2 mm (0.08 inch) and usually no longer than 10-15 cm (4-6 inches). Rhizomes are no more than 2-3 cm (0.8-1.2 inches) deep in the sediment. Leaf tips may be slightly notched, while those in eelgrass are rounded. Leaf sheaths are open, while those in eelgrass are closed.

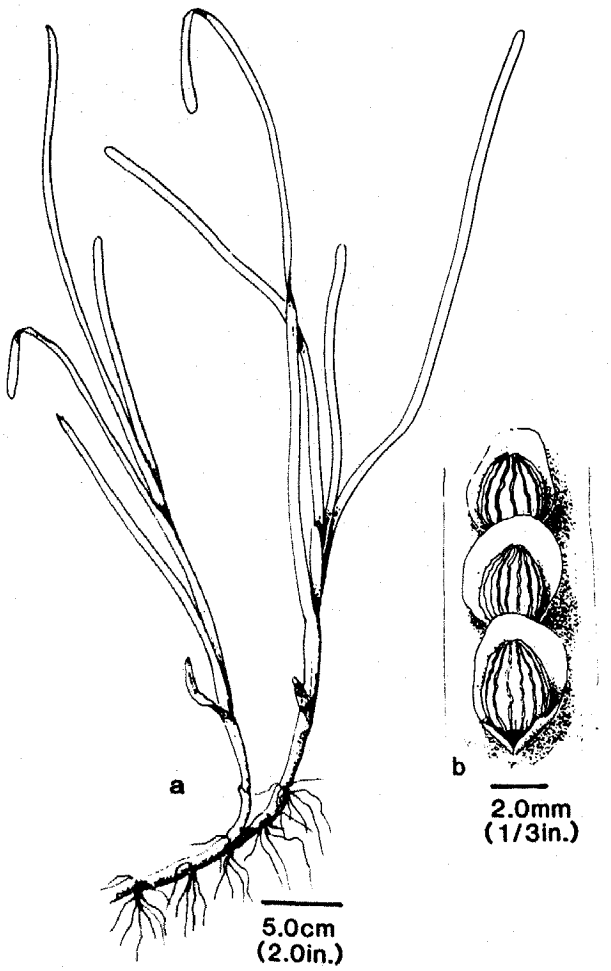

Figure 5. Eelgrass--(a) Vegetative plant (b) Part of spadix with mature seeds (after Phillips 1980) (Illustration courtesy of the U.S. Army Coastal Engineering Research Center, Fort Belvoir, Virginia).

In eelgrass, plants and leaves are much larger (a full analysis of seasonal changes in dimensions is given in Chapter 2, Section 2.1, Vegetative Growth Strategies).

The Pacific Northwest contains at least three very large stands of eelgrass: (1) Padilla Bay in northern Washington; (2) Willapa Bay and Grays Harbor in southwestern Washington; and (3) Humboldt Bay in northern California. There are large stands in some parts of southern British Columbia and on Vancouver Island, Canada (Harrison 1979, Haegele and Hamey 1982). Phillips (1972, 1974) calculated that eelgrass covered up to 9% of the bottom area of Puget Sound below mean lower low water (MLLW). The largest stand of eelgrass in Oregon is at Netarts Bay (Figure 3). Table 2 lists the various locations in the region where eelgrass has been found and the extent of areal coverage of growth where documented. Eelgrass is found throughout the Pacific Northwest in sheltered water on an unconsolidated substrate and where currents do not exceed 3.5 knots. Depth of growth does not exceed -6.6 m (-22 ft), and salinity is not less than 20 ppt (except near river mouths at low tide).

Zostera japonica was probably introduced into the region from Japan through the oyster industry (Harrison 1976). Japanese oysters were introduced into Willapa Bay in 1928, and the species was first collected by Hotchkiss in 1957 (Harrison and Bigley 1982). These oysters were increasingly imported after 1928 (Harrison and Bigley 1982). The species is presently found from Coos Bay (Phillips, unpublished research), to Netarts Bay, Oregon; in Willapa Bay and Grays Harbor, Washington; and extensively from Padilla Bay, Washington; to Nanaimo on Vancouver

Table 2. Distribution and extent of eelgrass growth in the Pacific Northwest.

Location	Size of estuary	Extent of eelgrass growth (bottom coverage)	Reference
British Columbia, Canada			
North coast of Vancouver Island	--	--	Haegele and Hamey 1982
Roberts Bank	--	--	Moody 1978
Boundary Bay		25 km^2 (6,447 acres): shares with *Zostera japonica*	Harrison 1979
Washington			
Near Bellingham	--	--	--
Drayton Harbor	--	--	Simenstad et al. 1979
Birch Bay	--	--	Simenstad et al. 1979
Lummi Bay	--	--	Simenstad et al. 1979
San Juan Islands			
Numerous locations, particularly around San Juan Is., Orcas Is., Lopez Is.	--	--	--
Padilla Bay near Anacortes	77.6 km^2 (20,000 acres)	Significant stand	Pryne 1979
Fidalgo Bay near Anacortes	--	--	Phillips 1981
Whidbey Island	--	--	Phillips 1972
Snohomish Estuary	11.63 km^2 (3,000 acres)	40 percent covered by eelgrass	Driscoll 1978
Puget Sound proper	--	9 percent of bottom below MLLW	Phillips 1972, 1974
Strait of Juan de Fuca			
Beckett Point	--	--	Simenstad et al. 1979
Port Williams	--	--	Simenstad et al. 1979
Crescent Bay	--	--	Phillips and Grant 1965

Table 2. (Continued)

Location	Size of estuary	Extent of eelgrass growth (bottom coverage)	Reference
Hood Canal			
Nearly continuous band around canal. Some very large meadows.	--	--	Phillips and Fleenor 1970
Willapa Bay	347 km^2 (74,207 acres)	6,208 ha (15,520 acres); significant stand	Smith 1976; Wilson 1981
Grays Harbor	95.5 km^2 (38 mi^2, 24,636 acres) at MLLW	Significant stand; 4,455 ha (11,000 acres) of eelgrass; half of this is in dense stands. There are 275 ha (680 acres) of *Z. japonica* (Dense defined as 70 shoots/m^2. Density could be as few as 7 shoots/m^2.).	Army Corps of Engineers July 1977a; Smith 1976
Oregon			
Necanicum River	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
Nehalem Bay	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
Tillamook Bay	--	Moderate percent of eelgrass	Proctor et al. 1980a
Netarts Bay	612 ha (1,520 acres) tidelands and 329 ha (806 acres) submerged	161 ha (395 acres) on tidelands (48%); 175 ha (429 acres) submerged (52%)	Stout 1976; Kentula 1983
Nestucca Bay	--	Moderate percent of eelgrass	Proctor et al. 1980a

continued

Table 2. (Concluded)

Location	Size of estuary	Extent of eelgrass growth (bottom coverage)	Reference
Salmon River	--	Moderate percent of eelgrass	Proctor et al. 1980a
Siletz Bay	--	Moderate percent of eelgrass	Proctor et al. 1980a
Yaquina Bay	15.8 km^2 (6.1 mi^2)	Moderate to high percent of eelgrass	Proctor et al. 1980a
Alsea Bay	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
Umpqua River	--	Low percent of eelgrass	Proctor et al. 1980a
Coos Bay	--	Low to high percent of eelgrass	Proctor et al. 1980a
Coquille River	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
Sixes River	--	Low percent of eelgrass	Proctor et al. 1980a
Rogue River	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
Pistol River; Winchuck River	--	Low percent of eelgrass	Proctor et al. 1980a
Chetco River	--	Low to moderate percent of eelgrass	Proctor et al. 1980a
California			
Humboldt Bay	Total surface area at high tide is 62.4 km^2 (24.1 mi^2)	--	Proctor et al. 1980b
North Bay	--	435 ha (1,088 acres)	Harding and Butler 1979
South Bay	--	786 ha (1,965 acres)	Harding and Butler 1979

Island, and Vancouver, Canada (Harrison and Bigley 1982). No attempt will be made to list all known eelgrass distribution, with one exception.

However, because so little is known of eelgrass distribution in Oregon, it is worthwhile to list in Table 2 distribution as it is known (Proctor et al. 1980a).

CHAPTER 2
THE BIOLOGY OF EELGRASS

2.1 VEGETATIVE GROWTH STRATEGIES

Sauvageau (1889, 1890, 1891), Setchell (1929), Phillips (1972), and Tomlinson (1974, 1980) described the morphology and anatomy of eelgrass. Eelgrass leaves possess an anatomy typical of submerged hydrophytes: namely, cutin on the leaf is thin, there are no stomata, chloroplasts are densely packed and lie principally in the epidermis, the internal cellular structure consists of large thin-walled aerenchyma cells with numerous air canals (lacunae), and the vascular tissue has reduced xylem (Tomlinson 1980). As with grass-like monocots whose leaves stand erect, there are no dorsal or ventral sides to the leaf blade. The lacunae are continuous from the leaf blade through the rhizome to the root tips and carry O_2 and CO_2 throughout the plant. Because these lacunae may also store and recycle O_2, the standard method of measuring primary productivity by measuring O_2 changes in the water around eelgrass plants is not accurate (Hartman and Brown 1967; Jacobs 1979; Zieman and Wetzel 1980). The leaf-tips are rounded, while the blades are strap-like. Leaf width depends on the severity of the climate in a region, the season, and tidal zone (Setchell 1920, 1929; Phillips 1972; Kentula 1983). The leaves are produced by a meristem terminal on a short shoot (erect branch from the horizontal rhizome). The oldest shoot (defined as an erect branch with a bundle of leaves) is terminal on the rhizome. Occasionally the meristem on the terminal shoot gives rise to a lateral rhizome branch with a meristem that produces leaves.

Depending on the length of the growing season, the number of leaves produced in a year, and the number of lateral branches produced, the individual eelgrass plant has a variable growth and expansion rate over the bottom. There is one rhizome node produced for each new leaf initiated; the same meristem which produces a leaf also produces a new internode for the elongating branch. Setchell (1929) theorized that eelgrass plants produced two lateral branches during a growing season and that the terminal shoot always flowered during the second year following development from a seed. In this scheme eelgrass is a biennial plant.

Eelgrass rhizome are buried from 3-4 cm (1.2-1.6 inches) up to 20 cm (8.0 inches) deep in sediment, depending on the sediment consistency. In firmer substrates, rhizomes may be only half as deep as in soft muddy substrates. Two bundles of roots are produced at each rhizome node.

New leaves grow on alternating sides from the meristem on the shoot. Subtidal shoots in Puget Sound typically carry five leaves each during summer and four in winter (Phillips 1972), while intertidal shoots in Oregon averaged four leaves each in June and as few as 2.5 each in August (Kentula 1983). Keller and Harris (1966) reported that the number of leaves per shoot in Humboldt Bay ranged from two to thirteen but averaged three to four.

Kentula (1983) analyzed the growth of a leaf in relation to its age-position on the shoot. The youngest leaf was designated No. 1. The greatest proportion of growth occurred in position No. 2. In April-May these leaves accounted for 48%-65% of the total growth of the shoot and from 75%-95% of the growth from June-October.

There are seasonal differences in leaf dimensions of eelgrass. Intertidal and subtidal leaves are longer and wider in summer than in winter (Table 3) (Tutin 1938, Burkholder and Doheny 1968, Phillips 1972, Kentula 1983). These changes in dimension not only affect functional aspects of the ecosystem (productivity, reduced eipiphyte load, amount of litter for decomposition), but also the structural aspects (density of leaf cover for the refuge and nursery functions of the animal communities).

Setchell (1929) noted that eelgrass growth was seasonal and correlated with 5° C intervals of temperature. While eelgrass activity in the Pacific Northwest does not fall neatly into these intervals, it does appear that eelgrass shows distinct seasonal patterns of activity, particularly in the case of vegetative growth and reproductive cycles. Phillips (1976) created a Phenological Index of 14 separate characteristics of seagrass activity, but shortened the list to three reproductive phases following a 4-year collection program of turtle grass (Thalassia testudinum Banks ex Konig) and eelgrass from a wide distributional range in North America (Phillips et al. 1983a). The three phases were significantly correlated with water temperature. The three events were initial date of flower buds, initial date of anthesis, and initial date of visible fruits. Dates of maximum and minimum biomass were analyzed, but no significant correlations with water temperature appeared. The data also indicated that both species may include genotypes with different temperature requirements for reproductive activity that are selectively adapted to different habitats. This study does not rule out the influence of other factors which could control phenology; namely, day length (photoperiod) and nutritional status of the plants.

Despite a lack of correlation of vegetative activity with environmental variables, eelgrass demonstrates seasonal regularity in the Pacific Northwest (Phillips 1972, Puget Sound; Kentula 1983, Netarts Bay, Oregon). Leaves typical of winter growth (narrower, shorter) appeared in September in Netarts Bay, with a complete change to the winter form by December. In Puget Sound the winter leaves begin to appear in November. In both areas new vegetative growth events occur before the water cools and warms, respectively. Table 4 lists the field observations made on eelgrass phenology in the Pacific Northwest.

In Denmark, Ostenfeld (1908) calculated that a shoot of eelgrass produced four to six new leaves annually. Petersen (1913) stated that eelgrass shoots in Denmark each produced ten leaves in summer and five more in winter. In Puget Sound, Phillips calculated that eelgrass shoots produced an annual crop of 15 leaves

Table 3. Seasonal changes in leaf dimensions of eelgrass in Puget Sound, Washington.

Season	Tidal Zone	Width in mm (inches)	Length in cm (ft)	No. of leaves/ shoot ($\bar{X}$)
Winter	Intertidal	3-5 (0.12-0.20)	Up to 25 (1)	
	Subtidal	5-8 (0.20-0.31)	46-100 (1.5-3.3)	4
Summer	Intertidal	4-7 (0.16-0.28)	Up to 50 (1.67)	4 in June; 2.5 in August[a]
	Subtidal	8-12 (0.31-0.47)	200-390 (6.6-10.0)	

[a]Kentula 1983

Table 4. Field observations on eelgrass phenology in the Pacific Northwest (Phillips 1972; Kentula 1983).

Event	Earliest month and range	Water temperature in °C (°F)
1. New growth of roots, rhizomes, and leaves typical of summer	February	6.5-7.8 (43.7-46.0)
2. Appearance of flowering stalks	March (to July)	6.5 (43.7)
3. Seed germination	April (to July) (occurs all year but predominantly from April to July)	7.5 (45.5)
4. Vegetative growth burst	July	10.0-13.5 (50.0-56.3)
5. Seed production	July (to October)	13.5-10.0 (56.3-50.0)
6. Seed dispersal	Mid-August (to October)	13.5-10.0 (56.3-50.0)
7. End of summer leaves and production of winter leaves	November	10.0 (50.0)
Zostera japonica (southern British Columbia, Canada; Harrison 1982a)		
1. Seed germination	Mid-March (maximum in April-May; to August)	
2. Vegetative growth	April (maximum in August; to January)	
3. Appearance of flowers	July (maximum in August; to December)	

(Phillips 1972). In Oregon, Kentula (1983), working in the intertidal zone, calculated that mean lifetimes of leaves were 34-34.8 days in April, 49 days in May, and 40.7-55.7 days in June-October. The shorter periods in April were due to leaves sloughing from the plant faster than their production. The longer period of 55.7 days was attributed to shoots in the lower intertidal region. This study also determined that the time interval between the sloughing of two successive leaves on one shoot varied from as few as 7.1 days (May-June 1981) to as many as 23.3 days (May 1981). Table 5 lists the methods of calculating these time intervals. In Oregon it appears that intertidal eelgrass may also produce about four to five crops of leaves/year (Kentula 1983). Sand-Jensen (1975), using a leaf marking technique, calculated that the mean lifetime of leaves in Denmark was 56 days and that new leaves were produced every 14 days.

Under most conditions eelgrass forms perennial stands. Under certain conditions of stress, eelgrass may act as an annual plant with a very heavy production of seeds (Felger and McRoy 1975, Mexico; Keddy and Patriquin 1978, Nova Scotia, Canada; Bayer 1979a, Oregon; Jacobs 1982, Europe; Phillips et al. 1983b, Washington). Stress factors may include high and low water temperatures, reduced water salinity, and intertidal locations. Recent work has shown that seagrass species may form genotypes that are selectively adapted to different habitats (McMillan and Phillips 1979; Phillips and Lewis 1983; Phillips et al. 1983a,b). Environmental factors that appear to correlate with genotypic formation include temperature, salinity,

Table 5. Calculations for methods of determining leaf growth and release (Tomlinson 1972, 1974; Patriquin 1973; Jacobs 1979; Kentula 1983).

Method	Calculations
Plastochrone Interval (P.I.) (Represents time interval between the initiation of two successive leaves on one shoot)	$\frac{\text{No. of shoots marked x observation period in days}}{\text{No. of new leaves on marked shoots}}$
Export Interval (E.I.) (Represents time interval between sloughing of two successive leaves on one shoot)	$\frac{\text{No. of shoots marked x observation period in days}}{\text{No. of leaves sloughed from marked shoots}}$
	Multiply the P.I. x mean no. of leaves/shoot to get mean lifetime of a leaf on a shoot

light, and combinations of temperature-light along a depth gradient. Work has also shown that eelgrass may exhibit a phenotypically plastic growth response to changes in environmental conditions (Phillips 1972; Backman 1983; Phillips and Lewis 1983). Eelgrass from stressed environments typically shows genotypic (ecotypic) differentiation, while eelgrass from environmentally optimum (least stressed) conditions shows a phenotypically plastic response to the environment.

2.2 REPRODUCTIVE STRATEGIES

Several recent studies have analyzed sexual reproductive patterns of eelgrass in the Pacific Northwest (Phillips 1972; Harrison 1979; Kentula 1983; Phillips et al 1983b). The events and timing are summarized in Table 4. Harrison (1982a) reported the phenology of *Z. japonica* (Table 4).

With the study of phenology of eelgrass and *Z. japonica* has come an application to the r-K selection theory (MacArthur and Wilson 1967) and use of the word "strategies" to describe growth patterns and interactions in the field. It appears that on the Pacific coast of North America eelgrass has three distinct life-history strategies (Phillips et al. 1983b): (1) Gulf of California, where all plants flower in March, produce seed in April and May, and decay as water temperatures exceed 27° C (80.6° F), an annual habit and r-selected trait; (2) Central portion of range from California to Alaska: a. Intertidal plants subjected to wide fluctuations in temperature, salinity, radiation, grazing, erosion, and wave action. These plants have a much higher incidence of flower and seed production than plants in subtidal zones; b. Subtidal plants are relatively undisturbed physically and biologically, and show the least flowering response, indicating perennial plants and a K-selected trait. Bayer (1979a) found an upper intertidal zone of eelgrass in the Yaquina estuary, Oregon, made up of annual eelgrass. He also found that the incidence of flowering declined over the gradient from the upper intertidal to the subtidal zone.

Harrison (1979) compared the reproductive effort of eelgrass and *Z. japonica* and concluded that *Z. japonica* was an r-strategist, while eelgrass was a K-strategist. *Z. japonica* inhabits a high intertidal location, while eelgrass grows below it. Harrison (1982a) concluded that eelgrass may be a facultative annual in areas where plants are exposed to conditions too harsh for its adaptive tolerance and that *Z. japonica* is an opportunist that over-winters predominantly as seed and can quickly complete its life cycle in 6-7 mo. (in southern Canada). It is important that we determine if annual eelgrass in the Gulf of California and in the Pacific Northwest is really annual or whether populations may really behave facultatively. Harrison (1982b) found that both eelgrass and *Z. japonica* could live together in spring, but *Z. japonica* declined in summer as the longer eelgrass

leaves overtopped them and created deeper shade.

In the subtidal zone sexual reproduction does not play an important role in the growth and maintenance of an eelgrass meadow (Phillips 1972; Kentula 1983). During a study in Puget Sound, Phillips (1972) tagged numerous seedlings in the subtidal and found 100% mortality. In one denuding experiment only one seedling colonized a 1-m^2 plot in the subtidal, while five seedlings appeared in an intertidal plot.

There appears to be a direct relationship between the amount of physical disturbance (high or low water temperatures, intertidal conditions) and a dependence on sexual reproduction (degree of flower and seed production and survival of seedlings) to maintain an eelgrass meadow in the intertidal zone. In the subtidal zone there is a dependence on vegetative growth to maintain the meadow (Phillips 1972; Phillips et al. 1983b).

2.3 PHYSIOLOGICAL REQUIREMENTS AND FUNCTIONS

Table 6 includes a general list of habitat factors under which eelgrass grows (Phillips 1974).

Temperature

Eelgrass worldwide survives under a wide range of water temperatures. It appears that an overall range of 5° C to 27° C (41° F to 80.5° F) would include most areas where the plant is established. Extreme limits at which eelgrass is known to survive are a minimum of -6° C (21.2° F) in Alaska (Biebl and McRoy 1971) and a maximum of 40.5° C (104.9° F) (Arasaki 1950) measured at a substrate depth of 3-5 cm. Optimum temperatures for growth seem to lie between 10° C and 20° C (50° F to 68° F) in most areas of the world (Phillips 1974). In Puget Sound vegetative and reproductive activity occurs in a temperature range of 6.0° C to 12.5° C (42.8° F to 54.5° F). In local areas water temperatures may warm to 18° C (64.4° F) during daytime summer low tides. In the Gulf of California, Mexico, eelgrass decays when the water temperature exceeds 27° C (80.5° F).

In Netarts Bay, Oregon, water temperature varies from 8° C to 11° C (46.4° F to 51.8° F) in winter to 16.0° C to 28.5° C (60.8° F to 83.3° F) in summer (Stout 1976). The latter temperature was rare and only occurred over a tideflat during daytime summer low tides.

All seagrass species appear to have upper/lower temperature tolerance levels (Thayer et al. 1975a; McMillan 1978). McMillan (1978) subjected three different Puget Sound eelgrass populations, each with different leaf widths, to three temperature treatments. After 4 mo. each population continued to maintain its original distinct genetic limits of ecoplasticity to their environment. These tolerance levels vary with the local area (McMillan 1979; Phillips et al 1983a). Eelgrass at the northern and southern extremes of distribution on both the Atlantic and Pacific coasts appears to tolerate a much broader temperature range than eelgrass in the middle of the range (Phillips 1980).

The relationship of water temperature to eelgrass reproductive physiology was shown by Phillips et al. (1983a). Analyzing collections from a wide distributional range on both coastlines in North America, they demonstrated a significant correlation of plant activity with water temperature. It was also suggested that eelgrass may form genotypes with different temperature requirements that are selectively adapted to conditions at local sites and over a latitudinal gradient.

Biebl and McRoy (1971) demonstrated that eelgrass in Izembek Lagoon possessed a broad response to temperature. Local plants survived freezing in ice at -6° C (21.1° F), but eelgrass from Washington State and California could not. Tidepool eelgrass in Izembek Lagoon showed increased photosynthesis and survival up to 35° C (95° F), while photosynthesis and survival in subtidal plants declined above 30° C (86° F).

Short (1975) diagrammed a relationship of eelgrass productivity and water

Table 6. Numerical characteristics of eelgrass habitat factors (Phillips 1974).

Habitat factor	Vegetative growth	Flowering state	Seed germination
Temperature			
Range	-6° C to 40.5° C (21.1° to 104.9° F)	--	--
Optimum	10° C to 20° C (50.0° F to 68.0° F)	15°-20° C (8° C-9° C in Puget Sound) (59° F to 68° F; 46.4° F to 48.2° F)	5°-10° C (41.0° F-50.0° F)
Salinity			
Range	Freshwater - 42 ppt	--	--
Optimum	10-30 ppt	Same as optimum	4.5-9.1 ppt
Depth Light			
Range	1.8 m above MLLW to 30 m deep	--	--
Optimum	MLLW - 6.6 m below MLLW (11 m at high tide)	Effect unknown	No effect
Substrate			
Range	Pure firm sand to pure soft mud	--	--
Optimum	Mixed sand and mud	No effect	No effect
pH	7.3-9.0	Effect unknown	Effect unknown
Water Motion			
Range	Waves to stagnant water	--	--
Optimum	Little wave action. Gentle currents to 3.5 knots	Effect unknown	Effect unknown

temperature (after Biebl and McRoy 1971; Figure 6).

Salinity

Eelgrass is an euryhaline species (Table 6). It grows at stream mouths when the water is fresh at low tide (Osterhout 1917; Phillips unpublished research, Hood Canal, Washington) but does not grow in persistent fresh water. Tutin (1938) found eelgrass at Chesil Beach, Borest, England, where summer water salinity was as high as 42 ppt. In Puget Sound eelgrass grows best in a salinity range of 20 ppt-32 ppt. A salinity range of 10 ppt-30 ppt is optimum for growth (Ostenfeld 1908). In the Baltic Sea salinities are seasonally diluted to 6 ppt. At this time eelgrass becomes stunted (Kikuchi and Peres 1977).

In Alaska eelgrass maintained an osmotic resistance to salinity changes from freshwater to 93 ppt (Biebl and McRoy 1971). In 124 ppt leaves were killed. Positive net production was found in a range from freshwater to 56 ppt, with a maximum in 31 ppt (normal seawater). Respiration was depressed in freshwater but was only slightly affected from 31 ppt to 93 ppt. Tide pool and subtidal plants showed the same reactions. Leaves of both populations were pretreated by soaking in

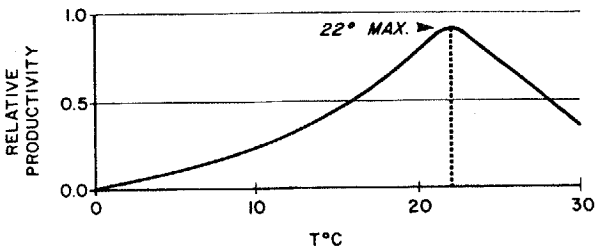

Figure 6. Relative productivity of eelgrass at varying temperatures (after Short 1975).

water of 93 ppt and then heating. Tide pool plants showed greater heat resistance than did subtidal plants.

Phillips (1972) found that salinity was the principal factor influencing eelgrass seed germination. Up to 70% of eelgrass seeds tested germinated in salinities from 5 ppt-10 ppt at all temperatures. However, at 10 ppt seed germination often doubled from 10° C to 15° C but did not do so in full strength seawater (30 ppt). The relationship of seed germination and salinity was also found by Tutin (1938; England) and Arasaki (1950; Japan). Recently, McMillan (pers. comm. 1983), working in Mexico, found that eelgrass seed germination in the annual populations there was related to temperature.

Sediments

Eelgrass colonizes sediments varying from firm sand with moderate wave action to soft mud in quiet bays (Ostenfeld 1908; Phillips 1974). Plants have been found on gravel mixed with coarse sand where growth is patchy (Tutin 1938). Sediments are not merely a static medium where the plants sink roots and anchor. Plants absorb nutrients from the sediments which stimulate leaf formation. When leaves slough from the plants, they are broken down by mechanical processes and microbes, and add organic and inorganic materials to the sediment. As this happens, shoot density may increase which not only adds more leaf litter but also forms a dense baffle and a dense rhizome-root mat that stabilizes bottom materials (Ginsburg and Lowenstam 1958, Fonseca et al. 1982a). Thus, in time, seagrasses affect the mean grain size, sorting, skewness, and shape of sediment particles, parameters that influence the redox potential of the sediments and mineral cycling processes (Swinchatt 1965, Fenchel and Riedl 1970, Burrell and Schubel 1977, Kenworthy et al. 1982). Not only do the rooted plants extract and entrap fine particles from the water, and form and retain particles produced with the grass bed, but the rhizome-root system binds and stabilizes the substrate (Burrell and Schubel 1977). Orth (1977a) found that eelgrass density was directly related to the degree of sediment stability.

Owing to the volume of falling particulate matter in the seagrass leaf baffle, an anoxic layer forms within several millimeters of the sediment surface (Fenchel and Riedl 1970). These conditions are appropriate for sulfur bacteria and the sulfur cycle, which remineralize nutrients from the entrapped litter. These bacteria reduce sulfate to sulfide and maintain a sufficiently low Eh and pH so that nitrogen mineralization particularly, proceeds faster than its use by the microbial community. Kenworthy et al. (1982) found that the highest pools of nitrogen were within the sediments of midbed locations. Smith et al. (1981a) described endobacteria in the roots of eelgrass that were associated with nitrogen fixation (Smith et al. 1981b, in Zieman 1982). Earlier, Patriquin and Knowles (1972) described nitrogen fixation in the root systems of eelgrass. The developing sediment-microbial-nutrient-seagrass complex thus develops as a system, and physical disturbances have serious effects on the substrate as a suitable site for seagrass growth. Stout (1976) and Marshall and Lukas (1970) reported the highest organic carbon content in sediments of eelgrass beds.

Eelgrass increases sedimentation rates in the beds, resulting in the concentration of fine particles (positive skewness), decrease of mean particle size, increase of organic content, increase of sediment sorting, and increase of sediment stabilization. These functions were clearly demonstrated by Stout (1976), Burrell and Schubel (1977), Orth (1977a), Churchill et al. (1978), Fonseca (1981), Fonseca et al. (1982b) and Kenworthy et al. (1982). In North Carolina, Thayer et al. (1975b) determined that mean sedimentation

rate and percent organic carbon (14 mm/yr; 1.8%, respectively) in an eelgrass bed were intermediate between an open estuarine site and a protected island site. In Izembek lagoon, Alaska, sediment composition was found to be quite variable (McRoy 1966; Figure 7). Orth (1977a) reported that sediment stability resulted in high infaunal diversity within eelgrass beds.

It is possible that the sediment texture may influence the eelgrass growth form. In Denmark, Ostenfeld (1908) found a narrow-leaved form on wave-exposed coasts on firm sand, a narrow-leaved form in shallow water on mixed sand and mud, and a wide-leaved form in deeper water on soft mud. He concluded that leaf width and length were directly related to the nature of the substrate.

Gross effects of eelgrass on sediment stabilization have been observed. Sand banks, formerly covered by eelgrass, were lowered by 30 cm (12 inches) almost overnight in Salcombe Harbor, Great Britain, after the plants disappeared in 1931 (Wilson 1949). Many species of filter-feeding invertebrates, mollusks, and several flatfishes also disappeared. Up to 29 cm (8 inches) of sediment eroded from unvegetated sand banks following a single storm in Chesapeake Bay, while little, if any, sediment disappeared from within a nearby eelgrass meadow (Orth 1977a).

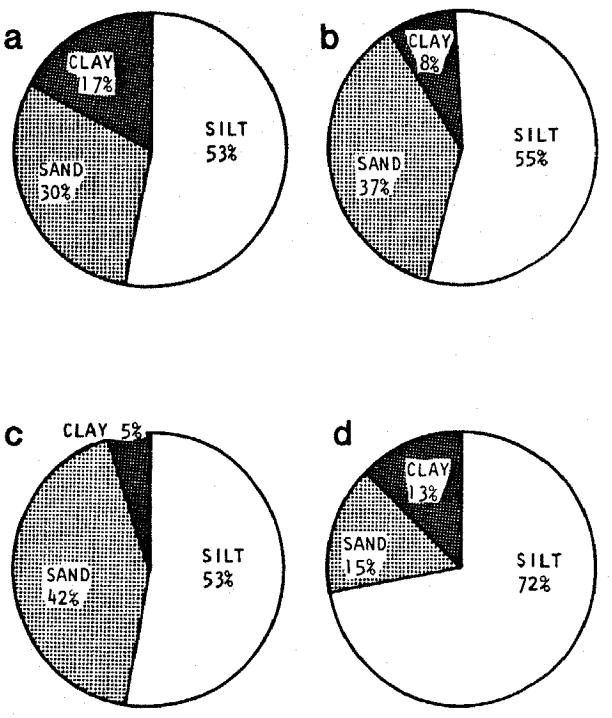

Figure 7. Sediment composition of four eelgrass beds in an Alaskan lagoon. Percentages are by weight (after McRoy 1966).

Current Velocity

Moderate current speeds appear to enhance eelgrass growth. In Puget Sound, Phillips (1972, 1974) observed the most luxuriant eelgrass where tidal currents reach 3.5 knots. Conover (1958) found that the optimum current speeds were about the average neap and spring tidal current speeds in the range of 0.6-0.8 knots (30-40 cm/sec). Inferential evidence suggests that rapid currents break down diffusion gradients across the leaf surface and make more CO_2 and nutrients available to the plants (Conover 1968). Conover also found that eelgrass biomass and production were strongly influenced by current velocity. If currents are too slow, eelgrass grows poorly and algae tend to dominate (Proctor et al. 1980b). Too much current tears leaves from the plant or erodes the substrate.

Several studies, especially the work by Fonseca on eelgrass (Ginsburg and Lowenstam 1958; Fonseca 1981; Fonseca et al. 1982a) documented the effect of seagrass leaf canopies on reducing current flow velocity and turbulence. This effect, coupled with the dense network of rhizomes and roots, established an environment of deposition within the boundaries of an eelgrass meadow, leading to large pools of nitrogen in the sediment.

Eelgrass does not grow where wave shock is regular (Ostenfeld 1908; Phillips 1974). Tutin (1938) observed only patchy growth of eelgrass on the south coast of England that was exposed to fairly heavy seas.

Oxygen

There are little data to indicate that oxygen is a limiting factor or constitutes a stress on the system. Diurnal changes can be extreme, however. Broekhuysen (1935) reported on O_2 changes in the water over an eelgrass meadow in Holland. Anoxic conditions prevailed from 1:00 am until 6:00 am. At 3:00 pm there was a 360% saturation of O_2 in the water (Figure 8). He reasoned that animals within the eelgrass meadow must be adapted to the anoxic conditions and to the lowered pH levels attendant with the low O_2. Imai et al. (1951) recorded that the dissolved O_2 concentration markedly decreased when large mats of eelgrass blades decayed. However, this led to a bloom of Monas sp., which was eaten by oysters and other filter-feeding macrobenthos. Apparently low O_2 concentrations in water over eelgrass beds do not harm animal communities in the system.

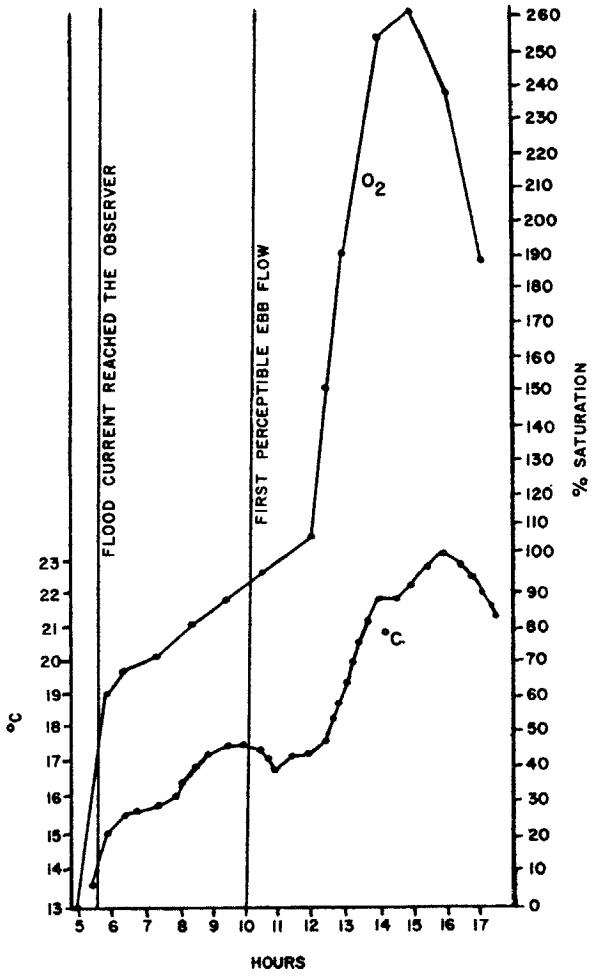

Figure 8. Oxygen changes in an eelgrass bed over time (after Broekhuysen 1935).

Suda (1974) found gross oxygen production and respiration of an eelgrass community in summer to be 5.49-10.87 $gO_2/m^2/day$ ($\bar{X}$ =8.07), while respiration was 3.92-7.99 $gO_2/m^2/day$ ($\bar{X}$=5.70). Short (1975) diagrammed the variation of eelgrass production by its relationship to O_2 evolution over a period of a year (Figure 9).

McRoy (1966) demonstrated that eelgrass is capable of anerobic respiration.

Solar Radiation

Although light energy is the single most important forcing function on all ecosystems, it is seldom measured, even in studies of productivity (Zieman and Wetzel 1980). Recent studies, however, noted a relationship in eelgrass production as a function of radiative energy (Dillon 1971; McRoy and McMillan 1977; Dennison 1979; Dennison and Alberte 1982). In North Carolina, Dillon (1971) found production to be 6.6-9.3 $mgC/m^2/langley$, while eelgrass production in Alaska was 12.9-14.4 $mgC/m^2/langley$. Eelgrass in North Carolina produced 7.5-44 mgC/dry wt/langley, while in Alaska production was 13.5-17 mgC/g dry wt/langley. McRoy

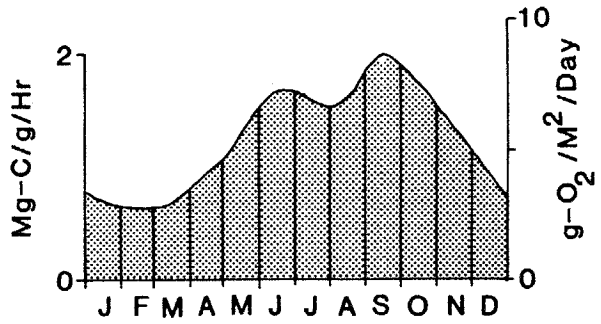

Figure 9. Production of organic carbon and release of oxygen by eelgrass in Charlestown Pond, Rhode Island (after Short 1975).

(1974) and Williams and McRoy (1982) reported that seagrass productivity in seven North American seagrass species was a function of irradiance (estimated by ^{14}C uptake). They also found that in multispecies systems, colonizer species had uptake rates up to four times greater than climax species.

Lower depth limits of seagrass growth depend on a number of interrelated factors: availability of suitable substrate, current velocity, light penetration, exposure to waves, and turbidity (Thayer et al. 1975a; Phillips 1980). In Puget Sound and in Oregon, light penetration in winter appears to be a limiting factor (Phillips 1972; Stout 1976). Eelgrass transplants were made in July 1970 at 1.5 m (5 ft), 3 m (10 ft), and 4.5 m (15 ft) deeper than the lowest depth limit of eelgrass in Puget Sound. All transplants survived until winter. In March 1971 the eelgrass at 3 m and 4.5 m lower than the natural depth limit had died. Stout (1976) theorized that sedimentation and turbidity brought about by logging are major limiting factors on depth of eelgrass growth in the Pacific Northwest. Burkholder and Doheny (1968) stated that eelgrass was limited to substrates where at least 1% of the incident light remains. They noted in South Oyster Bay, Long Island Sound, New York, that eelgrass leaves were longer in shallow water 1 m (3 ft) deep than at 1.8 m (6 ft) deep. Leaves in water 2.4 m (9 ft) deep were only 25% as long as those at 1 m deep. At many stations light intensity at 1 m deep was only 19%-30% of its incident value at the surface. Optimum light intensity for eelgrass production varies between 0.42 and 0.92 langleys/minute (Short 1975). McRoy (1974) and Burkholder and Doheny (1968) found the optimum light level for growth to be 50% of the maximum incident light occurring during the growth period.

Eelgrass has been reported down to 30 m (100 ft) deep off San Diego, California (Cottam and Munro 1954). Other depth records of eelgrass extend to 18 m (60 ft) in the Triest Gulf (Techet 1906) and to 20 m (67 ft) in the Black Sea (Caspers 1957). In Denmark, Ostenfeld (1908) found that eelgrass grew to 11 m (37 ft) in clear water but only to 5.4 m (18 ft) in turbid water. Depth is even less when water is more turbid (Burkholder and Doheny 1968).

One study done in an Oregon estuary determined that the most important water quality parameter related to eelgrass was turbidity (OSU 1977). The amount of light reaching the leaf blades is limited by shading, by plant density, leaf length and width, and the age of the leaf surface as it accumulates epiphytic growth (Proctor et al. 1980b). In Alaska, Dennison (1979) found that eelgrass leaf parameters respond to changes in light quality and quantity. These light changes occur seasonally and at different tidal stages as the leaf canopy is erect or bends as the tide recedes. The greatest leaf area was found in the lower one-third of the canopy height and diminished above and below that point (an adjustment to shading when leaves were bent over), while leaf biomass was greatest near the bottom and decreased near the top of the canopy. When light to the plants was increased using reflectors, increased leaf production rates were obtained. Dennison and Alberte (1982) noted that eelgrass is adapted to very low light conditions; in particular the light compensation rates, saturation points, photosynthetic rates, and respiration rates are much lower than other higher plants. They found that deeper water eelgrass adjusts to changes in the light regime by changing its leaf production rates (a lowered light regime results in a greatly lowered production rate). Eelgrass in shallow water was not affected by light changes. Shading experiments have shown that rapid reductions in density and standing stock occurred as a result of decreased irradiance (Backman and Barilotti 1976; Dennison 1979; Dennison and Alberte 1982). In California, eelgrass density decreased 18 days after installation of shading canopies which resulted in a decrease in down-welling illuminance of 63% (Backman and Barilotti 1976). After 9 months shoot densities declined to 5% of the adjacent unshaded control. Flowering percentage was also reduced under the shading canopies.

It is evident that turbidity caused by dredging, sewage, oil, and plankton blooms can have far-reaching effects on eelgrass. It is possible that if eelgrass declines

enough, increased erosion of bottom sediments could occur which would affect their recovery. Following the disappearance of eelgrass in some lagoons in Denmark in 1931, sediment eroded away down to the cobble base, and Fucus sp. invaded. No eelgrass ever returned (Rasmussen 1977).

Zonation

Harrison (1979) noted that Z. japonica grows higher on the shore than does eelgrass. Desiccation has been given as the major factor limiting the upper intertidal distribution of eelgrass (Johnson and York 1915; Phillips 1972). Harrison (1982b) experimentally confirmed the low resistance of eelgrass to desiccation and found that Z. japonica was much more resistant to desiccation. Occasionally, eelgrass is so dense that it retards the runoff of water over a tideflat of low relief at ebb tide. This occurs in Izembek Lagoon, Alaska (Dennison 1979) and in Netarts Bay, Oregon (Stout 1976). In these areas it is likely that plant production is greatly enhanced in these lagoons.

There have been a limited number of attempts to place eelgrass in a successional scheme leading to the creation of a marsh (Jefferson 1975). It is true that eelgrass meadows trap and stabilize a great quantity of sediment and that the sediment level may be raised over time. There is absolutely no evidence, however, that this type of habitat succession has ever occurred anywhere. The presence of eelgrass leaf fragments underlying marsh litter (Jefferson 1975) is not evidence that eelgrass succeeded to a marsh habitat. It means that eelgrass leaf litter became trapped by an adjacent marsh and was buried under litter from the marsh.

CHAPTER 3
THE EELGRASS SYSTEM

3.1 FUNCTIONS OF THE EELGRASS SYSTEM

All seagrasses perform a number of functions in their environments. Depending on the size and growth form of the plant, the seagrass species can modify the physical and biological environment to some degree. In the tropics, early successional genera, Halophila and Halodule, and temperate species such as Z. japonica and Z. noltii, have shallow root systems and small blades and produce little litter. As ecological succession in multispecies systems proceeds to climax species with their large dimensions, high litter production, and deep penetrating roots, the environment can be modified in more dramatic ways. Except for surfgrass, Phyllospadix, which grows on rocky substrates, seagrasses occur on unconsolidated substrates, mostly of uniform relief. Owing to their presence on and penetration into their substrates, seagrasses create a diversity of habitats and substrates, providing a structured habitat from a structureless one (Phillips 1972, 1978).

Zieman (1982) recently revised a list of seagrass functions that were originally enumerated by Wood et al. (1969):

1. High production and growth

   The ability of seagrasses to exert a major influence on the marine seascape is due in large part to their extremely rapid growth and high net productivity (leaves typically grow 5 mm/day but can attain 10 mm/day).

2. Food and feeding pathways

   Seagrass material may follow two energy pathways: direct grazing on the living plant material or utilization of detritus from decaying seagrass material, primarily leaves. Both living and detrital material may be exported from its original source.

3. Shelter

   Seagrass beds serve as a nursery ground for food and shelter for juveniles of a variety of finfish and shellfish of commercial and recreational importance.

4. Habitat stabilization

   Seagrass stabilizes sediments in two ways: a. leaves slow and retard current flow, reducing water velocity near the sediment-water interface, which promotes sedimentation of particles and inhibits resuspension of organic and inorganic material; b. rhizomes and roots form an interlocking matrix, which bonds sediment and retards erosion.

5. Nutrient effects

   Detrital production and sedimentation provide organic matter for sediments and maintain an active environment for nutrient recycling. Seagrasses and epiphytic algae can fix nitrogen, adding to the nutrient pool. Seagrass absorbs nutrients from the sediments and releases them into the water from the leaves, acting as a nutrient pump for the sediment.

3.2 BIOMASS

The terms used to describe biomass will follow the definitions in Zieman and Wetzel (1980): standing crop refers to above-sediment material, while biomass refers to the weight of all living plant material. Both are expressed as mass per unit area.

Representative densities are reported, but density can vary seasonally, with depth, and with substrate nutrients and texture. A few values will be listed for comparative purposes (Table 7).

As with density values, biomass also varies widely. It appears that the pattern first noted by Ostenfeld (1908) of decreased density on firm sand and increased density on softer substrates may be the only correlation possible. Most of the biomass of eelgrass is in the sediments. Depending on the season, the ratio of leaves:rhizomes-roots varies from 1:1 in summer to 1:2 or greater in winter in Puget Sound (Phillips 1972). These same ratios were found in eelgrass in Denmark (Sand-Jensen 1975). In Long Island, New York, Burkholder and Doheny (1968) found eelgrass leaf-shoot:rhizome ratios of 2:3 in sand and 10:3 in mud. In southern British Columbia, Canada, eelgrass ratios varied from 0.8 to 1.6 (Harrison 1982c). He has made the only analysis of leaf:rhizome-root ratios in Z. japonica (2.0-2.6). Recently, Kenworthy (1981) also reported a shift in leaf:root ratios from those in favor of leaves to roots with a shift in substrates from mud to coarse sand. Kentula (1983) reported leaf-shoot:rhizome-root ratios varying from 1:1 to 1:10 along intertidal transects of eelgrass in Netarts Bay, Oregon. In one study, Smith et al. (1979) determined that eelgrass root and root hair surface areas were 48.2 and 138.9 mm^2 root, respectively. In the tropical colonizing species Halodule wrightii, the root and root-hair surface areas were 34.8 and 19.2 mm^2 root, respectively.

In Table 7 only standing crops will be reported. The smallest seagrass standing crop was 6g dry wgt/m^2 in Humboldt Bay, California (Waddell 1964), while the highest value was 2,060 dry wgt/m^2 (Burkholder and Doheny 1968). Work done to date implies that biomass parameters reflect the nature of the substrate.

Caloric values of eelgrass tissue have only rarely been reported. In North Carolina, caloric values ranged from 3.54 cal/mg ash-free dry wt in January to 4.82 cal/mg ash-free dry wt in June to 5.73 cal/mg ash-free dry wt from April-May during flowering (annual mean was 4.48 cal/mg; Thayer et al. 1975b). There was seasonal variation noted. In Izembek Lagoon, Alaska, McRoy (1966) reported a mean of 4.125 cal/mg ash-free dry wt for leaves and 3.967 cal/mg ash-free dry wt for rhizomes.

3.3 PRODUCTIVITY AND MEASUREMENT

A number of reports have documented seagrass meadows as one of the richest and most productive of ecosystems, rivaling cultivated tropical agriculture in productivity (summarized by Zieman and Wetzel 1980). The earliest work to relate the value of eelgrass to inshore ecosystems was the work of Petersen (1891, 1913, 1918) and coworkers at the Danish Marine Biological Station (Petersen and Boysen-Jensen 1911; Ostenfeld 1908; Boysen-Jensen 1914; Blegvad 1914, 1916). These scientists concluded that organic detritus, derived chiefly from the decay of eelgrass, was the basic source of nutrition of animals in Danish coastal waters, especially the benthic invertebrates and that the abundance of fish in Denmark was due chiefly to eelgrass.

Estimates have shown that eelgrass can attain productivities up to 8 gC/m^2/day and an annual production of 500 gC/m^2. Several factors are directly correlated with eelgrass productivity: light, temperature, carbon supply, nutrient supply, and plant density. Thus, there are hourly, daily, and seasonal differences at local sites as well as over a geographic gradient. In addition, methods of analyzing productivity vary in reliability from leaf marking (Zieman 1968), ^{14}C uptake (Bittaker and Iverson 1976), harvest method (Petersen 1913; Phillips 1972; Mukai et al. 1979), to relating biomass to the plastochrone interval (P.I.; Patriquin 1973; Jacobs 1979). No

Table 7. Representative eelgrass density and standing crop (g dry wt/m^2). Numbers represent means for stations sampled.

Species	Location	No. of veg. shoots/m^2	No. of repro. shoots/m^2	Standing crop	Source
Zostera marina	Mexico Gulf of California	0	555 (April)	--	Phillips et al. 1983b
	California Humboldt Bay	31-361	--	6-420	Keller 1963, Waddell 1964, Keller and Harris 1966
				140-730	Harding and Butler 1979
	Oregon				
	Yaquina Bay	14-164	17-91% (less at MLLW; greatest at higher elevations)	209	Bayer 1979a
	Netarts Bay	500-3,845	5-65	7-256	Kentula 1983
	Washington				
	Grays Harbor	74	--	--	Smith 1976
	Hood Canal	62-287	7-10	--	Phillips et al. 1983b
	Whidbey island	71-861	5-66	95-540	Phillips 1972, Phillips et al. 1983b
	Canada				
	So. British Columbia	25-150	1-18	4-88(biomass)	Moody 1978, Harrison 1982c
	Alaska				
	Various locations	243-650	4-100	--	Phillips et al. 1983b
	Izembek Lagoon	740-4,380	48-653	186-1,840	
	North Carolina	--	--	50-550	Dillon 1971, Thayer et al. 1975a, Penhale 1977, Phillips et al. 1983b
	New York	--	--	250-2,060	Burkholder and Doheny 1968
	Rhode Island	629-2,044	67	--	Phillips et al. 1983b
		88-275	8-344	--	
	Canada				
Z. japonica	So. British Columbia	160-450	70-150	4-20(biomass)	Harrison 1982c

estimates are reported on work done using metabolic techniques; namely, the O_2 production method, owing to the uncertainty of equilibration of O_2 in seagrass leaves, its rate of internal use, and periods of extremely rapid release (Zieman 1982). Table 8 lists representative production values of eelgrass, epiphytes, and microphytic and macrophytic algae among the eelgrass, as well as listing the leaf area index (LAI) for comparative purposes. For the most part the values reflect above ground production. Few rhizome-root production estimates have been made. Those made by Mukai et al. (1979) were done using the

Table 8. Primary production of components of the eelgrass ecosystem.

Component	Location	Productivity ($gC/m^2/yr$)	Turnover rate	LAI	Source
Eelgrass plant	California Humboldt Bay	266 (assume growing season Apr. to Oct.)	--	--	Harding and Butler 1979
	Oregon Netarts Bay	712 (intertidal; aboveground)	10 times per year	0.3-15.9	Kentula 1983
		474 (intertidal; belowground)	6.3 times per year	--	
	Washington Puget Sound	84-480	--	1-4	Phillips 1972
	Alaska	180-320	--	--	McRoy 1966
		396-456	--	12-21	McRoy 1970a, 1970b
	North Carolina	90-306	--	--	Dillon 1971
		330	--	--	Penhale 1977
	Denmark	328 (aboveground)	--	--	Sand-Jensen 1975
		87 (belowground)	--	--	
	France	389 (aboveground)	--	--	Jacobs 1979
		183 (belowground)	--	--	
Epiphytes	Oregon Netarts Bay	23-75	--	--	Kentula 1983
	North Carolina	60	--	--	Penhale 1977
	Massachusetts	20	--	--	Marshall 1970
Microphyte algae	Oregon Netarts Bay	81 (assume 10-hr day; growing season Apr. to Oct.)	--	--	Davis 1981
Macrophyte algae	Oregon Coos Bay	490 (Ulva)	7-19	--	Pregnall 1983
		1,700 (for total green algal mat)			
	Netarts Bay	8,100 (assume 10-hr day; growing season Apr. to Oct.)	--	--	Davis 1981
		(Ulva, Enteromorpha)	--		
		3,600 (Gracilria)			
	Washington Grays Harbor	2,122 (Enteromorpha; (same assumptions as for Netarts Bay)	--	--	Thom 1981

harvest method, while those done by Jacobs (1979) and Kentula (1983) incorporated the P.I. method.

In most cases production values were made as g dry wt/m^2/yr. These were converted to gC/m^2/yr with a conversion factor of 37% (Westlake 1963).

Leaf marking methods have been used successfully to estimate net production (Zieman 1974, stapling; Sand-Jensen 1975, felt-tip pen; Kentula 1983, plastic line). Blades are marked at the base, harvested after a time period, and weighed. This method gives results where the standard error is at most ± 15% of the mean (Kentula, pers. comm.). This method does not account for below-ground production, excreted carbon, herbivory, or leaf loss.

The ^{14}C method measures production near net productivity (Bittaker and Iverson 1976). After correction for several factors, differences from estimates made by leaf markings were insignificant. The method is highly sensitive but requires sophisticated and expensive field and laboratory equipment.

The harvest method estimates net production by subtracting minimum from maximum biomass or by doubling maximum standing crop (Peterson 1913, Grontved 1958, Phillips 1972). These estimates do not account for leaf loss. Zieman and Wetzel (1980) stated that this method should be avoided, owing to gross inaccuracies.

The last method incorporated a series of biomass changes to the P.I. (Patriquin 1973, Jacobs 1979). The technique appears to be the only practical method of determining below-ground production where equipment necessary for ^{14}C is not available.

Relatively little work has been done on the primary production of the other components of the eelgrass ecosystem (Table 8). It is evident that epiphyte loads on eelgrass leaves have a dramatic effect. On the one hand heavy growths may weigh down the leaves and remove them from the optimal portion of the light column and shade them (Figure 10). Sand-Jensen (1977) reported that eelgrass photosynthesis was reduced 31% by epiphytes, primarily the diatom Cocconeis scuttelum, a common species on eelgrass in the Pacific Northwest. Penhale (1977) found that eelgrass epiphytes could constitute up to 24% of the standing crop of eelgrass (24.7 g dry wt/m^2) with an hourly productivity nearly equal to that of the eelgrass (0.65 mgC/g/hr for epiphytes; 0.88 mgC/g/hr for eelgrass). Owing to the small biomass, the annual production of epiphytes was estimated to be 18% of the eelgrass. McRoy and McMillan (1977) found that in Alaska growths of a diatom, Isthmia nervosa, may constitute up to 50% of the eelgrass plus epiphyte dry weight. In Oregon, Kentula (1983) found epiphyte biomasses varying from 25%-31% of the eelgrass biomass, depending on the season (0.4 g epiphytes/g leaf to 2.3 g epiphytes/g leaf).

Microphyte algae have received much less attention. Brown (1962) estimated net production at 0.24 g/m^2/day in New England salt pond (eelgrass was 2.2 g/m^2/day). Gargas (1972) reported values of 50 mgC/m^2/day in an eelgrass bed (maximum value in summer: 5 gC/M^2/yr). McRoy et al. (1973) found that eelgrass epiphytes could fix nitrogen in some tropical species.

Davis (1981), working in Netarts Bay, Oregon, found that net production of microalgae (predominantly diatoms) was 0.045 gC/m^2/hr, that of Enteromorpha and Ulva was 4.5 gC/m^2/hr, and of Gracilaria was 0.2 gC/m^2/hr (the latter three are macroalgae commonly found among eelgrass).

Figure 11 diagrams the proportional relationships of standing crop and productivity in an estuary (after Thayer et al. 1975a).

The excretion rate from eelgrass was shown to be 1.5% of the carbon fixed in photosynthesis, while that of the epiphytes on eelgrass was 2.0%; the excretion rate from heavily epiphytized eelgrass was 0.9% (Penhale and Smith 1977). In the estuarine system near Beaufort, North Carolina, they also established that eelgrass excreted 5.0 gC/m^2/yr, and the epiphytes excreted 1.5 gC/m^2/yr. They concluded that eelgrass and its epiphytes contributed 47% of their

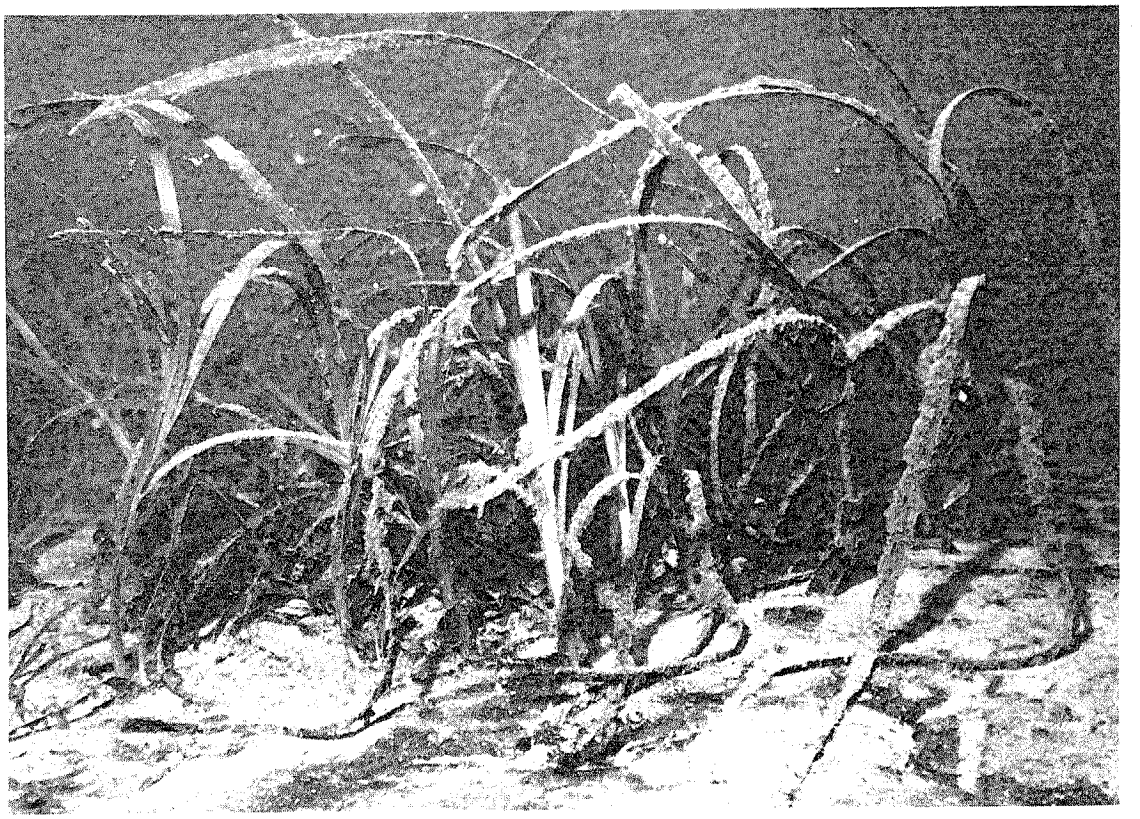

Figure 10. Eelgrass at Blakely Island, San Juan Islands, Washington, showing very heavy epiphyte loads.

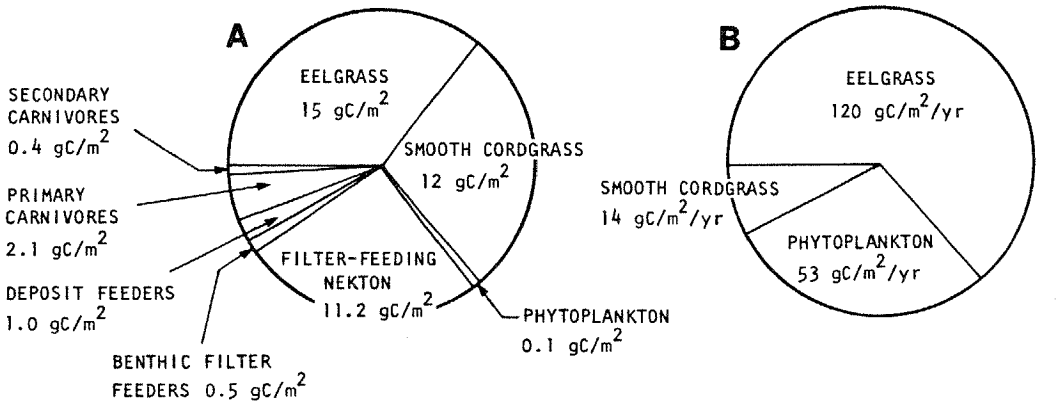

Figure 11. Proportional relations of standing crops and productivity in a North Carolina estuary: A. Relation among standing crops (in terms of carbon) or organisms in an estuary near Beaufort; B. organic production by the major plants in the system (after Thayer et al. 1975a).

total annual primary production and 14% of their total excreted material into the estuarine system.

3.4 ORGANIC AND INORGANIC NUTRIENT CYCLING

The anatomy of eelgrass, like that of all other seagrasses, is modified for metabolism, growth, and reproduction in the sea.

1. The cutin layer over the leaf is thin.

2. Leaf blades are flattened and thin with a very high surface-to-volume ratio.

3. There is an extensive lacunal system which gives buoyancy (they store and transport a great quantity of O_2 and CO_2.

4. Chloroplasts are densely packed in the epidermal layer surrounding the leaf.

5. There is an aerenchyma composed of large, thin-walled cells which adjoin the lacunae and facilitate gas and solute diffusion.

6. There is a reduced amount of mechanical support, allowing the leaves to flex and bend on an ebbing tide, which maintains their wetness and guarantees exposing as much photosynthetic surface to solar radiation as possible. At the same time the leaves are strong enough to resist breaking when they are whipped during wave action (Ferguson et al. 1980; Zieman 1982).

The major problem with procurement of certain nutrients, such as carbon, by seagrasses is that rates of gaseous diffusion in water are several orders of magnitude lower than in air. Also, when the pH of seawater rises during very active photosynthesis (from 8.2 to 8.9 or higher), free CO_2 in the water is greatly reduced or becomes unavailable, as does the HCO_3^- ion. It is now known that seagrasses obtain most of their nutrients from the sediments, which maintain a much lower pH in the deep anoxic layer beneath the very thin surface oxic zone.

Numerous papers have documented the uptake of nutrients (carbon, phosphorus, and nitrogen, in particular) from the sediments by the root system, translocation through the seagrass plant, and release to the epiphytes and water column. The plants and epiphytes can also absorb these nutrients from the water to release them to the interstitial water in the sediments (McRoy and Barsdate 1970; McRoy et al. 1972; McRoy and Goering 1974; Harlin 1975, 1980; Penhale and Smith 1977; Wetzel and Penhale 1979; Penhale and Thayer 1980; Short 1981). All the available work done states that sediments are the preferred source for nutrient uptake.

These laboratory experiments were reinforced by recent field experiments using fertilizers. Orth (1977b) used Osmacote (14-14-14; a slow-release fertilizer), placed in the sediments, and observed dramatic increases in plant standing crops. Eelgrass root/rhizomes increased 30%, the leaf crop was three to four times higher, and shoot density increased. Increases in the standing crop were also observed following fertilization of eelgrass in Rhode Island (Harlin and Thorne-Miller 1981).

Even though eelgrass needs a variety of macro- and micronutrients, most of the research has concentrated on carbon, phosphorus, and nitrogen. Phosphorus supply does not appear to be limiting. In Alaska, McRoy and Barsdate (1970) found that eelgrass plants were a phosphorus pump from the sediments to the water column, but in North Carolina the roots retained most of their absorbed phosphorus (Penhale and Thayer 1980). McRoy et al. (1972) estimated that phosphorus turnover times in the eelgrass meadows in Izembek Lagoon, Alaska, vary from two turnovers per year to one every 2 years.

Eelgrass has three sources of inorganic carbon (CO_2, HCO_3^-): recycled from respiration and photorespiration, the water column (which is not a likely source during active photosynthesis, owing to an

increase in pH), and the sediments (Wetzel and Penhale 1979). Penhale and Thayer (1980) found that most of the inorganic carbon found in the eelgrass plant entered through the root system. Of that amount 72.4% remained in the roots, 24.4% was transported to the leaves, and 3.2% was transferred to the epiphytes (bacteria, micro- and macroalgae). Eelgrass, however, is very inefficient in using inorganic carbon in photosynthesis. The photosynthetic use of this transported carbon was only 5%-20%, the remaining CO_2 passing through the leaves was released to the water as CO_2 (Wetzel and Penhale 1979). They also found that the supply of inorganic carbon from the combined sources of respiration, photorespiration, and the water is in excess of that needed for photosynthesis.

Eelgrass leaks an appreciable amount of its photosynthetically fixed carbon as dissolved organic carbon (DOC). Penhale and Smith (1977) found that eelgrass lost 1.5% of its fixed carbon as DOC (epiphytes removed), heavily epiphytized plants lost just 0.9% as DOC, while the epiphytes alone lost 2.9% as DOC. Wetzel and Penhale (1979) found somewhat higher amounts. They reported that eelgrass could excrete as much as 5.2% of the fixed carbon as DOC. Excretion rates were much higher in the light than in the dark; these rates increased when the plants were dried.

In 1976 Benedict and Scott suggested that C_4 metabolism occurs in some seagrasses. It is now known that of 11 species of seagrasses, including eelgrass, only one species (Cymodocea nodosa) has C_4 metabolism.

Various isotopes of carbon occur in the water. Seagrasses do not use these isotopes in the ratios found in nature but tend to accumulate the lighter, more mobile ^{12}C isotope over the ^{13}C form (Zieman and Wetzel 1980). The ratios of $^{13}C/^{12}C$, called the $\delta\ ^{13}C$ or del ^{13}C ratio, are relatively high in seagrasses. In a review of 12 genera and 47 species, McMillan et al. (1980) found that 45 species were within the range of -3 to -19 ppt (two species of Halophila were lower). Several studies determined that animals approximate the isotopic composition of their diets and that the del ^{13}C ratio of seagrasses may be used as a natural food tracer (Thayer et al. 1978; Fry and Parker 1979; McConnaughey and McRoy 1979). McMillan et al. (1980) determined that the del ^{13}C ratio for eelgrass varied from -7.8 to -12.4 ($\bar{X}$ = -9.9) and that for Z. japonica in Willapa Bay, Washington, varied from -15.3 to -16.3 ($\bar{X}$ = 15.8).

Nitrogen is needed in much greater quantities and can be rate limiting (McRoy and McMillan 1977; Short 1981). There are four potential sources of nitrogen in an eelgrass meadow: (1) nitrogen fixation, (2) nitrogen in the water column, (3) recycled nitrogen in the sediments, and (4) leaf deposition (Kenworthy et al. 1982; Zieman 1982).

Patriquin and Knowles (1972) first reported nitrogen fixation in the rhizosphere of eelgrass. This was refuted by McRoy et al. (1973) but is now considered to occur. Smith et al. (1981a) reported endobacteria in roots of eelgrass. These endobacteria were associated with nitrogen fixation (Smith et al. 1981b). Nitrogen fixation definitely occurs in the rhizosphere of Thalassia of the tropical Atlantic (Capone et al. 1979; Zieman 1982). Nitrogen fixation also occurs on the phyllosphere of eelgrass blades. McRoy and Goering (1974) found that the amount fixed by epiphytic blue-green algae was greatest in tropical species but was not unimportant in eelgrass, considering the great need for nitrogen in the system. In Thalassia, Capone et al. (1979) found that nitrogen fixed at the blade contributed primarily to the epiphytic community. Zieman (1982) reported that 20% to 50% of the nitrogen requirements of the Thalassia meadow could be supplied by nitrogen fixation in the rhizosphere. Nitrification in Thalassia meadows was highest on the developing margins and lower in the center where trapping and retention of the particulate material was greater. This was also found in eelgrass meadows in Alaska by Short (1981).

The nitrogen in the leaves and that fixed by epiphytes is carried down to the sediments as whole leaf matter and detritus (Harrison and Mann 1975b). Nitrogen in the sediments arises also from

plant and animal excretion (NH_4^+) and dead root/rhizome decay (NO_2^-, NO_3^-). In seagrasses the primary source of nitrogen for leaf production is recycled material from sediments (Thalassia: Capone and Taylor 1980, Orth 1973). Until recently it was difficult to understand how nitrification could occur in the reduced root zone, but Iizumi et al. (1980) deomonstrated that eelgrass roots excrete O_2 into the anoxic sediments. This creates oxygenated microzones around the roots, resulting in the nitrification of ammonia (which can be readily assimilated by eelgrass roots, rhizomes, and leaves) to nitrate for uptake by roots.

Kenworthy et al. (1982) found highly significant correlations between density of eelgrass vegetation (related to production of detached leaf material and detritus and ability to trap and hold it), organic matter in the sediment, fine sediments, and the total nitrogen pool. They reported an increasing gradient in all parameters from unvegetated sediments to the edge of a meadow to the midbed region. The nitrogen pool in the midbed regions was composed of exchangeable ammonium, ammonium dissolved in the sediment interstitial pores, and total nitrogen.

Recently several studies have shown the cycling of trace metals in an eelgrass system. In North Carolina, Wolfe et al. (1976) analyzed more than 50 species of organisms in an eelgrass bed for manganese, iron, copper, and zinc. These organisms included eelgrass, dominant macroalgae, epifauna, infauna, and nekton. The detritus and sediments were also analyzed. Results showed that eelgrass accumulated significant fractions of these metals but that the metal contents in all other trophic compartments were very small relative to that in eelgrass. They did find high manganese contents in bay scallops. In another study in the same estuary, Drifmeyer et al. (1980) found that content of the four metals varied significantly in different parts of the eelgrass plant (aboveground tissues contained the most), and that imported and exported blade particles did not differ in metal content. Eelgrass biomass was the largest biological reservoir, and blade senescence and decomposition were responsible for the largest biological flux of these elements in the system. Brinkhuis et al. (1980) found that cadmium and manganese, specifically, remain complexed in the sediments under anoxic conditions. When the sediments become oxidized, these metals may become bioavailable. Eelgrass absorbs cadmium and manganese through both the roots and leaves. Cadmium is transported both upwards and downwards, but the roots form a cadmium sink (also found by Faraday and Churchill 1979). Old roots/rhizomes deposit their greater contents of cadmium in the sediment sink. Manganese is more readily fixed by leaves with little transport between leaves and rhizomes/roots. Some manganese does enter the anoxic sink. They also warned that the mechanics of the metal ions varied widely from element to element and species to species in the same genus.

The role of detritus in marine food webs was first recognized by Danish investigators (Boysen-Jensen 1914, Petersen 1918). This view was enlarged by Mann (1972). Detritus is not described as the driving force in the exchange of nutrients in most seagrass ecosystems (Wood et al. 1969, Barsdate & Nebert 1974, Thayer et al. 1975a).

The degradation of plant material involves its reduction through a spectrum of sizes to a level of smaller molecues (Darnell 1964). Wetzel et al. (1972) defined detritus as organic carbon lost by nonpredatory means from any trophic level (egestion, excretion, secretion) or inputs from external sources that enter the cycle in the system. Senescent seagrass leaves recently released may be initially broken by physical fragmentation, but ultimately become detrital matter through microbial (bacteria, fungi, flagellates, ciliates) colonization and activities and physical handling by consumers (amphipods, etc; cf, Zieman [1982] and Klug [1980] for reviews). Burkholder and Doheny (1968) determined that eelgrass was nearly completely processed into particulate matter in 30 days. Harrison and Mann (1975a) found a 35% reduction of eelgrass detrital dry weight after 100 days at 20° C (68° F), concluding that eelgrass detritus decomposes slowly. Godshalk and Wetzel (1978) also found that eelgrass

particulate matter and DOM were highly resistant to decomposition. They related this to the ultrastructure of eelgrass; i.e., a high content of structural tissue (23.2% hemicellulose, 22.1% cellulose, 7.3% lignin), and adaptation to a harsh environment.

As senescence of eelgrass blades begins, the nitrogen content declines (Boysen-Jensen 1914; Harrison and Mann 1975b; Thayer et al. 1977) but increases in the detritus (Harrison and Mann 1975b; Thayer et al. 1977) as does the phosphorus content (Thayer et al. 1975b; Fenchel 1977). Thayer et al. (1977) also reported that the organic carbon content increased on a gradient from living to dead leaves to detritus (on an ash-free dry weight basis). The increase of nitrogen in detritus relative to the dead leaves suggested nitrogen mobilization from the water into the detritus by the microbial coating.

Detritus as such tends to be poor in essential nutrients. Bacteria locate as a film around the particles, and while acting enzymatically on them, enrich them with nitrogen, phosphorus, and organic carbon. In this sense detritus may act as a nutrient pump from the water column to the sediment when detritus settles to the bottom. Thus, microbial decomposition of detritus is of prime importance in nutrient release and cycling.

There is much evidence that the real nourishment for animals which utilize detritus is the microbial layer (Newell 1965; Fenchel 1970, 1972; Mann 1972; Tenore 1977). After stripping off the microbial layer, the invertebrates egest the particles which again become clothed with a microbial layer. As this continues the particle size becomes reduced, owing to enzymatic activity of the microbes. As the particle sizes decline, they become available to various classes of consumers, e.g., filter feeders and deposit feeders, polychaetes, zooplankton, and gastropods, which are only able to ingest fine particles less than 0.5 mm in diameter (Zieman 1982). Harrison (1977) found that the detrital material was repeatedly ingested until it was completely utilized. Gammarid amphipods were particularly important in ingesting eelgrass particles, resulting in their reduction in size. There is some evidence that physical fragmentation of the particles leads to an increased microbial respiration rate which is also stimulated by the feeding activities of animals (Fenchel 1977; Harrison and Mann 1975a). Decomposition rates of detrital particles are directly related to the particle size (Harrison 1977; Godshalk and Wetzel 1978). This is due to the much higher surface volume ratios of the smaller particles and the increased microbial respiration rates on them. Larger plant material and detritus may either become deposited onto the sediment surface and incorporated into the sediments, or exported from the eelgrass system. The smaller the particle (less than 0.5 mm), the more easily it is resuspended and dispersed (Zieman 1982).

Owing to the high rate of detrital deposition on the bottom, and the great numbers of microbes on the plant material and in the sediments, anaerobic (reducing) conditions are maintained in the sediments of eelgrass beds below a thin (few millimeters) surface oxidized layer. O_2 diffusion is decreased by these conditions. Seagrass and other plant detritus is mineralized under these anaerobic conditions. These conditions favor the development of sulfur bacteria, forming sulfides that create a sink for organic nutrients and metals in the sediments.

Several decomposition processes occur which are characteristic of the anaerobic layers (Fenchel 1977): (1) bacteria ferment the detritus in the absence of O_2 as a respiratory electron acceptor; (2) CO_2, NO_3, and SO_4 are also used as respiratory electron acceptors; and (3) end products of the anaerobic pathways are methane, ammonia, or nitrogen gas, and H_2S (Figure 12). H_2S reacts with metals, forming a sink for many heavy metals, releasing phosphate to the system in the process. There is evidence that anaerobic decomposition in the presence of sulfate produces six times more organic matter than aerobic decomposition produces (Fenchel 1972).

3.5 PLANT CONSTITUENTS

A number of studies have been done on the

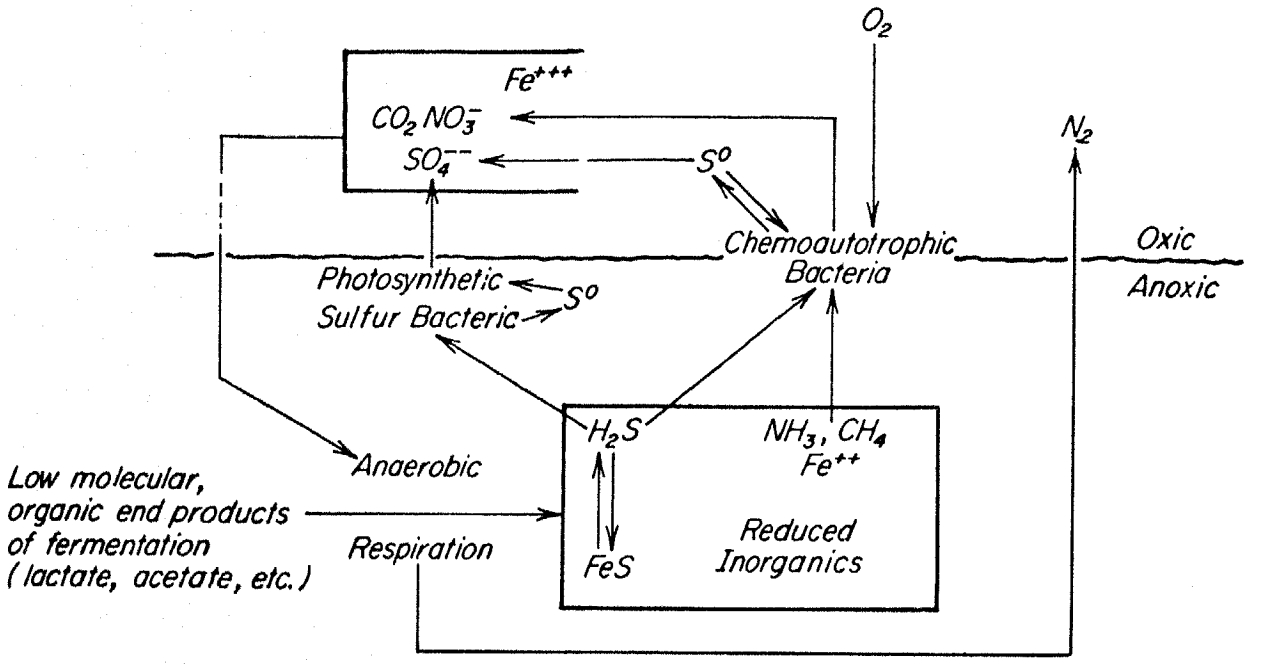

Figure 12. Oxic and anoxic detrital decomposition and the cycle of sulfur in seagrass beds (after Fenchel 1977).

proximate constitutents of eelgrass (Boysen-Jensen 1914; Candussio 1960; Einarsen 1965; Burkholder and Doheny 1968; Park 1979; Stahlheber 1982; Felger and Moser 1973, 1976; Table 9). No studies have been made on Z. japonica, a large staple of the black brant geese in the Pacific Northwest.

Protein contents of eelgrass leaves range from a low of 8.1% of dry weight to 20.3%. The value for the rhizomes ranges from 2.8% to 6.14%. Unfortunately, no seasonal comparisons have been conducted for eelgrass, as have been done for the tropical seagrasses (cf, Zieman 1982 for a summary). This area needs a lot of work.

Lipid contents of all plant parts are low (0.84% of the dry weight to 2.29% in leaves; 0.91% for rhizomes; 1.0% for seeds). Fiber contents are relatively high in leaves and rhizomes (a low of 5.45% of dry weight in one analysis to 61.7%). Ash contents range from a low of 8.8% of dry weight to 32.6%. Carbohydrate contents are highly variable (1.3% of dry weight to 44.6% in leaves to 50.9% in seeds). There have been so few studies made and no systematic analyses either seasonally or regionally that it is difficult to draw any conclusions from the few results reported.

McRoy (1970a) collected data on the elemental composition of eelgrass as compared to the ocean (28 elements; Table 10). It is apparent that eelgrass is actively accumulating great quantities of many minerals.

Caution must be used in assuming that the nitrogen content of eelgrass vegetation is a good indicator of food value. Harrison and Mann (1975b) have shown that up to two-thirds of the nitrogen content of young green leaves may represent low-molecular-weight soluble compounds (nonprotein nitrogen). Actual protein content should be determined for food-value analyses.

Recent studies show that eelgrass contains phenolic acids, suggested to be among the primary allelopathic agents of land plants (cf, Zapata and McMillan 1979 for a review). In a following study, McMillan et al. (1980) demonstrated that eelgrass and Z. japonica contain flavone sulphates. They suggested that if these seagrasses

Table 9. Nutrient content of eelgrass (percentage dry weight).

Plant part	Protein	Lipid	Fiber	Ash	Carbohydrate	Reference
New leaves	10.0	--	--	--	--	Boysen-Jensen 1914
Old leaves	0.49	--	--	--	--	
Leaves	19.03	1.6	16.6	18.15	44.62	Candussio 1960
Leaves	18.55	--	--	--	--	Einarsen 1965
Leaves	10.63	2.29	61.7	8.8	5.6	Burkholder and Doheny 1968
Rhizomes	6.14	0.91	59.94	32.62	--	
Leaves	9.97	0.84	5.45	10.63	--	Park 1969
Leaves	--	8.1-20.3	--	--	1.3-13.1	Stahlheber 1982
Rhizomes	--	2.8-4.5	--	--	8.21-26.0	
Seeds	13.2	1.0	--	--	50.9	Felger and Moser 1973, 1976

For caloric values, convert using caloric equivalents per gram of 9, 4, 4 for lipids, carbohydrates, and protein, respectively.

release these compounds into the sediment, the plant community might shift from reliance upon nitrate nitrogen to use of ammonia nitrogen (indicated by Rice 1974, for land communities). Harborne (1977) suggested that phenolics could form a chemical barrier against microbial invasion. Indeed, Harrison and Chan (1980) and Harrison (1982d) reported that water-soluble extracts of live and dead eelgrass leaves inhibited the growth of diatoms, phytoflagellates, and bacteria, and inhibited grazing by amphipods on dead leaves. They noted that the activity was strongest in young leaves and decreased in leaves aged from 35 to 90 days, suggesting that the compounds could control epiphyte growth on living leaves. It further explains the resistance of eelgrass to decomposition; phenolic content is thus shown to be a major factor in regulating the nutrient cycling processes in eelgrass ecosystems.

3.6 SPECIES AND PROCESS SUCCESSION

The focus of the most recent research on seagrass ecosystems has been the succession of the ecosystem; i.e., the succession of species (structure) and functions (processes) within the system. Structural succession also includes changes in the provision of habitat and refuge for surface-attaching algae and nonswimming and swimming animals. It is recognized that these structural relationships are not static. Large seasonal and longer period changes can and do occur, owing to leaf sloughing, changes in plant density, and meandering of meadow boundary lines.

There appears to be no species succession in the eelgrass or primary-producer stage of the ecosystem. Eelgrass is the initial colonizer as well as the climax stage of development (den Hartog 1973). Since Zostera rhizomes are incapable of vertical growth, the plants are restricted to habitats where erosion and sedimentation are in equilibrium. There are simply no firm data for establishing species succession from an eelgrass meadow to a marsh. Chapman (1960) recorded such a succession, as did Jefferson (1975) and Proctor et al. (1980b) from the Pacific Northwest, but den Hartog (1973) noted that Chapman confused succession with zonation. It is obvious that eelgrass and marshes are adjacent in many places, but one should observe whether true succession is really occurring.

Intermingling of Z. japonica and Carex lyngbyei occurs in several places in the

Table 10. Comparison of elemental composition of eelgrass and the ocean (after McRoy 1970a).

Elements	Eelgrass (ppm)	Ocean (ppm)
Major elements		
Oxygen	390,000	875,000
Hydrogen	59,500	108,000
Carbon	385,000	28
Phosphorus	2,860	0.07
Nitrogen	30,450	0.5
Minor elements		
Sodium	19,590	10,500
Chlorine	45,680	19,000
Magnesium	7,380	1,350
Potassium	22,640	380
Sulfur	7,300	885
Calcium	20,010	400
Boron	310	4.6
Silicon	840	3.0
Iodine	203	0.06
Zinc	56	0.01
Iron	245	0.01
Aluminum	500	0.01
Manganese	1,825	0.002
Trace elements		
Bromine	9.59	65
Rubidium	0.14	0.12
Fluorine	3.61	1.3
Nickel	0.4	0.002
Barium	7.2	0.03
Molybdenum	3.12	0.01
Cadmium	0.23	0.00011
Copper	7.50	0.003
Cobalt	0.3	0.001
Beryllium	0.12	6×10^{7}

Pacific Northwest, particularly in Oregon and southwestern Washington, just as Z. japonica grows intermixed with eelgrass along its lower limit of growth (Harrison 1979). This mixing cannot be interpreted in either case to be species succession.

Functional or process succession relates to the quantitative and qualitative changes in primary production, decomposition of plant matter, and reliance on detritus for food and nutrients as the ecosystem develops in time. It appears that processes change along recognizable sequences, concomitant with species and structural changes.

McRoy and Williams (1978) defined processing as all biotic and abiotic interactions resulting in the transformation of particulate organic matter. Temperature, chemical composition, animal, and microbial activity, desiccation, aerobic and anerobic conditions, and particle size affect processing rates.

It is known that eelgrass processes change along temporal and spatial gradients. The spatial gradient may lie from the edge to the center of a single meadow or along a latitudinal gradient from an area with optimal environmental conditions where ecosystem development has proceeded rapidly to stressed areas at the northerly and southerly limits of distribution where ecosystem development has been retarded. Kenworthy et al. (1982) described a sequence in nitrogen accumulation along a local spatial gradient in an estuary in North Carolina. The greatest pool of nitrogen was in the midbed; the intermediate level was at the edge of the meadow, and the least nitrogen was in unvegetated sediment. These nitrogen changes were correlated with concentrations of fine particle size in the sediments, a characteristic associated with the eelgrass. Dennison (1979) documented the changes in leaf area index and light responses of eelgrass as a spatial gradient of ecosystem development in Izembek Lagoon, Alaska. It has been possible to transplant eelgrass from Puget Sound, Washington, to Izembek Lagoon, but not vice versa. This suggests that eelgrass has a much broader adaptive tolerance from an area with optimal environmental conditions and can tolerate the stress in Izembek Lagoon. The plants from Izembek Lagoon do not appear to have as broad an adaptive tolerance to conditions elsewhere (Phillips and Lewis 1983).

What appears to be a simple ecosystem, structurally and functionally, merely

because it is dominated by a single species, is in reality a highly complex structural and functional system, composed of differing adaptive responses related to the population characteristics, including differing genetic patterns, vegetative and reproductive growth patterns, trophic relationships, and variable process relationships. As in most of the climax ecosystems of the world, detrital food patterns predominate in the eelgrass ecosystem. Therein are the structural and functional natures of the ecosystem brought together. Because of this unit and complementarity of structure and function in both a single plant and in the entire ecosystem, complexity is revealed which is manifested as high species and trophic diversity and primary productivity.

CHAPTER 4
COMPONENTS OF THE EELGRASS COMMUNITY-STRUCTURE AND FUNCTION

A community is characterized by its species composition and related features (den Hartog 1980). The community can be described as a structural framework in which to study plant and animal interrelationships, while the ecosystem is a functional framework in which the interrelationships are viewed as processes and in which the effects of the abiotic environment are integrated.

This chapter will, for the most part, be organized along a community orientation. Many studies have shown a great diversity of plant and animal life associated with eelgrass meadows, from epiphyte lists (Davis 1913; Kita and Harada 1962; Ledoyer 1962; van den Ende and Haage 1963; den Hartog 1970; Main and McIntire 1974; Harlin 1980) to large lists, some of which also analyzed the functional interrelationships of animals associated with eelgrass (Blegvad 1914, 1916; Allee 1923; Blois et al. 1961; Ledoyer 1962, 1964a,b; Kikuchi 1966, 1968, 1974, 1980; Nagle 1968; Orth 1973, 1977a; Adams 1976a,b; Kikuchi and Peres 1977; Simenstad et al. 1979; Jacobs and Huisman 1982).

The animals organize conveniently into functional groupings, largely without concern for their taxonomic placement. The principal groups are (1) epiphytes, (2) epibenthic organisms, (3) infauna, and (4) nekton. Birds will be treated as a separate category. These four groupings follow the classification set by Stauffer (1937).

The term epiphyte means any organism living on a plant surface, plant or animal (Harlin 1980). It includes both sessile and mobile plants and animals, as well as animals that may crawl onto the leaves from the sediment. Epibenthic organisms are those that live on the surface of the sediment, both mobile and sessile forms. Infauna live buried in the sediments. Some organisms, such as shrimp and some crabs, lie partially buried during the day and move on the sediment surface to feed. These are treated as epibenthic organisms. Nekton live in or above the plant canopy.

There are at least two other ways in which to classify animals in an eelgrass meadow by function. Kikuchi (1966, 1980) proposed the following system reflecting the use of Japanese eelgrass meadows. I have attempted to classify the animals in eelgrass systems of the Pacific Northwest according to this system: (1) permanent residents, (2) seasonal residents, (3) transients, and (4) casual species. Thayer et al. (1975b) subdivided the infauna into deposit feeders and suspension feeders, but this refinement is not adopted here.

It is interesting that Nagle (1968), working on epiphytes of eelgrass at Woods Hole, Massachusetts, concluded that general trophic abundances were the same geographically everywhere. In a recent paper, Lewis and Hollingworth (1982), working in Thalassia meadows at Barbados, confirmed Nagle's observation.

4.1 HORIZONTAL AND VERTICAL STRUCTURE

Throughout the limited geographic extent of the Pacific Northwest, there appears to be little, if any, horizontal structure of the associated organisms of the eelgrass community. Epiphytes, benthic algae,

epibenthos, and other components all appear to be homogenous throughout the region.

There are two aspects of the vertical structure of the components. The first is that which exists from the water column downward and into the sediment. Stauffer (1937) described this structure from the viewpoint of the invertebrate community: (1) among the plants (nekton); (2) on the plants (epiphytes); (3) on the sediment surface (epibenthos); and (4) in the sediment (infauna). One more category must be considered here--that of birds which feed on eelgrass or its epiphytes from the water surface or at low tide. The second type of vertical structure is that found on the eelgrass plant itself. This structure was diagrammed by Nagle (1968; Figure 13) for eelgrass from the Woods Hole, Massachusetts, region. The diagram generally shows that the peak loads of epiphytes and epibiota occur near the center of the leaves. This was also found by van den Ende and Haage (1963) on the Brittany coast of France. This might be a community adjustment toward keeping the leaf high in the water column as long as possible. It is also possible that the center of the leaf is the most structurally intact, giving the greatest attachment area, as the leaf ages. In Japan, Kita and Harada (1962) diagrammed the vertical distribution of diatoms on eelgrass blades. They found that diatom abundances increased dramatically toward the distal end of the leaf (oldest part).

4.2 BENTHIC ALGAE

Relatively few species of benthic algae grow within eelgrass meadows of the Pacific Northwest. Since macroalgae need a hard substrate, they can grow only where rock cobbles or shell fragments occur in the sediments. It is not uncommon, however, for certain genera, such as Ulva and Enteromorpha, to occur loose in large

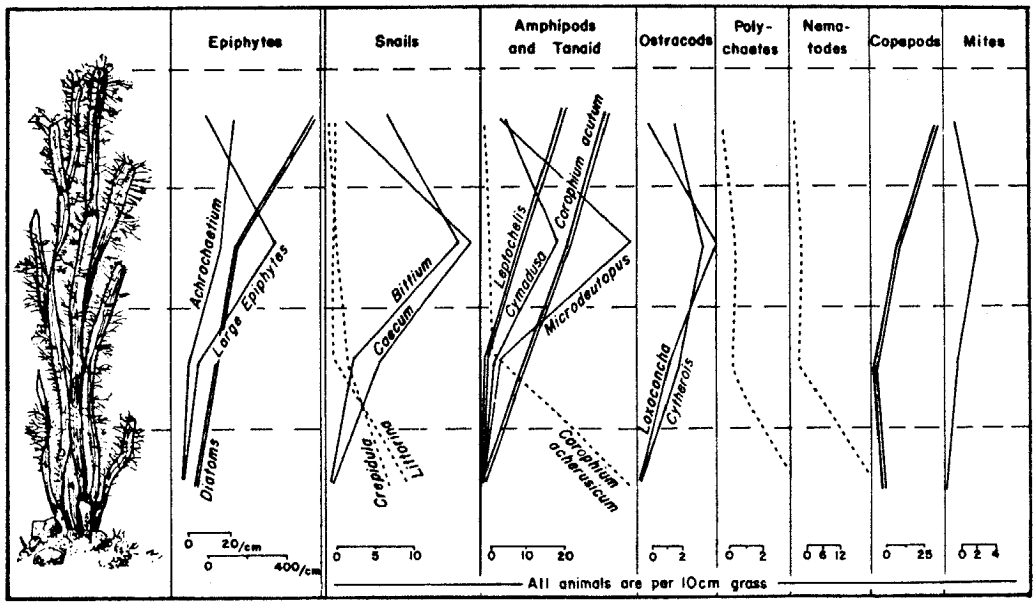

Figure 13. Vertical distribution of eelgrass epibiota (after Nagle 1968). Dashed lines indicate animals which generally decrease in abundance away from the bottom; solid lines indicate variation with epiphytes; single ruled lines signify variance with large epiphytes; double ruled lines signify variance with diatoms.

masses among the eelgrass stalks. This commonly occurs in areas where tidal currents are sluggish. There are no rhizophytic benthic macrophytic algae in the Pacific Northwest.

In the Hood Canal, Washington, Sargassum muticum grows on shell fragments among eelgrass. In summer these algae grow to 2-3 m (6-10 ft) long and could possibly shade the eelgrass. However, by October the plants die back and overwinter as short stubs 2-4 cm (1-15 inches) long. Occasionally, Laminaria, Alaria, Gracilarea, Desmarestia, and Neoagardhiella occur between the eelgrass shoots.

Observations on benthic algae of eelgrass meadows of the Pacific Northwest have been made by Phillips (1972; unpubl. research), Davis (1981), and Pregnall (1983).

Often, large mats of diatoms cover the substrate between the shoots. This was observed by Phifer (1929) and has been corroborated many times. Recently, Whiting (1983) enumerated the microbenthic algae associated with the sediment of eelgrass meadows in Netarts Bay, Oregon. Little has been done on the production values of these algae.

4.3 EPIPHYTES

Harlin (1975) listed the factors which influence the coexistence between host and epiphyte:

1. Physical substrate
2. Access to photic zone
3. Free ride through moving waters
4. Nutrient exchange with host
5. Organic carbon source

Occasionally in waters with little tidal movement, a coating of blue-green algae may be found on the eelgrass blades (Davis 1913). Blue-green algae are occasionally found on the eelgrass in the Pacific Northwest. McRoy et al. (1973) found that these algae may fix a small amount of nitrogen. Considering the nitrogen deficiency in eelgrass beds, this may be an important source.

Epiphyte biomass at times equals the biomass of the leaves (Marsh 1973; Harlin 1975; McRoy and McMillan 1977). Penhale (1977) observed that eelgrass epiphytes can constitute up to 18% of the annual production of carbon of the eelgrass primary production system (200 $mgC/m^2/day$). Carbon, nitrogen, and phosphorus travel from eelgrass blades to epiphytes to the water and vice versa (Harlin 1973, 1975, 1980; Wetzel and Penhale 1979; Penhale and Thayer 1980;. In the Pacific Northwest, Kentula (1983) found that epiphyte biomass could be as much as 2.3 times that of the leaf. She also estimated that the net primary production of these epiphytes accounted for approximately 8% of the combined eelgrass (above- and below-ground) and epiphyte production.

The epiphyte list can be enormous and varied under the usage adopted in this report. It may include sessile plants and animals, mobile epifauna and epibenthos that crawl onto the plants, bacteria, and detritus (Harlin 1980). Kikuchi and Peres (1977) also included in the mobile epifauna a group of swimming animals which often rest on the eelgrass leaves. Table 11 (from Burkholder and Doheny 1968) lists the numbers of bacteria associated with the sediment, water, and eelgrass in New York.

The epiphytic plants, bacteria, and diatom coating on the leaf surface often form a brownish felt. This felt shelters and feeds members of the epifauna, as well as many grassbed predators (amphipods and at least four species of ducks and some

Table 11. Bacteria in the eelgrass habitat (after Burkholder and Doheny 1968).

Station	Type of sample	Bacteria/g or ml
1	Mud	1,300,000
	Water	27,700
	Eelgrass	68,964,000
2	Mud	200,000
	Water	30,000
	Young eelgrass	1,680,000
	Old eelgrass	28,728,000

shorebirds). From a recent thorough study done by Lewis and Hollingworth (1982) in Thalassia at Barbados, West Indies, and the work done by Kikuchi and Peres (1977) and Kikuchi (1980), it is known that the various categories of epiphytes include the following subgroups: (1) microfauna and meiofauna: protozoans-ciliates, flagellates, forams, nematodes, polychaetes, rotifers, tardigrades, copepods, ostracods (this group is made up of herbivores, detritivores, and carnivores); (2) sessile fauna: hydrozoa, anemones, bryozoa, tube-forming polychaetes, compound ascidians; (3) mobile epifauna: gastropods, polychaetes, tubellarians, nemertinians, amphipods, isopods, some starfish, and sea urchins; (4) swimming epifauna which may rest on the leaves: mysid shrimp, hydromedusae, small squids, and special fishes. Eggs of snails, tectabranchs, and Pacific herring and smelt are deposited on the leaves also.

Lewis and Hollingworth (1982) and Nagle (1968) found a direct correlation between density of epiflora and epifauna. In Thalassia (in Japan) the epiphytic nematodes constituted over 62% of the total epifauna on leaf blades (Kikuchi 1966). At Woods Hole, Massachusetts, Nagle (1968) found that amphipods dominated the epifauna. All these studies identified the specific animals in the epifauna and found that they were the dominant food of fish in the seagrass systems. In all systems the epifauna was dominated by herbivores and detritivores. It is obvious that the role of eelgrass as a substrate for brown felt of diatoms, bacteria, detritus, and other algae is of fundamental importance in providing a nursery for juvenile and adult forms of recreationally and commercially important animals.

Numerous studies have attested to the role of eelgrass in providing physical substrate for epiphytes. Probably most of the epiphytes reported are sessile. Certainly all of the plants are. Many of the animals are sessile, but a great number are mobile, and many move onto and off the plant from the substrate.

Davis (1913) listed 42 species of plants that occur on eelgrass at Woods Hole, Massachusetts. Most of these algae belonged to the green and red algae. In Rhode Island, Brown (1962) listed 25 species of microalgae which occur on eelgrass blades. In the Yaquina estuary, Oregon, Main and McIntire (1974) identified 221 epiphytic diatoms, but only listed the 36 most abundant (Table 12). The only species characteristically associated with eelgrass blades was Cocconeis scutellum. They found that the same taxa of diatoms were equally found on rocks, Ulva, Enteromorpha, and Polysiphonia. Working in Netarts Bay, Oregon, Whiting (1983) reported that Cocconeis, Synedra, Navicula, Nitzschia, Gomphonema, and Rhoicosphenia (diatoms) were dominant from November through July, while Cocconeis, Gomphonema, and Rhoicosphenia and different species of Navicula and Nitzschia became dominant from August through October. Harlin (1980) noted that Smithora naiadum and Ectocarpus sp. were the dominant macroalgae on eelgrass blades.

For a thorough review of epiphytes found on eelgrass, one should consult the reviews of Kikuchi and Peres (1977), Harlin (1980), and Kikuchi (1980). The lists of plants and animals associated with eelgrass as epiphytes are too numerous to reproduce fully here.

The development of the epiphytic community on eelgrass is thought to begin with a covering of Cocconeis upon which the bacteria and other algae attach. Sieburth and Thomas (1973) found few epiphytes on young leaves until Cocconeis coatings were present.

There is one overriding constraint placed on any epiphytic community on a seagrass blade. It does not matter whether the individual leaf persists for 20 or 56 days. The sessile portion of the community must adapt its life span to the longevity of the blade upon which it grows. The mobile epifauna can move to the younger blades. It appears, however, that the entire food web associated with the blade, a microcosm of the entire eelgrass ecosystem, is dependent on the development of the microphytic (diatoms, bacteria) coating, detritus which is trapped, and the macrophytic algae which attach to the blade. Without the initial

Table 12. Thirty-six most abundant diatom epiphytes on eelgrass in the Yaquina Estuary, Oregon (after Main and McIntire 1974) and a small list of epiphytes found in Puget Sound, Washington (after Phillips 1972).

Location	Species
Yaquina Estuary	Achnanthes brevipes
	A. deflexa
	A. lanceolata
	A. parvula
	A. rutilans
	A. paludosa
	Amphiprora paludosa
	Cocconeis californica
	C. costata
	C. placentula
	C. scutellum
	Fragilaria striatula
	Gomphonema oceanica
	Licmophora gracilis
	Melosira moniliformis
	M. nummuloides
	Navicula sp.
	N. directa
	N. diserta
	N. endophytica
	N. gregaria
	N. heufleri
	N. mutica
	Nitzschia sp.
	N. aequorea
	N. frustulum
	N. oregona
	N. pseudohybrida
	Plagiogramma vanheurckii
	Surirella ovata
	S. fasciculata
	Synedra fasciculata
	Thalassionema nitzschioides
	Thalassiosira aestivalis
	T. salvadoriana
Puget Sound	Enteromorpha linza
	Ectocarpus sp.
	Petalonia debilis
	Antithamnion subulatum
	Erythrotrichia kylinii
	Melobesia mediocris
	Rhodophysema georgii
	Smithora naiadum
	Arachnoidiscus ehrenbergii
	Biddulphia alternans
	Cocconeis sp.
	Grammatophora marina
	Isthmia nervosa
	Melosira moniliformis
	Navicula sp.
	Schizonema pacifica
	Surirella sp.

layer and its ability to colonize and complete a life cycle in a very short time, it appears that much of the nursery and trophic functions of an eelgrass meadow would never develop.

4.4 EPIBENTHOS

Many epibenthic animals are relatively large and conspicuous. Some of them, such as Dungeness crabs (Figure 14), broken-back and coon-stripe shrimps, English sole, and starry flounders, are commercially important. These animals are listed in Table 13a, b.

Major reviews of the epibenthos which include lists of epifauna were included in Allee (1923), Ledoyer (1962, 1964a,b), Kikuchi (1966, 1980), and Kikuchi and Peres (1977).

Scallops, crabs, sponges, mussels, sea urchins, shrimps, flatfish, sea slugs, sea cucumbers, snails, brittle stars, ribbon worms, polychaete worms, flatworms, nematodes, and amphipods have been associated with the sediment surface. Thayer et al. (1975b), working in a newly established eelgrass meadow in North Carolina, determined that gastropods represented 72% of the total numbers of epifauna found in the system. Deposit feeders represented 77% of the numbers; suspension feeders 18%; and carnivore-scavengers 5%. There was a seasonal variation in numbers with maximum abundance in spring and early summer. This is also true for Puget Sound (Simenstad et al. 1979). Wolfe et al. (1976) analyzed transfers of Mn, Fe, Cu, and Zn through trophic levels in this eelgrass bed and found very little transfer from eelgrass.

In Alaska, Dungeness crabs can best be fished in eelgrass beds. In summer the crabs appear to consume eelgrass. Gotshall (1977) found 7-15 percent of crab gut contents composed of eelgrass. In Puget Sound, Dungeness and red rock crabs scavenge in eelgrass meadows (Beak Consultants 1975).

Pryne (1979) noted that Padilla Bay, one of the three largest eelgrass meadows on the Pacific coast, contains significant

Figure 14. Dungeness crab (Cancer magister) in eelgrass bed in Puget Sound.

populations of soft-shell clams and crabs. In another newspaper article, Lane (1980) stated that Dungeness crabs support a sport and commercial crab fishery in Padilla Bay. Numerous species of worms, clams, snails, crabs, shrimp, and other invertebrates were identified in Padilla Bay (NOAA 1980). The density of epibenthic harpacticoid copepods, a favorite food of juvenile chum salmon in the Pacific Northwest, was four times as high in a thick stand of eelgrass than nearby in a sand habitat without eelgrass (Simenstad et al. 1980). Dense schools of juvenile chum salmon were feeding upon and among the eelgrass blades.

In Grays Harbor, Washington, Dungeness crabs produce commercially important catches which range from 11,364 to 100,000 kg (25,000-220,000 lb) (Army Corps of Engineers 1977b). Grays Harbor functions as a coastal estuary for coastal Dungeness crabs. The estuary has extensive eelgrass meadows. Bayer (1979b) studied the densities and seasonalities of Dungeness, hermit, kelp (Figure 15), and red rock crabs, and two species of crangonid shrimps in the eelgrass meadows of the Yaquina estuary, Oregon. Humboldt Bay is another estuary with very large sport and commercial fisheries for Dungeness crabs, pink shrimp, and bottom fish (Proctor et al. 1980b).

4.5 INFAUNA

Very little work has focused on or even listed infauna. The three best studies are those of Kikuchi (1966) in Japan, Thayer et al. (1975b) in North Carolina, and Orth (1973) in the Chesapeake Bay. Extensive work has been done in the Pacific Northwest by Dr. Carl Nyblade in the North Puget Sound area, but this is largely unpublished in the scientific literature and not so widely known.

Orth (1973) found 117 macroinvertebrate taxa associated with eelgrass beds in the Chesapeake Bay. Strictly speaking, not all these were infaunal, because he mentions seasonality of the fauna as many forms moved from the sediments and onto the leaves from March to July. He found that the recorded density of infauna was higher from eelgrass than from any other benthic habitat in the Chesapeake Bay system. This was also found by Kikuchi (1980) in Japan.

In North Carolina, Thayer et al. (1975b) found that the infauna was composed of 40 species and dominated by five species. Pelecypods represented 58% and polychaetes 41% of the total individuals. The infauna was dominated by deposit feeders (53% and 44% of the abundance and biomass, respectively), while suspension feeders represented 42% and 35%, respectively. They noted a much lower density of organisms and biomass as compared to the Chesapeake Bay, and concluded it was due to the relatively recent establishment of the eelgrass bed of their study.

In one study done off Skiff Point, Bainbridge Island, Washington, Thom et al. (1979) reported that the eelgrass habitat contained more invertebrates at the +1.0 m (3.0 ft) level, than at the unvegetated sites. For crustacean species there were few individuals, but a great number of species; in mollusks and annelids, species richness was intermediate or above the curves for other groups at the +1.0-m level. They theorized that the substrate-stabilizing effect of eelgrass may be important in causing the increased

Table 13a. List of invertebrates found in eelgrass meadows of the Pacific Northwest, arranged in functional categories.

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
PORIFERA					
Demospongiae					
Ficulina lata	(Sponge found on *Pagurus* sp.)	R	C	E	F
Haliclona sp.	--	R	X	E	F
Lissondendoryx sp.	--	R	X	E	F
Mycale adhaerens	(Sponge found on *Pecten* sp.)	R	C	E	F
Myxilla parasitica	" " " " "	R	C	E	F
Tetillia mutabilis	" " " " "	R	X	S-E	F
CNIDARIA					
Hydrozoa					
Abietinaria sp.	Sea Fir	R	X	E	X
Agalaophenia inconspicua	Ostrich plume hydroid	R	C	E	C
Obelia sp.	--	R	C	E	C
O. dichotoma	Sea plume	R	C	E	C
O. longissima	--	R	C	E	C
Plumularia lagenifera	Plume hydroid	R	C	E	C
P. setacea	Plume hydroid	R	C	E	C
Sertularia furcata	--	R	C	E	C
Gonionemus vertens	Orange-striped jellyfish	R*	A	C	C
Scyphozoa					
Haliclystus stejnegeri	Fixed jellyfish	R	A	E,N	C
H. auricula	Stalked jellyfish	R	A	E,N	C
Anthozoa					
Cerianthus aestuari	Burrowing anemone	R	A	E	C
Epiactus prolifera	Small green anemone	R	A	E	C
PLATYHELMINTHES					
Turbellaria					
Freemania sp.	--	R	C	C	C
NEMERTEA					
Anopla					
Cerebratulus californiensis	Ribbon worm	R	X	B	C
Enopla					
Paranemertes peregrina	Restless worm	R	C	B,N	C
Membranipora membranacea	Bryozoan	R	C	C	C
Tricellaria occidentalis	Bryozoan	R	C	C	C
Tetrastemma sp.	--	R	C	C	C
MOLLUSCA					
Gastropoda					
Alvinia spp.	--	R	C	C-S	H
Notoacmea paleacea	--	R	U	C-S	H
Batillaria zonalis	Horn snail	R	C	C-S	C
Haminoea vesicula	Bubble shell	R	C	C-S	H
H. virescens	--	R	A	C-S	H
Lacuna porrecta	Wide-chink snail	R	C	C-S	H
L. variegata	--	R	A	C	H
Nassarius fossatus	Channeled basket shell	R	U	C-S	C
N. fraterculus	Basket shell	R	C	C-S	C
Ocenebra japonica	Japanese oyster drill	R	U	S	C
Urosalpinx cinereus	Oyster drill	R	U	S	C
Polinices lewisi	Giant moon snail	R	A	S-B	C
Thais lamellosa	Roman purple thais	R	C	S	C
Phyllaplysia taylorii	--	R	A	C	H
Chloraera leonina	Hooded nudibranch	R	X	C,N	C
Corambe pacifica	--	R	C	C	C
Dirona albolineata	Alabaster nudibranch	R	C	C	C
Aeolidia parillosa	--	R	A	C	H
Galvina olivacea	--	R	C	C	C
Hermissenda crassicornis	--	R	A	C-S	C
H. opalescens	Opalescent nudibranch	T	C	C	C
Pleurophyllidia california	Striped nudibranch	T	U	S-B	C

continued

Table 13 a. (Continued)

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
Pelecypoda					
Clinocardium nuttalli	Basket cockle	R	A	B	SF
Crassostrea gigas	Japanese oyster	R	U	S	SF
Ostrea lurida	Native oyster	R	U	S	SF
Macoma iris	--	R	X	B	D-DF
M. balthica	--	R	A	B	D-DF
M. inouinata	Polluted macoma	R	C	B	D-DF
M. nasuta	Bent-nosed clam	R	A	B	D-DF
M. obliqua	--	R	U	B	D-DF
M. secta	Sand clam	R	C	B	D-DF
M. inconspicua	--	R	A	B	SF
Mya arenaria	Eastern soft-shell clam	R	C	B	SF
Panope generosa	Geoduck	R	A-U	B	SF
Pecten sp.	Scallop	R	U	C	SF
P. staminea	Rock cockle	R	U	B	SF
Tapes philippinarum	Japanese littleneck	R	U	B	SF
Psephida lordi	--	R	A	B	SF
Saxidomus giganteus	Washington clam	R	U	B	SF
Tagelus californianus	Common jackknife clam	R	C-U	B	SF
Tresus capax	Horse clam	R	C	B	SF
T. nuttalli	Gaper clam	R	C	B	SF
Solen sicarius	Jackknife clam	R	U	B	SF
Parvilucina tenuisculpta	--	R	U	B	SF
Tellina modesta	--	R	C	B	SF
Transenella tantilla	--	R	X	S	SF
ANNELIDA					
Polychaeta					
Abarenicola claparedii vagabunda	Roughskinned lugworm	R	C	B	D
Armandia brevis	--	R	C	B	D
Capitella capitata	Lugworm	R	C	B	D
Capitella sp.	Lugworm	R	C	B	D
Cistenides brevicoma	--	T	C	B	D
Glycera americana	--	R	C	B	C
Glycinde armibera	Polychaete worm	R	C	B	X
Haploscolopus elongata	Polychaete worm	R	X	B	X
Scolopolos armiger	Polychaete worm	R	X	B	X
Sthenelais fusca	--	R	C	Found in root mass	X
Mediomastus sp.	--	R	X	B	DF
Neinereis dendritica	--	R	C	Found in root mass	X
Nereis branti	Clam worm	R	C	B	C,H
N. procera	--	R	C	E	H
Owenia justiformis	--	X	X	B	X
Platynereis bicangiculata	--	R	C	B	H
Tharyx multifilis	--	R	C	B	D
Medimastus sp.	--	R	A	B	X
Malacocens glutaeus	--	R	A	B	X
Notomastus tenuis	--	R	C	B	X
Saccogelssus sp.	--	R	A	B	X
Platynereis agassizi	--	X	X	B	X
ARTHROPODA					
Crustacea					
Longipedia sp.	--	R	C	S/C	D
Clausidium vancouverense	--	T	C	Commensal with Callianaessa californiensis	--
Ectinosoma sp.	--	R	A	S	X
Helectinosoma sp.	--	R	A	S	X
Danielssenia typica	--	R	C	X	X
Harpaciticus uniremis	--	R	C	S/C	D,H
H. septentrionalis	--	R	C	S/C	D,H
H. compressus	--	R	C	S/C	D,H
H. spinulosus	--	R	A	S/C	D,H
H. spp.	--	R	A	E	X
Zaus aurelii	--	R	C	S/C,E	D
Z. caeruleus	--	R	C	S/C,E	D
Z. spinatus hopkinski	--	R	C	S/C,E	D

continued

Table 13a. (Continued)

Phylum, class, and species Scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
Zaus sp.	--	R	C	S/C	D
Tisbe spp.	--	R	C	S/C	D
Scutellidium arthuri	--	R	C	E	X
Porcellidium sp.	--	R	C	E	X
Tegastes spp.	--	R	C	E	X
Dactylopodia crassipes	--	R	A	S/C	D,H
D. vulgaris inornata	--	R	C	S/C	D,H
Paradactylopodia sp.	--	R	C	X	X
Diarthrodes spp.	--	R	C	Plant miners	--
Parastenhelia hornelli	--	R	C	X	X
P. spinosa	--	R	C	X	H
Amonardia normani	--	R	C	S/C	D,H
A. perturbata	--	R	C	S/C	D,H
Amphiascoides spp.	--	R	C	X	X
Amphiascus spp.	--	R	C	S/C	D,H
Schizopera knabeni	--	R	C	X	X
Diosaccus spinatus	--	R	A	S/C	X
Nitrocra spp.	--	R	C	X	X
Mesochra spp.	--	R	C	X	--
Orthopsyllus illgi	--	R	C	Intaunal	--
Enhydrosoma uniarticulatum	--	R	C	Intaunal	--
Huntemannia jadensis	--	R	A	S	X
Acrenhydrosoma perplexum	--	R	C	Intaunal	--
Heterolaophonte longisetigera	--	R	C	X	D,H
H. discophora	--	R	C	X	D,H
H. variabilis	--	R	C	X	D,H
Laophonte inopinata	--	R	C	X	X
Pseudonychocamptus spiniter	--	R	C	X	X
Cumacea vulgaris	--	R	A	S	X
Porcellidium sarsi	--	R	A	C	D
Hemicyclops callianassae	--	R	Commensal with ghost shrimp		
Euphilomedes carcharodonta	--	R	A	X	X
Epinebalia pugettensis	--	R	X	X	X
Diastylopsis dawsoni	--	R	A	S	D
Lamproya quadriplicate	--	R	A	S	D
Leprochelia dubia	--	R	A	S	D
Idotea aculeata	Eelgrass isopod	R	C	C	D
I. fewhesi	--	R	C	S	D
I. rufescens	--	R	C	S	D
I. wosnesenskii	--	R	A	S	D
I. montereyensis	--	R	X	C	H
I. resecata	Transparent isopod	R	A	C	H
I. aculeata	--	R	X	C	H
I. urotoma	--	R	X	C	X
Munna ubiquita (Juv.)	--	R	C	--	X
Orchestia traskiana	--	R	A	S	D
Aorides spp.	--	R	A	X	X
Corophium stimpson	--	R	A	S	D
Ischyrocerus anguipes	--	R	A	X	X
Synchelidium shoemakeri	--	R	A	X	X
Eogammarus confervicolus	--	R	A	C	X
Anisogammarus pugettensis	--	R	A	X	X
Caprella californica	--	R	A	C	H
C. equilibra	--	R	X	X	H
C. laeviuscula	--	R	A	X	X
Photis spp.	--	R	A	X	X
Metacaprella anomala	--	R	U	X	X
Callianassa californiensis	Red ghost shrimp	R	C	S	D
C. gigas	Long-handed ghost shrimp	R	C	S	D
Crangon nigricauda	Black-tailed shrimp	T	C	S	C
C. californiensis	Pistol shrimp	R	C	S	C
Hippolyte clarki	Grass shrimp	R	A	C	C
Pandalus danae	Coonstripe shrimp	R	C	S	C
P. platyceros (larva/juv.)	Spot shrimp	R	A	S/C,S	X
Spirontacaris paludicola	Grass shrimp	R	C	C	C
Upogebia pugettensis	Blue mud shrimp	R	C	B	D
Eualus spp.	--	R	A	S	--
Cancer magister	Dungeness crab	R	A	S-B	C
C. productus	Red rock crab	R	C	S-B	C
Oregonia gracilis	Spider crab	R	C	C	H
Pinnixa littoralis	--	R	X	Commensal with Clinocardium sp.	

continued

Table 13a. (Concluded)

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
Pugettia gracilis	Kelp crab	R	A	C	H
P. producta	--	R	C	S	D
Pagurus dalli	Hermit crab	R	C	S	D
P. granosimanus	Hermit crab	R	C	S	D
P. hirsutiusculus	Hairy hermit crab	R	C	S	D
Insecta					
Aedes dorsalis	Mosquito	R	C	N	F
ECHINODERMATA					
Asteroidea					
Evasterias troschelii	Mottled star	T	C	S	C
Leptoasterias hexactis	Six-rayed star	R	A	S	C
Pycnopodia helanthoides	Sunflower star	T	C	S	C
Solaster dawsoni	Sunstar	T	C	S	C
S. stimpsoni	Morning sun star	T	C	S	C
Echinoidea					
Dendraster excentricus	Sand dollar	R	U	S	D
Echinarachnius parma	Sand dollar	T	C	S	D
Holothuroidea					
Leptosynapta albicans	Sea cucumber	R	C	S-B	D

[a]Resident status: R = resident; T = transient; T* or R* = seasonal occurrence.

[b]Abundance status: A = abundant, often seen on field trips; C = common, present but not always seen on field trips; U = uncommon, present in small numbers and seldom seen; X = unknown.

[c]Living mode status: C = clinging to blades; B = burrower; E = Epiphyte; N - Nekton; S = feeding on or slightly above sediment surface; S/C = Epibenthic zooplankton.

[d]Feeding habit: H = herbivore; D = Detritivore; DF = deposit feeder; SF = suspension feeder; C = consumes fauna in eelgrass and eelgrass substrate; F = filter feeder.

Reference: ACOE 1976; 1977b; Banse and Hobson 1974; Behrens 1980; Cordell (pers. comm., 1982); Farmer 1980; Gardner 1978; Guberlet 1962; Hartman and Reish 1950; Hobson and Banse 1981; Kohn 1982; Kozloff 1973; Kozloff 1974; Kozloff (pers. comm., 1983); Liburdi and Truitt 1973; NOAA/State of Washington Dept. of Ecology 1980; Ricketts and Calvin 1968; Simenstad and Kinney 1978; Simenstad et al. 1979; Simenstad et al. 1980; Simenstad (pers. comm., 1982); Staude (pers. comm., 1982); Thayer and Phillips 1977; Thorn (pers. comm., 1983).

Table 13b. List of fish found in eelgrass meadows of the Pacific Northwest, arranged in functional categories.

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
CHORDATA					
Chondrichthyes					
Squalus acanthias	Spiny dogfish	T	U	N	C
Raja binoculata	Big skate	T	U	N	C
Osteichthyes					
Clupea harengus pallasi	Pacific herring	T	C	N	C
Clupea larvae	--	R¢,T¢	C	--	
Engraulis mordax	Northern anchovy	T	A-U	N	C
Oncorhynchus gorbuscha (Juvenile)	Pink salmon	T¢	C	N	C
O. keta (Juvenile)	Chum salmon	T¢	C	N	C
O. kisutch (Juvenile)	Coho salmon	T¢	A-U	N	C
O. tshawytscha (Juvenile)	Chinook salmon	T¢	U	N	C
Salmo clarki	Sea-run cutthroat trout	T	C	N	C
Hypomesus pretiosus pretios	Surf smelt	T	C	N	C

continued

Table 13b. (Continued)

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
Spirinchus thaleichthys	Longfin smelt	T	U	N	C
Atherinops affinis	Top smelt	R	C	N	C
Porichythus notatus	Plainfin midshipman	T	U	N	C
Gobiesox maeandricus	Northern clingfish	T	U	N	C
Gadus macrocephalus	Pacific cod	T	U	N	C
Microgadus proximus	Pacific tomcod	T	U	N	C
M. proximus (Juvenile)	--	R*	A	N	C
Theragra chalcogramma	Walleye pollock	T	U	N	C
Lycodes palaeris	Wattled eelpout	T	U	N	C
Aulorhynchus flavidus	Tubesnout	R	A	N	C
Gasterosteus aculeatus	Threespine stickleback	R	A-C	N	C
Syngnathus griseolineatus	Bay pipefish	R	C	N	C
Cymatogaster aggregata	Shiner perch	R*	A	N	C
C. aggregata (Juvenile)	Striped seaperch	R*	A	N	C
Embiotoca lateralis	Striped seaperch	R*	A	N	C
E. lateralis (Juvenile)	Striped seaperch	R*	A	N	C
Hyperprosopon argenteum	Walleye surfperch	R	U	N	C
Rhacochilus vacca	Pile perch	R*	A	N	C
Trichodon trichodon	Pacific sandfish	T	U	N	C
Anoplarchus purpurescens	High cockscomb	R	C	N	C
Lumpenus sagitta	Snake prickleback	T*	C	N	C
Apodichthys flavidus	Penpoint gunnel	R*	C	N	C
Pholis laeta	Crescent gunnel	R*	C	N	C
P. laeta (Juvenile)	Crescent gunnel	R*	C	N	C
Pholis ornata	Saddleback gunnel	R*	A-C	N	C
Ammodytes hexapterus	Pacific sand lance	R*	A	N	C
Sebastes caurinus	Copper rockfish	R	U	N	C
S. melanops	Black rockfish	T	U	N	C
Sebastes sp.	Larvae/juveniles	R*	C	N	C
S. maliger	Quillback rockfish	T	U	N	C
Hexagrammus bugocephalus	Rock greenling	T	U	N	C
H. decagrammus	Kelp greenling	T	U	N	C
H. stelleri	White spotted greenling	T	U	N	C
Ophidon elongatus	Lingcod	T	U	N	C
Hemilepidotus hemilepidotus	Red Irish lord	T	U	N	C
Artedius fenestralis	Padded sculpin	R*	U	N	C
A. fenestralis (Juvenile)	Padded sculpin	R*	U	N	C
Blepsias cirrhosus	Silverspotted sculpin	R*	A-U	N	C
Enophrys bison	Buffalo sculpin	R	A-C	N	C
Gilbertidia sigalutes	Soft sculpin	T	U	N	C
Leptocottus armatus	Pacific staghorn sculpin	R	A	N	C
Myoxocephalus	Great sculpin	T	U	N	C
Oligocottus maculosus	Tidepool sculpin	T	C	N	C
Psychrolutes paradoxus	Tadpole sculpin	T	U	N	C
Clinocottus acuticeps	Sharpnose sculpin	R*	C	N	C
Scorpaenichthys marmoratus	Cabezon	T	C	N	C
Agonus acipenserinus	Sturgeon poacher	T	U	N	C
Pallasina barbata aix	Tubenose poacher	R	C	N	C
Xeneretmus latifrons	Blacktop poacher	T	U	N	C
Eumicrotremus orbis	Spiny lumpsucker	R*	C	N	C
Liparis callyodon	Spotted snailfish	T	U	N	C
L. florae	Tidepool snailfish	T	U	N	C
L. cyclopus	Ribbon snailfish	T	U	N	C
L. pulchellus	Tadpole snailfish	T	U	N	C
L. rutteri	Ringtail snailfish	R	U	N	C
Ieopsetta isolepis	Butter sole	T	U	S	C
Lepidopsetta bilineata	Rock sole	R	U	S	C
L. bilineata (Juvenile)	Rock sole	R	U	S	C
Microstomus pacificus	Dover sole	T	U	S	C

continued

Table 13b. (Concluded)

Phylum, class, and species scientific name	Common name	Resident or transient[a]	Abundance[b]	Living mode[c]	Feeding habits[d]
Pleuronichthys coenosus	C-O sole	R	C	S	C
P. coenosus (Juvenile)	C-O sole	R	U	S	C
Parophrus vetulus	English sole	R	A	S	C
P. vetulus (Juvenile)	English sole	R	A	S	C
Platichythus stellatus	Starry flounder	T	U	S	C
Psettichthys melanostictus	Sand sole	T	C	S	C

[a]Resident status: R = resident; T = transient; T* or R* = seasonal occurrence; T¢ or R¢ = life cycle occurrence such as juvenile, larval.

[b]Abundance status: A = abundant, often seen on field trips; C = common, present but not always seen on field trips; U = uncommon, present in small numbers and seldom seen.

[c]Living mode status: N = nekton; S = feeding on or slightly above sediment surface.

[d]Feeding habits: H = herbivore on eelgrass; C = consumes fauna in eelgrass and eelgrass substrate.

References: ACOE 1977b; Bayer 1981; Brown 1982; Gardner 1978; Miller (pers. comm., 1982); NOAA/State of Washington Dept. of Ecology 1980; Simenstad and Kinney 1978; Simenstad et al. 1979.

Table 13c. List of birds found in eelgrass meadows of the Pacific Northwest, arranged in functional categories.

Phylum, class, and species scientific name	Common name	Abundance[a]	Living mode[b]	Feeding habits[c]
CHORDATA				
Aves				
Gavia immer	Common loon	C	D	C
G. stellata	Red-throated loon	C*	D	C
Aechmophorus occidentalis	Western grebe	C*	D	C
Podiceps auritus	Horned grebe	C*	D	C
P. grisegena	Red-necked grebe	C*	D	C
P. nigricollis	Eared grebe	C*	D	C
Podilymbus podiceps	Pied-billed grebe	U	D	C
Phalacrocorax auritus	Double-crested cormorant	U	D	C
P. pelagicus	Pelagic cormorant	U	D	C
Branta canadensis	Canada goose	U*	G	H
B. bernicla	Brant	A-C*	d-G	H
Chen hyperborea	Snow goose	A-C*	G	H
Philacte canagica	Emperor goose	U*	G	H
Anas platyrhynchos	Mallard	C*	d	C,H
A. strepera	Gadwall	U*	d	H
A. crecca	Green-winged teal	A-C*	d	C,H
A. acuta	Pintail	C*	d	C,H
A. clypeata	Northern shoveler	C*	d	C
A. penelope	European wigeon	U*	d	H
A. americana	American wigeon	A-C*	d	H
Aythya valisineria	Canvasback	C*	D	C,H
A. marila	Greater scaup	U*	D	C
A. affinis	Lesser scaup	U*	D	C

continued

Table 13c. (Continued)

Phylum, class, and species scientific name	Common name	Abundance[a]	Living mode[b]	Feeding habits[c]
A. collaris	Ring neck duck	U*	D	C,H
Bucephala clangula	Common goldeneye	U*	D	C
B. islandica	Barrow's goldeneye	U*	D	C
B. albeola	Bufflehead	C*	D	C,H
Histrionicus histrionicus	Harlequin duck	U*	D	C
Melanitta deglandi	White-winged scoter	C*	D	C,H
M. perspicillata	Surf scoter	C	D	C,H
M. nigra	Black scoter	U*	D	C,H
Oxyura jamaicensis	Ruddy duck	U*	D	C,H
Olor columbianus	Whistling swan	U*	d	H
Mergus merganser	Common merganser	U	D	C
M. serrator	Red-breasted merganser	C*	D	C
Lophodytes cacullatus	Hooded merganser	U	D	C
Pandion haliaetus	Osprey	U	BP	C
Ardea herodias	Great blue heron	C	W	C
Fulica americana	American coot	C	D	H
Haematopus bachmani	Black oystercatcher	U*	W	C
Charadirus semipalmatus	Semipalmated plover	C*	W	C
C. vociferus	Killdeer	U*	W	C
Squatarola aquatarola	Black-bellied plover	C*	W	C
Numenius americanus	Long-billed curlew	U*	W	C
N. phaeopus	Whimbrel	C*	W	C
Limosa fedoa	Marbled godwit	U	W	C
Calidris ptilocnemis	Rock sandpiper	U*	W	C
C. alpina	Dunlin	C*	W	C
C. canutus	Red knot	C*	W	C
C. minutilla	Least sandpiper	C*	W	C
C. mauri	Western sandpiper	C*	W	C
C. alba	Sanderling	C	W	C
Actitus macularia	Spotted sandpiper	C*	W	C
Heteroscelus incanum	Wandering tattler	U*	W	C
Limnodromus griseus	Short-billed dowitcher	C*	W	C
L. scolopaceus	Long-billed dowitcher	C*	W	C
Aphriza virgata	Surfbird	U*	W	C
Arenaria interpres	Ruddy turnstone	C*	W	C
A. melanocephala	Black turnstone	U*	W	C
Tringa melanoleuca	Greater yellowlegs	C*	W	C
T. flavipes	Lesser yellowlegs	U*	W	C
Lobipes lobatus	Northern phalarope	C*	W	C
Capella gallinago	Common snipe	U*	W	C
Larus glaucescens	Glaucous-winged gull	C	S	C
L. occidentalis	Western gull	C*	S	C
L. nurgentatus	Herring gull	C	C	C
L. californicus	California gull	C*	S	C
L. delawarensis	Ring-billed gull	U*	C	C
L. canus	Mew gull	C*	S	C
L. heermanni	Heermann's gull	C*	S	C
L. philadelphia	Bonaparte's gull	C	S	C
L. thayeri	Thayer's gull	C*	S	C

continued

Table 13c. (Concluded)

Phylum, class, and species scientific name	Common name	Abundance[a]	Living mode[b]	Feeding habits[c]
Sterna hirundo	Common tern	C*	S	C
Hydroprogne caspia	Caspian tern	U*	S	C
Uria aalge	Common murre	U*	D	C
Cepphus columba	Pigeon guillemot	C	D	C
Derorhinca monocerata	Rhinoceros auklet	C	D	C
Brachyramphus marmoratum	Marbled murrelet	U	D	C
Megaceryle alcyon	Belted kingfisher	C-U*	BP	C
Corvus caurinus	Northwestern crow	C	S	C

[a]Abundance status: A = abundant, often seen on field trips; C = common, present but not always seen on field trips; U = uncommon, present in small numbers and seldom seen; * = seasonal occurrence.

[b]Living mode: d = dipper; D = diver; G = grazer; W = wader; S = scavenger; BP = bird of prey.

[c]Feeding habits: H = herbivore on eelgrass; C = consumes fauna in eelgrass and eelgrass substrate.

References: Ballew (pers. comm., 1983); Bayer 1980; Eaton 1975; Einarsen 1965; Gardner 1978; Kortwright 1967; NOAA/State of Washington Dept. of Ecology 1980; Outram 1958; Paulson (pers. comm., 1983); Terres 1980; Wahl and Paulson 1971.

abundance and biomass of bivalves over that of nearby unvegetated sandy areas.

Figure 15. Kelp crabs (Pugettia gracilis) in eelgrass bed in Puget Sound.

In the Hood Canal, Washington, Yoshinaka and Ellifrit (1974) diagrammed the presence of bent-nosed clams, butter clams, geoduck clams, jointed tube worms, red-banded tube worms, brittle stars, and clam worms as characteristic infauna in eelgrass meadows.

Occasionally, the very large starfish, such as Pycnopodia can be observed within eelgrass beds, attempting to extract clams out of the bottom (Figure 16).

4.6 NEKTON

The high mobility of fishes, cephalopods, and many decapod crustaceans enables them to migrate to and from beds on a seasonal or diurnal basis. Considering their abundance and functional relations within the eelgrass beds of southern Japan, Kikuchi (1966) classified the nekton into four categories: (1) permanent residents: filefish, sea catfish, syngnathids, gobies, blennies, and hippolytid and palaemonid shrimp; (2) seasonal residents:

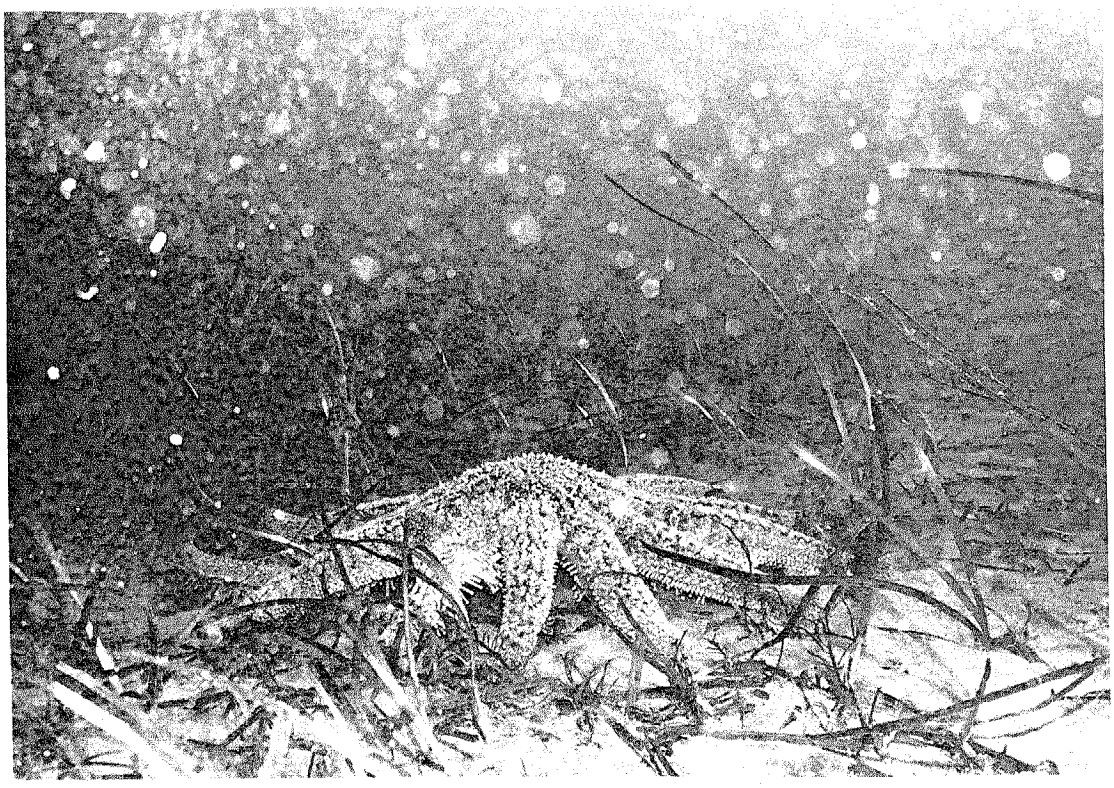

Figure 16. Pycnopodia helianthoides in eelgrass meadow in Puget Sound attempting to extract a clam out of the bottom.

a. juvenile and subadult states: sea bass, rock fishes, alterids, gerreids, sea breams, groupers, and greenlings; b. residents in spawning season: squid, portunid crabs, and some shrimps; (3) transients: puffers; (4) casual species. He noted that some of the seasonal residents were commercially important, especially in the juvenile stage (Kikuchi 1980). For commercially valuable inshore and offshore fish species, the eelgrass meadow is most important in the juvenile stage in providing food and shelter; i.e., in providing a nursery for their development.

In North Carolina, Adams (1976a,b) reported that fishes in eelgrass were characterized by low diversity (39 species) and high standing crops of biomass and energy, both of which showed seasonal variation. Winter stocks (December-April) averaged about 15% as high as during May-November, a function of water temperature. He also reported that stocks at night were twice as high as during the day. Fish did not feed in the eelgrass at night. Interestingly, Adams (1976b) noted that the feeding relationship of certain species changed with the developmental stage. The general trend for the pinfish, which dominated the biomass of the fish community (45% and 67% in two systems), was that copepods were used first, then eelgrass detritus, and finally an omnivorous stage was reached where polychaetes and plant material were used.

Orth and Heck (1980) reported a different fish community in eelgrass of the Chesapeake Bay (48 species), but noted similarities in seasonal abundances. They noted that the number of fish species associated with eelgrass was dramatically higher than nearby unvegetated substrates. This was also reported by Briggs and O'Connor (1971) in New York and by Kikuchi (1974) in Japan. In all of these eelgrass beds many species were important food and game fish. In New York, 38 species were collected in eelgrass (17 preferring

eelgrass), while 29 species were found over sand (only six preferred sand).

Specifically, in the Pacific Northwest, Thayer and Phillips (1977) stated that most of the nekton associated with eelgrass in Puget Sound are carnivores, which feed on detritivores and conduct diurnal and seasonal movements into and out of the eelgrass. Numerous fish use the eelgrass as nursery grounds. Commercially important members were partially dependent on eelgrass for at least part of their life history: Pacific herring, striped seaperch, and the juvenile stage of the chum salmon.

At least 57 species of fish were identified in Padilla Bay (NOAA 1980), a site with significant stands of eelgrass in northern Puget Sound (five species of salmon, steelhead, sea run cutthroat trout, smelt, Pacific herring, sole, flounder, and 10 species of sculpins have sport and commercial importance). In northern Puget Sound, Beak Consultants (1975) reported 20 species of shoreline fishes as well as early stages of pelagic and demersal fishes in eelgrass meadows. These fish included various sculpins, gunnels, rockfish, greenlings, and cabezon. This study emphasized the juvenile stages, which used the eelgrass meadows for shelter and food for a portion of their life cycle or throughout the year. Open-water fishes such as Pacific herring and young salmon (several species), are found in eelgrass throughout the year.

In a study done at Alki Point, Puget Sound, Brown (1982) found that six fish species were permanent residents. These were composed of adult tube snouts (Figure 17) and adult soles (English, rock, and C-O; Figure 18), buffalo and Pacific staghorn sculpins, and the adult bay pipefish. Seasonal residents included nine species, most of which were juveniles (seaperch, perch, tomcod, gunnels, and sculpins). A total of 41 fish species were found in the eelgrass bed. Brown concluded that the eelgrass habitat was an important spring and summer nursery ground for very young juveniles of several

Figure 17. Tubesnouts in eelgrass meadow, Puget Sound.

Figure 18. Flounders moving into transplanted eelgrass, Puget Sound.

species, particularly juveniles of striped seaperch, padded sculpin, crescent gunnel, and English sole. Seasonal maxima in abundance and species richness occurred in summer and autumn. Fish abundance increased at night as in North Carolina and the Chesapeake Bay. The habitat complexity, i.e., eelgrass density, its leaf canopy and rhizome-root penetration into the substrate, and epiphyte complex, was related to fish abundance and species richness (Brown 1982). None of the fish were detritivores. All were carnivores, except the buffalo sculpin which contained Ulva in 58% of its stomach contents.

In northern Puget Sound, Miller et al. (1975) reported 64 fish species in eelgrass. Of this number, three spine sticklebacks, staghorn sculpin, shiner perch, Pacific herring, Chinook salmon, and surf smelt were dominant. They concluded that the eelgrass fish fauna was the richest, most abundant pelagic fish fauna of any habitat sampled.

In Yaquina estuary, Oregon, Bayer (1981) collected 30 fish species in an eelgrass meadow, of which four were dominant. He described seasonality in species number but also found seasonality in developmental state. The smallest size stages were most abundant in eelgrass in August and January-May, but no diurnal changes in species were noted.

Many studies have been done on the abundance, seasonality, and dependence on eelgrass of the Pacific herring. This is obviously due to the commercial value of the fish as bait for sport salmon fishing and the use of eggs as roe. Both Pacific herring and smelt deposit eggs on eelgrass as well as algae. This deposition occurs throughout the Pacific Northwest region. Just to establish the value of the crop of eggs, Webb and Hourston (1979) reported that for British Columbia alone the roe herring industry took 81,000 tons (73,636,364 kg) in 1976-77 with a landed value of $29 million. The food fishery took another 7,000 tons (6,363,636 kg) worth $0.9 million. The peak fishery occurred from 1953-54 to 1964-65 when catches fluctuated from 170,000 tons (154,545,455 kg) to 263,636 tons

(239,090,909 kg) (Outram and Humphreys 1974).

Herring spawnings begin in the first week of February and continue until the third week of June, but 78% of all recorded deposition occurs in March (Webb and Hourston 1979). Some variability is noted from year to year, depending on the water temperature. One 3-year-old female may deposit 20,000 adhesive eggs onto eelgrass or one of several species of benthic algae (Figure 19). Egg development occurs in 14-15 days at a water temperature of 8° C. Upon deposition of the eggs and hatching of the fry, enormous swarms of birds (seagulls and ducks) are attracted to the eelgrass beds. Mortality of eggs and juvenile herring may be as great as 50% (Outram 1958; pers. comm., 1981).

4.7 BIRDS

In north temperate eelgrass beds, waterfowl are the primary herbivores on living plants. This is in direct contrast to the tropics where a large number of fish and sea urchins are direct grazers. The birds on the Pacific coast eat a variety of products from the eelgrass beds: waterfowl such as black brant, Canada geese, emperor geese, wigeons, scoters, canvasback ducks, and coots eat eelgrass vegetation; pintails, mallards, and green-wing teals gorge on eelgrass seeds and epiphytic pelecypods on the blades before migrating from Izembek Lagoon (McRoy and Helfferich 1980); and many shorebirds and some ducks go to eelgrass beds to feed on associated fauna (mollusks, annelids, crustaceans). Gulls,

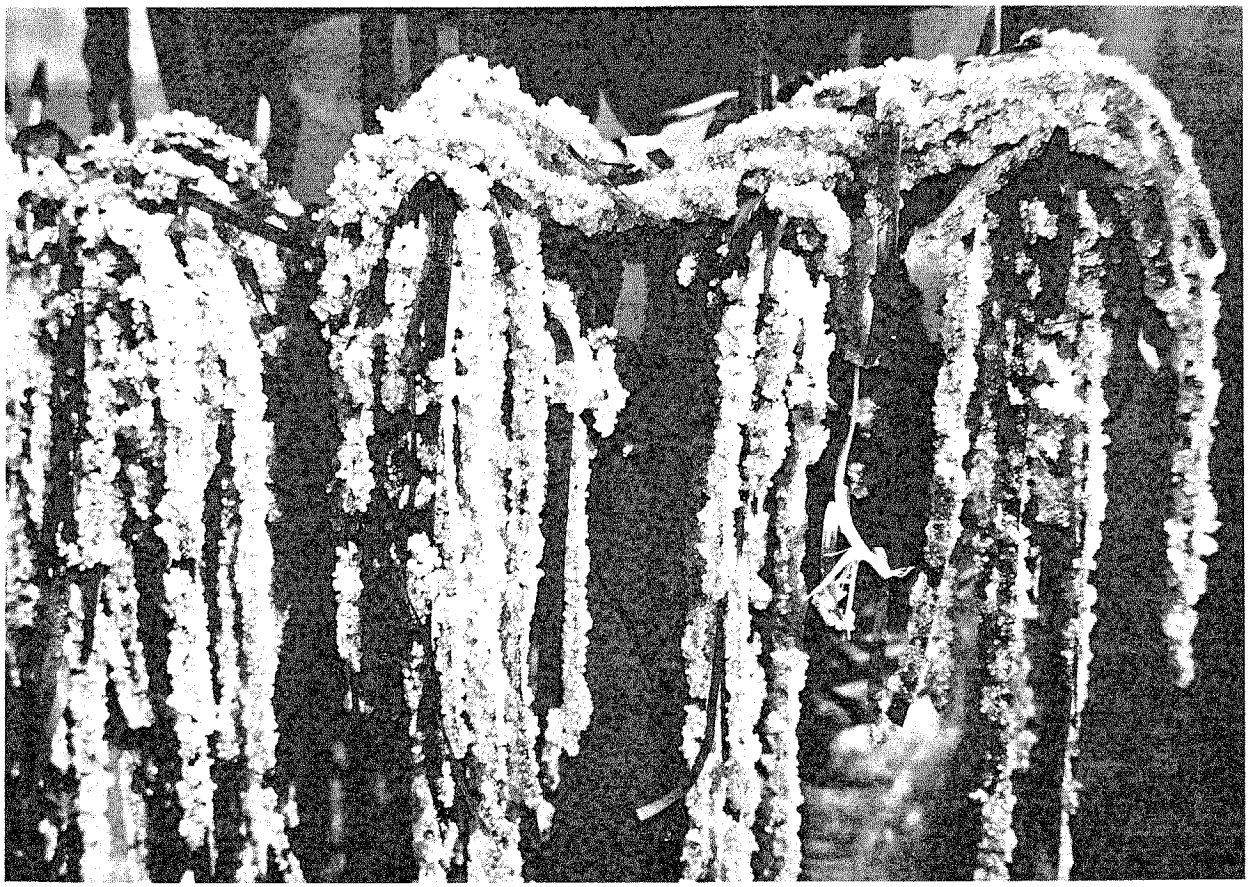

Figure 19. Eelgrass completely covered by Pacific herring eggs, British Columbia, Canada (Photo, courtesy of Dr. D.N. Outram).

coots, and surf scoters prey on herring eggs deposited on eelgrass. Bird use of eelgrass meadows is heavy in terms of abundance and species richness. This is possible, owing to the shallow nature of much of the eelgrass. At low tide numerous shorebirds, including the great blue heron, pick animals from the beds. The niches of the waterfowl also appear to be divided. Diving ducks eat animals, while the dabblers eat eelgrass blades. Once I did observe, however, a diving scaup come up with an entire eelgrass plant in its bill. The bird fauna associated with the eelgrass beds in the Pacific Northwest is listed in Table 13. Also included in the list of waterfowl which eat eelgrass in the Pacific Northwest are ring-necked ducks, bufflehead ducks, and ruddy ducks.

These birds obviously take a great quantity of energy from the eelgrass system. In Alaska, McRoy (1966) estimated that each black brant consumed 180 g dry wt eelgrass/bird/day (about 4% of the standing stock). The total amount consumed by the other grazing birds is as yet undetermined, as is the amount of food taken by the epiphyte scrapers (Steller's eiders) and animal feeders.

The waterfowl and shorebirds also add a great but as yet undetermined amount of nutrients to the eelgrass meadows. At low tides one can observe numerous large white patches of excrement dumped by gulls onto the eelgrass, while the waterfowl add theirs directly to the water column.

Owing to the economic value of the black brant on the Pacific coast from sport hunting, the populations of this species have been traced for years. Brant appear to eat primarily eelgrass leaves; however, some populations in the mid-1940's were observed consuming rhizome-root sections (Witherby et al. 1943; Cottam et al. 1944). The eastern brant depended on eelgrass for over 85% of its diet in the north, while in North Carolina where the blades were shorter, Ruppia maritima averaged up to 12% of the winter food. Algae, mostly Ulvaceae of very low nutritional value, only constituted 1% of the food used. Following the wasting disease of the 1930's, eelgrass only constituted 9% of the food consumed; Ruppia increased to 16%, while the Ulvaceae increased to 36%. Most of the birds diverted their migration route and went inland to feed on winter wheat and rye. Some brant from New Jersey to North Carolina are even now raiding home lawns for Kentucky bluegrass (Reiger 1982). On the Pacific coast there were minor declines of eelgrass in 1938. The black brant there also used Ulvaceae as an alternative diet (Moffit and Cottam 1941).

Black brant populations seem to be dramatically declining in the Pacific Northwest, correlated with the draining of coastal marshes, conversion of bays to boat marinas, and a general increase in water use by people (Reiger 1982).

Proctor et al. (1980b) stated that the major concentration areas of black brant in the Pacific Northwest are Grays Harbor, Willapa Bay, the Columbia River, Coos Bay, and Humboldt Bay. The important hunted waterfowl include American wigeon, mallard, pintail, canvasback, Canada geese, and the black brant. In 1976 a total of 101,420 ducks and 3,770 geese were harvested from five counties in southwestern Washington. In 1972 a total of 121,570 ducks and 2,450 geese were taken from seven coastal counties in Oregon (Proctor et al. 1980b).

The Washington State Department of Game (pers. comm., 1982) related that there are two principal wintering areas for black brant in Washington: Padilla Bay and Willapa Bay. A few brant feed on eelgrass throughout Puget Sound; however, there are also two segments of the brant population: those that winter in Washington and those that winter in Baja California but return to Washington in April to feed in eelgrass during daytime low tides. Brant arrive in Washington in mid-November and the winter population peaks in January. An increase is noted in April before the entire population leaves in May.

Lane (1980) reported that 60,000 to 70,000 black brant stop by to feed on eelgrass in Padilla Bay in the spring migration. A report made for Padilla Bay (NOAA 1980) listed 239 species of birds and also stated that an average of 5,000 brant winter on the bay (5,000-8,000 on Padilla Bay and Samish Bay, winter 1981-82;

Washington State Game Dept., pers. comm., 1982), with spring counts averaging 47,392 birds (up to 50% of the Pacific Flyway passes through Padilla Bay). An average of 50,000 ducks winter on Padilla and nearby Samish Bays (over 6,000 are diving ducks: canvasbacks, scaup, goldeneyes, buffleheads, and scoters on Padilla Bay alone; several of these species feed on eelgrass or animals within the system). In northern Puget Sound, Simenstad et al. (1979) recorded that the principal wintering sites for black brant were Padilla Bay, Samish Bay, Discovery Bay, and Sequim Bay. In April up to 18,000 brant were recorded in Samish Bay, 55,000 in Padilla Bay, and 6,000 in Discovery Bay.

At Grays Harbor an estimated 50,000 ducks and 6,000 brant use the estuary during winter (Proctor et al. 1980b). Grays Harbor also supports more than 150,000 shorebirds during peak migrations and is an important link in their migration (ACOE 1977b). In Willapa Bay, 50,000 black brant overwinter (Proctor et al. 1980b). Only 1,500-2,200 brant overwintered in 1981-82 (Washington State Game Dept., pers. comm., 1982). At peak periods Willapa Bay harbors 200,000 or more waterfowl. It is known now that Willapa Bay and Humboldt Bay are important wintering areas for the canvasback duck (850 winter in Willapa Bay with peak populations at 1,400 to 1,600; Proctor et al. 1980a,b). Wintering populations of ducks in Humboldt Bay are 124,000 with an additional 35,000 black brant.

In the Yaquina estuary, black brant arrive in late October-early November, increase in numbers to 350-525 birds in mid-January, and further increase to 780-914 birds in late March (R.D. Bayer, pers. comm., 1983).

Thus, there is a large list of birds that directly eat or are dependent on eelgrass and its food webs (Table 14). The nutrient and energy flows that these birds control and drive are enormous in scope.

4.8 TROPHIC RELATIONSHIPS AND GENERAL STRUCTURE

As with all the world's ecosystems, the eelgrass system supports both grazing and detrital food webs. Owing to the high productivity of eelgrass and its sloughing of leaf material from the shoots, a third pathway of energy flow is evident, that of leaf and detrital export.

Recent work in the tropics has documented the increasing importance of the direct use of leaves and epiphytes (grazing, herbivory), but in seagrasses generally and eelgrass in particular, the detrital food webs within the eelgrass meadows are still the primary pathway of trophic energy transfer (Kikuchi 1980).

Very few organisms use the fresh eelgrass plants in the Pacific Northwest as food. Table 14 lists the waterfowl which are overwhelmingly the dominant grazers on eelgrass in the region. McRoy and Helfferich (1980) listed only the green urchin, Stronglyocentrotus drobachiensis, which consumed fresh eelgrass.

It would be useful to have abundant data on the amount of energy or production which is channeled through direct herbivory, the detrital food webs, and the export route. Unfortunately, only the old study done by Petersen (1918) in Denmark and the relatively recent one conducted by Thayer et al. (1975b) have documented the energy flows quantitatively. Thayer et al. (1975b) concluded that the eelgrass system exports to adjacent systems, on the basis of a net incrase of sediment carbon, but no direct work was done. They also calculated that the macrofauna in the eelgrass bed in North Carolina consumed energy equivalent to 55% of the net production of eelgrass, phytoplankton, and benthic algae in the bed. They calculated a gross-growth ecological efficiency of 12% for the macrofauna in the bed and 24% for the fish community, suggesting a fairly efficient system with a surplus of energy to support the food webs. The high efficiency for the fish, in large measure a result of high proportions of juveniles in the community, suggests that the eelgrass system provides resident fish with superior shelter, food, and protection. These fish probably spend a relatively small proportion of their energy coping with environmental extremes, searching for food, and escaping from predators, and can use a relatively large part of their consumed energy for growth

Table 14. Waterfowl that use eelgrass meadows in the Pacific Northwest.

Species	Location	Winter population	Spring population	Food
Black brant	Padilla	5,000	55,000	Eelgrass vegetation
	Samish Bay	--	18,000	" "
	Discovery Bay	--	6,000	" "
	Grays Harbor	6,000	--	" "
	Willapa Bay	50,000	--[a]	" "
	Yaquina Estuary	350-525	780-914	" "
	Humboldt Bay	35,000	--	" "
Ducks	Padilla and Samish Bays	50,000 (6,000 are diving ducks)		Eelgrass vegetation or animal life on or among the plants
	Grays Harbor	50,000	--	" "
	Willapa Bay		--	
Canvasback duck		850	1,400-1,600	Eelgrass vegetation
	Humboldt Bay	124,000	--	Eelgrass vegetation or animal life on or among the plants
Shorebirds	Grays Harbor	--	150,000	Animal life on or among the plants
Miscellaneous				
Canada geese				Eelgrass vegetation
Emperor geese				" "
American wigeon				" "
Scoters (3 species)				Eelgrass vegetation; herring eggs
Coots				" "
Canvasback				Eelgrass vegetation
Ring-neck				" "
Bufflehead				Eelgrass vegetation
Ruddy				" "
Pintail				Eelgrass seeds; epifauna
Mallards				Eelgrass seeds; epifauna
Green-wing teal				Eelgrass seeds; epifauna
Scaups (2 species)				Eelgrass vegetation; fauna

[a]Bay shelters 200,000 or more waterfowl at peak periods.

and production. Figure 11 shows the proportional relations of the various trophic components in this North Carolina eelgrass system (Thayer et al. 1975b). Table 15 lists the various compartments in this system and the energy relations involved.

Finally, an abundant literature has documented the role of eelgrass as a nursery for young fish and many other animals (Thayer et al. 1975b; Adams, 1976a,b; Thayer and Phillips 1977; Thayer et al. 1979; ; Kikuchi 1980; McRoy and Helfferich 1980; Orth and Heck 1980). The meadow actually is a giant food factory, feeding a small number of herbivores, with most of the primary production decaying to enter the detrital food webs. Owing to the density of foliage and sediment stabilization, the habitat also becomes a refuge for many other animals. Thus, the meadow attracts permanent, seasonal, and

Table 15. Energy in various compartments of an eelgrass bed in North Carolina (after Thayer et al. 1975b).

Compartment	Energy value in compartment (kcal/m^2/yr)	Energy input to compartment (kcal/m^2/yr)	Energy lost from compartment (kcal/m^2/yr)
1. Primary producer			
Eelgrass	135	--	--
Benthic algae	18	--	--
Phytoplankton	1	--	--
2. Detritus production	21,160	--	--
3. Bacteria, microfauna, Meiofauna	47	--	467
4. Nekton	6	103.5	95.8
5. Epifauna	4.2	167.6	66.0
6. Infauna	30.7	585.5	234.5

transient residents, some on a seasonal basis, and some on a diurnal basis.

A relatively new technique has been employed to delineate the flows of carbon from plants to animals in seagrass food webs, the del ^{13}C or $^{13}C/^{12}C$ ratio. The technique assumes that individual plant species or groups possess stable ratios, that these ratios are retained in carbon flows, and that the isotope ratios of animals are a function of their diet. While the procedure will not identify the specific food-web importance of a seagrass species, it is useful in analyzing the food-web importance of seagrasses as a group (Fry et al. 1982).

Much research is needed on eelgrass food-web relationships in the Pacific Northwest. The best work done to data on a descriptive basis is that of Simenstad et al. (1979; Figure 20) and a diagram prepared for an Army Corps of Engineers report (ACOE 1977b; Figure 21). There is a need for quantification of work of this sort, as well as quantifying the energy flows through the various trophic compartments and the amount of leaf material and detritus exported from the eelgrass system in the Pacific Northwest. Figure 22 diagrams the principal energy pathways in a typical eelgrass meadow in the Pacific Northwest.

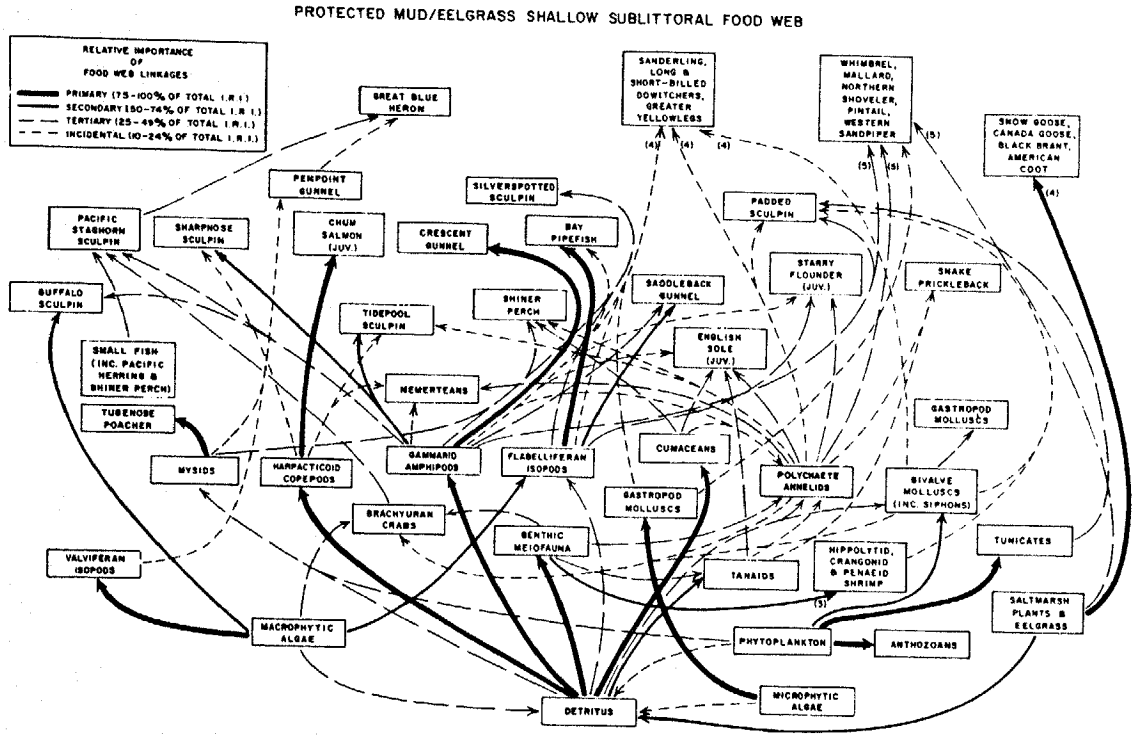

Figure 20. Composite food web characteristic of protected mud/eelgrass, shallow sublittoral habitats in northern Puget Sound and the Strait of Juan de Fuca (after Simenstad et al. 1979).

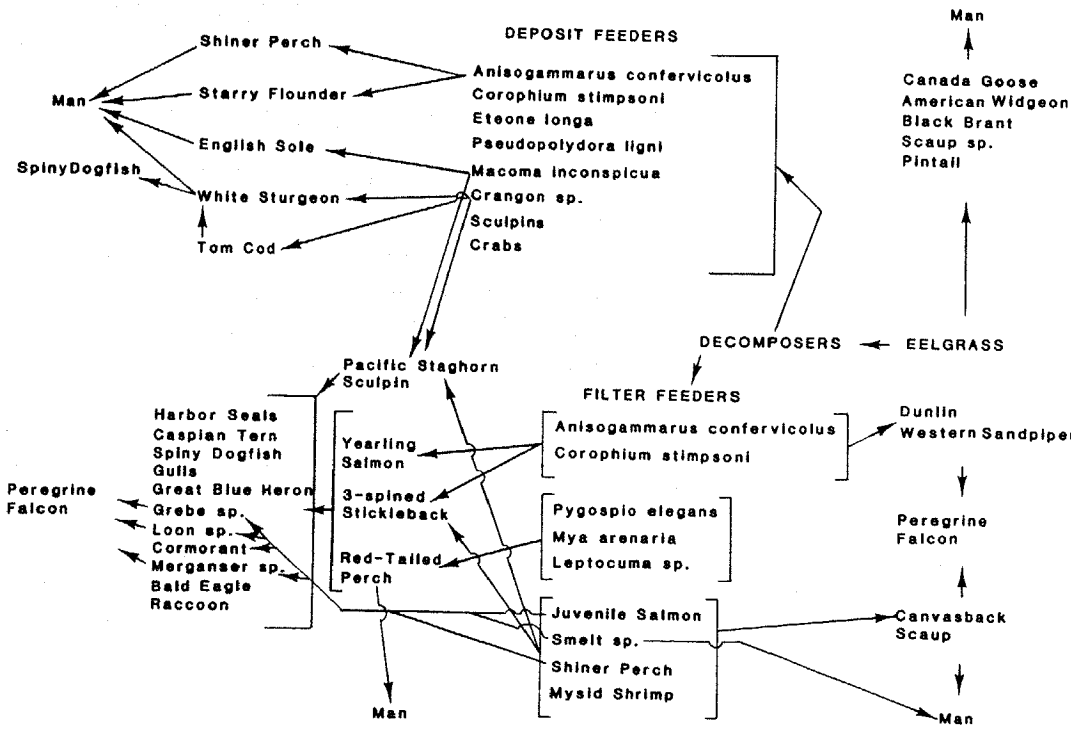

Figure 21. Food web diagram of eelgrass at Grays Harbor, Washington (adapted from Army Corps of Engineers 1977b).

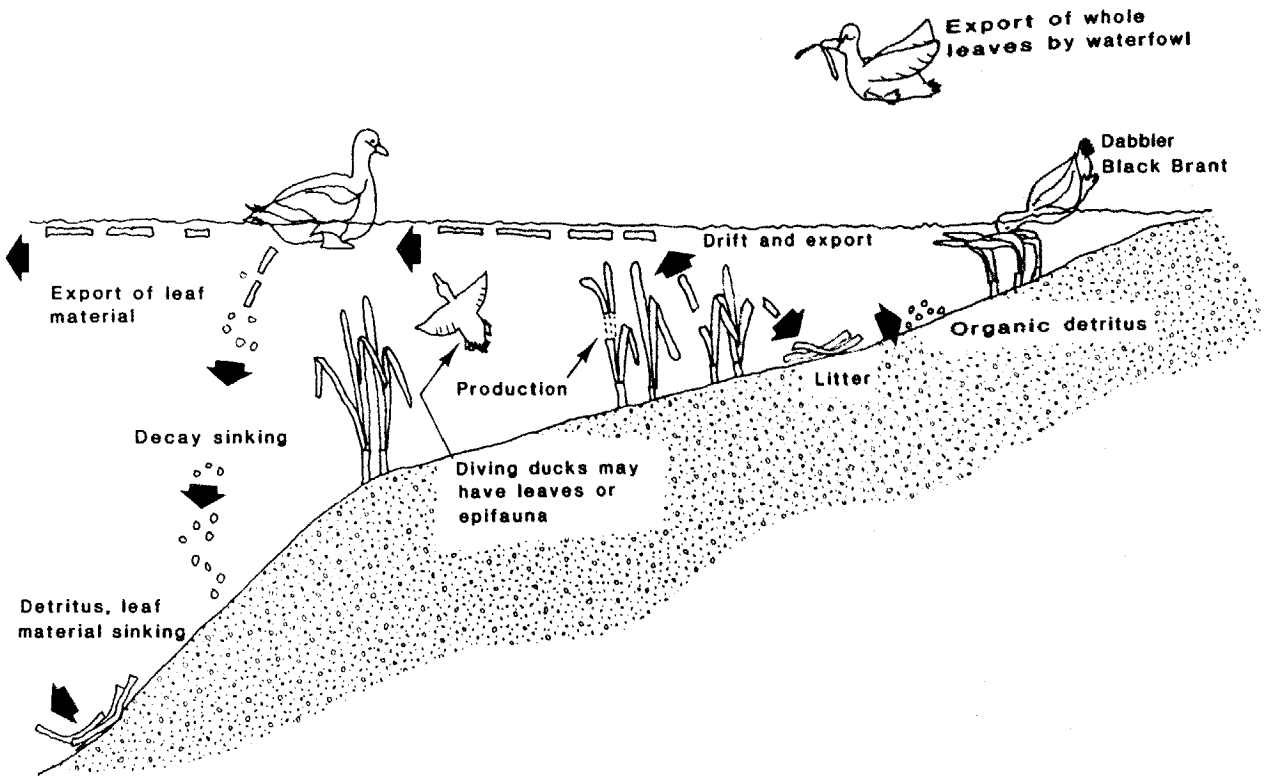

Figure 22. Principal energy pathways in an eelgrass meadow (adapted from Zieman 1982).

CHAPTER 5
INTERACTION WITH ADJACENT SYSTEMS

There is very little known about the quantitative aspects of the transport of living and/or dead eelgrass material, DOM (dissolved organic matter), and detritus. For that reason, the discussion in this chapter is general.

Anyone who has walked beaches where seagrasses occur offshore has observed detached leaves and perhaps whole plants washed ashore, occasionally in large windrows. In October 1975, I observed great piles of eelgrass leaves up to 1 m (3 ft) deep on the beaches and covering the intertidal zone as far as the eye could see in Izembek Lagoon, Alaska. The presence of a deep compacted layer of eelgrass peat on the beach attested to this occurring annually. In May 1976, the leaf matter over the intertidal zone had decayed completely, leaving a 15-cm (6-inches) layer of soft jelly-like ooze. Barsdate et al. (1974) stated that the breakdown products of eelgrass in Izembek Lagoon supported the entire fisheries of the southern Bering Sea, implying a net transport of eelgrass decomposition products into the adjoining pelagic system.

It is unlikely that much eelgrass in the Pacific Northwest becomes dislodged through herbivore activity. Waterfowl eat the leaves they detach. In isolated locations sand dollars (Dendraster sp.) wedge into intertidal and shallow subtidal meadows and uproot considerable plant material (Figure 23). Exclusion cages have shown that eelgrass may recover from this perturbation. It is possible that

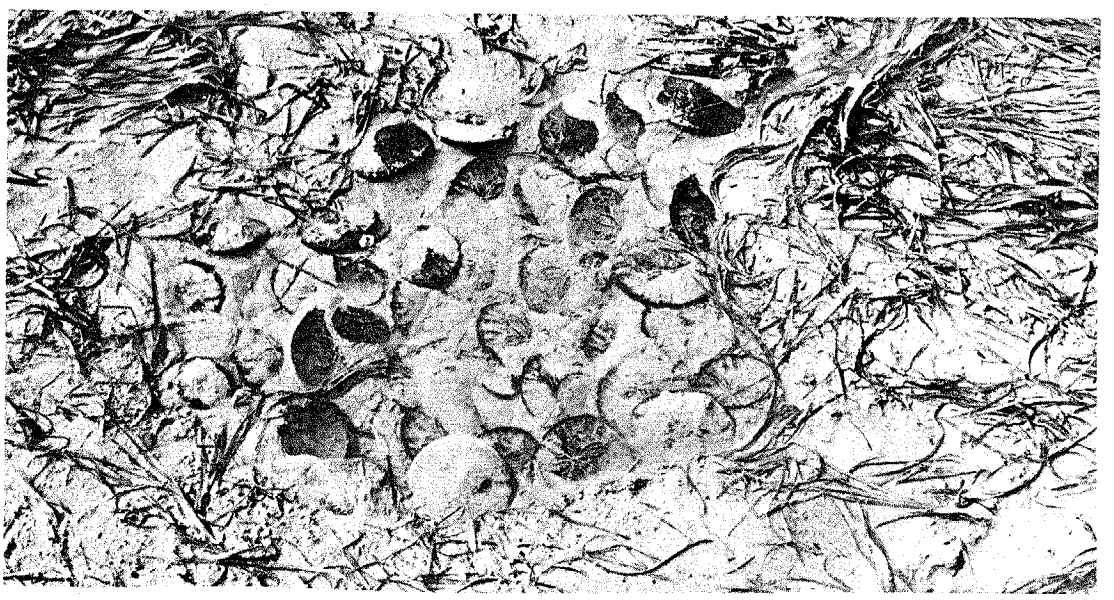

Figure 23. Sand dollars (Dendraster sp.) digging up eelgrass in Puget Sound.

storms erode and dislodge some eelgrass, but most is very persistent (Figure 2). Gallagher et al. (In prep.), however, found that periodic storms do dislodge a large amount of eelgrass in winter and summer and deposit the material in adjacent marshes in Netarts Bay, Oregon. The eelgrass litter constituted between 14% and 35% of the dead material in the marshes. Their conclusion is that in estuaries where seagrass beds adjoin marshes, the trapping of eelgrass litter in the marsh provides a mechanism for retaining and recycling nutrients within the wetlands and preventing their loss to the oceanic system. These nutrients may be passed back and forth between the eelgrass and marsh systems. Also, in Netarts Bay, Kentula (1983) calculated a total annual leaf loss which varied from 25 to 111 g dry wt/m^2. While the below-ground biomass was retained within the meadow, she observed that some of the aboveground biomass was carried shoreward and trapped by the salt marsh and some was transported out of the estuary. The presence of eelgrass material in cores taken in Oregon salt marsh sediments implied the net transport of eelgrass (Jefferson 1975).

Probably normal leaf defoliation and replacement is the source of most of the detached leaf material observed in the Pacific Northwest. Short (1975) estimated that eelgrass experienced a 70% seasonal defoliation rate. Proctor et al. (1980b) used this number and based on standing-crop estimates from Phillips (1974; 580 g dry wt/m^2, 260 tons/acre) and others, to calculate that eelgrass meadows in the Pacific Northwest produce annually about 30,000 kg (66,000 tons, dry matter) of eelgrass leaf material, of which 20,909 kg (46,000 tons) dry weight is defoliated annually to become detritus: 8,400 ha (21,000 acres) of eelgrass in Washington; 2,000 ha (5,000 acres) in Oregon; and 1,600 ha (4,000 acres) in northern California.

In North Carolina, Thayer et al. (1979) reported that up to 25% of the production in open water beds is exported to the adjacent estuary, while in embayment-type beds over 90% of the production decays in the bed or is washed up onto adjacent beaches and marshes.

The only record of eelgrass blades in the deep sea was made by Pearcy and Ambler (1974) who found the material as accidental contents in the abyssal rattail, Coryphaenoides armatus.

In the Carribbean, tropical seagrasses are exported and found at great depths (reviewed by Zieman 1982). At St. Croix, U.S. Virgin islands, 60%-100% of the Syringodium filiforme daily production was detached and exported, whereas only 1% of the Thalassia production was exported by bedload transport (Zieman et al. 1979). Leaves and rhizome pieces of Thalassia were collected in 3,160 m (10,368 ft) of water off North Carolina (Menzies et al. 1967); at 3,500 m (11,484 ft) deep off the Virgin Islands (Roper and Brundage 1972); and from 1,326-8,339 m (4,376-27,489 ft) deep in the Puerto Rican and Cayman trenches (Wolff 1980). Wolff reported consumption of the leaf and rhizome material by numerous invertebrates.

Finally, the important mechanism that leads to detritus production and either entrapment or export from the seagrass system is the decomposition and mineralization of the leaf material that becomes detached from the plants. Only two field studies have been conducted on seagrass leaf decay rates (litter bag analyses): one on Thalassia (Zieman 1968) and one on eelgrass (Burkholder and Doheny 1968). Two studies were conducted in the laboratory (Harrison and Mann 1975a; Godshalk and Wetzel 1978). Zieman (1968) observed that Thalassia leaves in litter bags anchored in areas subject to alternating periods of drying and wetting lost weight three times as fast as those incubated in tanks where they were constantly wet. Predried Thalassia leaves placed in tanks lost weight five times faster than leaves not predried. Drying is considered to destroy the cellular integrity more rapidly and allow a more rapid microbial attack. Zieman also found a 50% weight loss of leaves after 5 wk of incubation in tanks of circulating seawater. Only an additional 10% loss was observed over the next 4 wk.

In New York Burkholder and Doheny (1968) placed fresh eelgrass leaves in litter bags in two locations. At one site only 23% of the material remained after 56

days; at the other site, only 10% remained after 51 days (based on dry weight).

In the laboratory Harrison and Mann (1975a) found that dead eelgrass leaves lost 35% of the original dry weight in 100 days at 20° C. Whole leaves lost 0.5% of the organic content per day; particles smaller than 1 mm lost 1%/day. Since most leaves of Thalassia and Zostera remain attached to the plant during senescence and death (McRoy 1966; Zieman 1968; Harrison and Mann 1975a), the data indicate that the loss of organic matter from attached leaves is slow during the remainder of processing. Godshalk and Wetzel (1978) described three phases in eelgrass leaf decomposition based on changes in decay rates in time: (1) increasing weight loss from leaching and production of DOM; i.e., initial leaching and maximum weight loss/unit time (may last from a few minutes to several days); (2) decay rates decreased; during phase 2, the microbial flora on the decomposing leaves enriched the material with ATP and nitrogen (may occur in a few days to a few months); (3) rate of breakdown of residual refractory material closely approaches zero, but can be accelerated by changes in physical conditions or nutrient replenishment to stimulate microbial growth (may last from several months to several years).

Thus, the mechanisms that give rise to detached plants and to leaf decay and detritus are apparent. What are lacking are the studies that define seasonality and abundance of the fractions of eelgrass material (DOM, particulate matter, whole leaves) which are retained within the system and are exported to adjacent systems, and their contributions to these adjacent systems.

CHAPTER 6
HUMAN IMPACTS-MANAGEMENT CONSIDERATIONS

With the increasing residential, recreational, and commercial development of the shorelines of the nation and the Pacific Northwest, it is inevitable that pressure on the shallow water resources of the area have also increased. In comparison to the high-density development in southern California, the Gulf of Mexico, and in the northeastern United States, that in the Pacific Northwest could be termed minimal. Yet demands and impacts have been made, and they are increasing. Logging has been an important feature of the economy since the early 1900's. In certain areas of heavy rainfall and where clearcutting of upland timber has occurred, siltation has also occurred. Stout (1976) noted the effects of siltation in Netarts Bay, Oregon, coincident with historic logging and burning of timber in the watershed, but stated this has intensified since the 1940's when clearcutting and roadbuilding were initiated. Proctor et al. (1980b) have documented the extensive maintenance dredging needed to maintain shipping channels in several areas and the suspended silts arising from wood chips and sawdust in Yaquina Bay.

The extensive land cultivation needed for agriculture can lead to siltation in estuarine areas, with an increase in water turbidity that leads to decreased eelgrass growth (Thayer et al. 1975a). The role of solar radiation passing through the water column, which controls the productivity, density, depth limit, and even presence of eelgrass in an area, and thus the presence and richness of the ecosystem itself were discussed earlier in this report.

The increasing human use of northern Puget Sound is having a drastic impact on the black brant presence in Padilla Bay and other local bays (Reiger 1982). State and Federal agencies continue to receive an increasing number of applications in the northern sound area, particularly for marina development. One observes an increasing shoreline development of homes and even condominiums in some areas.

Continued maintenance of shipping lanes and logging is presumed necessary for the economic life of the Pacific Northwest. It is hoped that this report will aid in the formulation of policy that will accommodate those activities while preserving and protecting the water and habitat qualities of the eelgrass resources.

Considering the coastal sediment stabilization function, the nutrient exports which enhance oceanic production, and the value of eelgrass to recreational and commercial fisheries, it is worthwhile--even imperative--to consider preserving the resource.

6.1 DREDGING AND FILLING

Of all the possible impacts, dredging poses the greatest threat to the seagrass ecosystem (Thayer et al. 1975a; Zieman 1975; Phillips 1978). Not only are the plants removed, but the entire physical, biological, and chemical structure of the ecosystem is changed. The extent of the area affected by the dredging depends on the tidal range, current strength, and sediment texture in the area.

Sediments raised by dredging can bury plants away from the site. More importantly, sediments drastically reduce

plant density as a result of their effect on water clarity. The reduction in seagrass density could result in an increased silt load, due to a reduction in sediment trapping, and increased erosion of bottom sediments. Where turbid water prevails, eelgrass populations are limited to less than 1-3 m (3-10 ft) deep (Burkholder and Doheny 1968; Thayer et al. 1975a). Eelgrass has been observed down to 30 m (98 ft) where the water is clear (Cottam and Munro 1954). Dredging reverses the normal redox potential (Eh) of the sediments of a seagrass system, which reverses the entire nutrient-flow mechanics of the ecosystem.

Hydraulic clam dredges have been used in Puget Sound. The dredge blasts sediment to a depth of 45 cm (18 inches) and a width of 1 m (3 ft). Since eelgrass rhizome mats are located at a maximum depth of 15 cm (6 inches), this activity removes the entire ecosystem. The State of Washington requires leaving strips of eelgrass between the dredged strips. In one location, however, I observed that all the eelgrass had been removed. Several years ago, the use of these dredges was banned in Florida and in the Chesapeake Bay after it was determined that they directly removed the seagrasses or led to their removal by erosion.

In North Carolina, bay scallop larvae attach directly to eelgrass blades (Thayer and Stuart 1974). Commercial fishermen use hand rakes and bar dredges to gather the scallops. The bar dredges denude the bottom of eelgrass over large areas, stirring up sediments and promoting sediment oxidation so that recolonization of eelgrass and thus that of the bay scallops was impeded. In the Niantic River, Connecticut, the eelgrass is too dense for the settlement of bay scallops. When the eelgrass disappeared in the 1930's, allowing better wave circulation, the bay scallop flourished, attaching to small algae (Marshall 1947).

Waddell (1964) documented the impacts of harvesting oysters from eelgrass beds in Humboldt Bay by hydraulic dredges and a modified dragline-type dredge. Harvesting procedures had severe impacts on eelgrass. Under conditions of no dredging, eelgrass biomass declined 38% (cf. discussion on logging, maintenance dredging, and agricultural impacts on water quality in this section), while biomass declined by 96% after three dredgings. The mean percentage reduction of shoot density ranged from 33% on beds with no dredging to 71% on beds that were dredged three times. The greatest reduction occurred after the first dredging operation. In some cases, the eelgrass failed to recover following dredging.

Proctor et al. (1980b) documented the various studies done in estuaries of the Pacific Northwest where dredging has occurred. In Oregon, a number of landfills have resulted in the loss of eelgrass habitat either by direct dredging or by sediment deposition. Peripheral erosion around the landfill and diking to protect the landfill have also reulted in loss of eelgrass in some areas. They stated that Willapa Bay required maintenance dredging of 230,000 m^3 (300,000 yd^3) per year up to 1977, when the Army Corps of Engineers decided to discontinue it. Yaquina estuary, Oregon, contained about 5% of its sediments in the form of wood chips, sawdust, and plant material. These materials are significant fractions in estuaries where wood processing industries are located. Coos Bay, in southern Oregon, is heavily impacted by industrialization, logging, and shipping. Humboldt Bay is heavily sedimented. The high tide area decreased from 108 km^2 (43 mi^2) to 67 km^2 (26 mi^2) in the last 120 years. This decrease is related to human activity in the area, in particular, agriculture and logging.

6.2 EUTROPHICATION AND SEWAGE

Eelgrass seems relatively resistant to substances that can poison other forms of marine life (McRoy and Helfferich 1980). It appears to concentrate metals without damage (Barsdate and Nebert 1971; Brinkhuis et al. 1980), but Zieman (1975) postulated that this makes the metals available for movement up the food chain.

6.3 OIL AND ORGANIC CHEMICALS

Several studies made on eelgrass following oil spills have shown only temporary damage to blades if the oil contacts the blades in air (Dalby 1968). If the leaf remains covered with water, there is no

apparent damage. Rhizomes and roots do not appear to be damaged in any case. The best documented case study is that of den Hartog and Jacobs (1980) after the tanker Amoco Cadiz was stranded on the Brittany coast, France, discharging 216,000 tons (196,363,636 kg) of crude oil and 4,000 tons (3,636,364 kg) of bunker fuel. The eelgrass remained almost unaffected. Animal groups were selectively affected: gastropods were not affected, and echinoderms recovered. The amphipods, isopods, and polychaetes were seriously damaged and had not recovered during the year following the spill.

The most sensitive areas containing eelgrass may be in sheltered locations that are poorly flushed (Beak Consultants 1975). These areas will tend to retain oil for long periods. If spills occur in late summer or winter when leaf sloughing is at a peak, mats of drift blades will tend to capture and retain oil for later remobilization in the intertidal zone. The authors also warn that oiling of blades may make them unpalatable to natural grazers such as waterfowl. It is also possible that a spill in spring could interrupt the production and/or viability of young flowers and pollen. Research should be done on the effects of oil on the bacterial decomposition of dead eelgrass blades into detritus before it enters the food web. It is known that the eelgrass habitat can retain and release oil slowly over long periods, resulting in chronic contamination.

Beak Consultants (1975) documented the possible impacts of an oil spill in northern Puget Sound for a number of animals that use the eelgrass system. For the waterfowl and shorebirds, the loss of food or consumption of tainted food, are the greatest impacts. For the fishes the greatest impacts are to the bottom dwellers; i.e., narcotization followed by suffocation or increased predation by the less sensitive crabs. Flatfishes may develop tumors on their ventral surfaces in contact with polluted sediments. For the shoreline and open-water fishes, the movement away from the eelgrass meadow increases the chance of predation and the loss of food. Crabs appear to be highly resistant to oil, but the smaller crustaceans are more severely and quickly affected. Mollusks appear to be entirely unaffected by oil contamination of low aromatic content, but highly aromatic crudes and refined products can cause paralysis and death. The same was found for annelids.

On a ranking for physical impact, the eelgrass bed was second only to the salt marsh: for toxicity impact the eelgrass bed was midway between the mixed-coarse habitat and open water habitat (Beak Consultants 1975).

Oil spilled on the surfgrass, Phyllospadix scouleri, in the Pacific Northwest had similar effects. Little damage was done to the plants (leaves turned brown, but were replaced; no damage to rhizomes and roots), but some groups of animals received long-term damage (Foster et al. 1971; Clark et al. 1978).

Documentation of oil spills on the tropical seagrass Thalassia is more extensive (cf. Zieman 1982 for a thorough review). The results are approximately the same; the plants are little affected by the oil, but associated fauna can be severely damaged. The most severe effect was noted when oil was spilled on Thalassia near Guanica, Puerto Rico. In less than 1 wk, 3,000 m^3 of sand washed out, owing to the mixing of the oil with the sediments, making them buoyant and easier to wash out. Mass mortalities of animals occurred following the spill.

Zieman (1982) thoroughly reviewed the research done on the toxicity levels of crude oil and the refined fractions. All work shows that refined bunker C and No. 2 fuel oil were more toxic to all animal forms than crude oils. Changes in temperature and salinity enhanced the toxic effects. The greatest danger to aquatic organisms appears to be the aromatic hydrocarbons as opposed to the paraffins or alkanes. The bicyclic and polycyclic aromatics, especially napthalene, are the major source of the observed mortalities. The best indicator of an oil's toxicity is probably its aromatic hydrocarbon content.

In recent years humans have dumped increasing amounts of heavy metals and synthetic products, including chlorinated

hydrocarbons and other herbicides, into our shallow coastal zone. Additions of toxic materials are known to affect animal communities (Thayer et al. 1975a), but little has been done to document their direct effect on eelgrass. More research is needed, not only on the bioaccumulation of metals and toxic chemicals by the plants but also their accumulation and possible transfer through the grazing and detritus food chains and nutrient cycles.

In an attempt to decimate eelgrass in Nova Scotia to enhance oyster growth, Thomas (1968) found that the herbicide, butoxyethanol ester of 2,4-D, was most effective in killing the plants. This was applied to the plants in the field. Correll and Wu (1982) found that the herbicide atrazine, commonly used in corn production, stimulated photosynthesis at 75 ug/liter in eelgrass, but inhibited it at 650 ug/liter. This herbicide was tested following a gradual decline in populations of many species of submerged vascular plants in the upper and midreaches of Chesapeake Bay. They noted that the temporal and spatial use pattern of atrazine around the bay correlated well with the observed decline in the estuarine plant populations. It is clear that herbicides can be extremely damaging. Runoff from waterways that drain agricultural areas can severely damage eelgrass systems by sediment transport and by herbicide contents. These waters should be monitored for these chemicals.

6.4 BOAT USE

Impacts to eelgrass meadows in the Pacific Northwest do not normally result from physical disturbance involving cuts made by boat propellors. In south Florida, Zieman (1982) stated that these cuts are the most common form of disturbance to seagrass beds.

The numbers of black brant are declining in the Pacific Northwest, owing to an increase in human use and development of the coastal area (Reiger 1982). Between the 1940's and 1981 brant stopping in Washington declined by 74%; in Oregon, by 90%; and in California, numbers declined by almost 99%. Reiger attributed this to the draining of coastal marshes, the conversion of bays to marinas, and the impact of an increasing number of weekend boaters, who have driven wintering brant to Mexico where populations have grown from 80,000 in the early 1950's to as many as 130,000 today.

Even if these numbers are only approximately correct or merely indicate trends, an aggressive program is needed to create protected zones around the large eelgrass beds which harbor the brant.

6.5 TEMPERATURE AND SALINITY

Temperature is probably the most critical of the suite of environmental factors that affect marine life. It is a controlling factor. In the case of seagrasses, it affects growth, development, and phenological cycles. McMillan (1978) and Phillips et al. (1983a) reported that eelgrass populations have upper and lower thermal tolerance levels and that temperature regimes at local sites along broad latitudinal gradients on both coastlines of North America control the occurrence and timing of flower and seed production.

McMillan (1978) subjected three different eelgrass populations from Puget Sound, each with different leaf widths, to three different temperature treatments. After 4 mo, each population maintained its original leaf width, indicating that local populations maintained distinct genetic limits of ecoplasticity to their environments. These tolerance levels vary with the local area. Biebl and McRoy (1971) not only found a difference in the thermal tolerances of intertidal pool and subtidal eelgrass in Izembek Lagoon, Alaska, but also found that both forms could withstand a range of water temperatures from -6° C to 27° C, while plants from Puget Sound and California were killed at -6° C. McMillan and Phillips (1979) found that eelgrass in Alaska had more heat resistance than plants from Puget Sound or California, owing to the selective influence of a greater environmental variability in Alaska.

In the Bering Sea and along the Atlantic coast of North America, there is a fairly

great annual range of water temperature (-6° C to 27° C in Izembek Lagoon; Nova Scotia: -2° C to 24° C; Rhode Island: -2° C to 27° C; North Carolina: 0° C to 27° C)(Phillips unpubl. data). There is evidence that eelgrass at the northern and southern limits of distribution on the Pacific coast and on the Atlantic coast may have much greater thermal tolerances than that in the midportion of the Pacific coast range (Phillips et al. 1983b). In Puget Sound, the normal annual range of water temperature is 6° C to 13° C. Occasionally, during low tides on sunny days in summer, there may be brief periods of elevated water temperatures over eelgrass (up to 18° C), but this is rare.

In 1974, Phillips warned that heated water released into eelgrass habitats could disrupt the reproductive cycle, presumably interfering with the normal temperature-dependent periodicity of flowering and germination. Considering the present contributions of McMillan (1978) and McMillan and Phillips (1979), we now know that the developmental cycle of eelgrass, as well as its presence in an area, is temperature related. Populations of the plant have specific thermal adaptive limits. The Pacific Northwest does not have a significant problem with thermal water release from power plants or industry. We know from work done in Biscayne Bay on Thalassia (reviewed by Zieman 1982) that plants were killed when the water temperature was elevated 5° C above ambient and were harmed by an elevation of 3° C. If the Northwest should encounter such thermal releases, we must consider the impacts on eelgrass. McRoy and Helfferich (1980) noted the susceptibility of eelgrass in the North Atlantic to a very slight increase in water temperature in 1931. During that period over 90% of all eelgrass died. Recent evidence shows that these strains have a greater thermal tolerance range than do Pacific coast stocks.

Considering its worldwide distribution, eelgrass grows in a wide range of salinity. It is euryhaline. Biebl and McRoy (1971) reported that eelgrass in Izembek Lagoon, Alaska, maintained an osmotic resistence to salinity changes from freshwater to 93 ppt. At 124 ppt leaves were killed. Positive net production was maximum at 31 ppt, as was photosynthetic rate, but was found in a range from freshwater to 56 ppt (photosynthetic rate was zero in freshwater and at 62 ppt). Respiration was depressed in freshwater but only slightly affected from 31 ppt to 93 ppt. Ostenfeld (1908) considered that a salinity range for eelgrass in Denmark from 10 ppt to 30 ppt was optimum for growth. In Japan, Arasaki (1950) reported that eelgrass growth was best from 23.5 ppt to 31 ppt but poor at 18.0 ppt and stopped below 9.1 ppt, although plants did not die. Tutin (1938) observed eelgrass in a bay in England in 42 ppt with no damage. He grew plants for a considerable period in the laboratory in salinities ranging from 10 ppt to 40 ppt without harm. It is known that eelgrass can acclimate to a changing salinity regime. Often extensive meadows grow off the mouths of streams where the salinity drops to freshwater level at low tide. The plants appear to flourish. Low salinities appear to enhance seed germination in spring (Tutin 1938; Arasaki 1950; Phillips 1972).

6.6 MANAGEMENT NEEDS

Wilson (1981) noted that in order to manage our coastal estuaries properly, we need a better understanding of the ecology of eelgrass, which requires knowledge of the causes of its distributional patterns. These patterns are affected in the short term by the increasing demands by modern man on the coastal and estuarine environments. Sedimentation, dredging, storms, currents, sewage, power-plant effluents, and factors such as adaptational tolerances of the plants as regulated by their genetic patterns, all affect these distributional patterns.

Continued monitoring of our estuarine areas is necessary if we desire to remain aware of biological and environmental changes. This awareness is needed for intelligent management of this resource. Spartina alterniflora (saltmarsh cordgrass) was introduced into Willapa Bay during the 1940's or early 1950's. The species has rapidly spread into upper intertidal and mudflat communities and is displacing the more productive native

marsh species and the small Zostera japonica, a favorite food plant of black brant and other waterfowl. Cordgrass was also introduced into South Padilla Bay, where it also seems to be spreading from rhizomes. The result of continued growth of Spartina in the Pacific Northwest would result in lowering waterfowl carrying capacity. In its native habitat in the northeastern Gulf of Mexico and northward from Florida to Massachusetts, the species does not compete with seagrasses for its niche. In its native habitat all seagrasses are subtidal.

Monitoring of vegetation such as cordgrass expansion, changes in standing stocks of eelgrass, impacts and disturbances of eelgrass, and continued escalation of human activity over the dense stands of eelgrass is needed to establish improved means of assessing changes and legislating policy as necessary in sensitive areas. The use of the best agricultural, logging, and roadbuilding practices are imperative if future impacts are to be minimized. Conflicting uses of the eelgrass habitat, such as oyster culture, boating over meadows, and real-estate development, which requires dredging and later sewage deposition, need suitable management.

In Willapa Bay, one of the three largest stands of eelgrass in the Pacific Northwest, six activities have impacted eelgrass (Fish and Wildlife Service 1970): (1) destruction of tidelands and marshlands by filling and diking have reclaimed 2,520 ha (6,300 acres) for industry and highways, and another 120 ha (300 acres) for agriculture, while the Pacific Soil and Water Conservation District encouraged the reclaiming of another 2,640 ha (6,600 acres) for pasture, hay, and silage production; (2) draining of fresh-water marshes and construction of lagoon housing (there were fears for oyster culture and fisheries due to deteriorating water quality); (3) dredging activities: in 1969 alone, about 630,000 yd^3 of dredged spoil were deposited on diked and reclaimed tidelands and marshlands; (4) construction of bulkhead, pier, and shoreline facilities; (5) contamination of the aquatic life or the environment: domestic waters, agricultural runoff, debris from log storage areas, wood chips, and radioactive materials were causing water quality problems (the radionuclides entered Willapa Bay from the Hanford Atomic Works where they traveled along the Columbia River to the Pacific Ocean and into Willapa Bay, 390 miles away; P^{32}, An^{65}, and Cr^{51} were predominant and were found in the oysters and razor clams); (6) sedimentation arose upstream from topsoil off farmland, from logging, and from road and highway construction.

It is imperative that studies be continued in sanctuaries totally devoid of impacts to yield baseline data that can be used as control information on the inherent genetic, morphological, and physiological capabilities of the plants and their system.

Undesirable Effects of Eelgrass

There are, at present, no known undesirable effects of eelgrass in the Pacific Northwest region.

Commercial and Recreational Fisheries

Helfferich and McRoy (1978) calculated the dollar values of various components of an eelgrass system. For gross energy values, using the technique of Gosselink et al. (1974) and the productivity values of eelgrass of McRoy and McMillan (1977), they calculated that 0.4 ha (1 acre) of eelgrass was worth $4,267/yr (Gosselink et al. used the real estate evaluation technique of income capitalization: $V = \frac{R}{i}$, where V is the value of a parcel of land, R is the annual return from it, and i is the standard rate of interest, assuming 5%). The nutrition generated by an eelgrass meadow in Puget Sound for oyster culture using data from Imai et al. (1951) was worth $8,760 per 0.4 ha (1 acre)/yr. For fisheries, the category was divided into commercial, sport, and sport charters. For commercial fisheries 0.4 ha (1 acre) of eelgrass has a value of $35/yr. For sport fisheries the value was $284/yr, while for sport charters the value was $6/yr. For waterfowl, considering the value of the meat as food and the money spent hunting, the value of 0.4 ha (1 acre) was $13/yr. This gives a value of $12,325/0.4 ha (acre)/yr for an eelgrass meadow (cf. Helfferich and McRoy

1978, for all assumptions, formulations, and considerations used in the calculations).

If these calculations are even only approximately correct, the economic value of seagrasses is enormous in the Pacific Northwest. Proctor et al. (1980b) calculated that there are 8,400 ha (21,000 acres) of eelgrass in Washington (this probably does not include Puget Sound), 2,000 ha (5,000 acres) in Oregon, and 1,600 ha (4,000 acres) in northern California. On a persistent annual basis this represents a sizeable economic resource, even without considering coastal-sediment stabilization value, which is incalculable.

Specifically in the Northwest there are some data that relate to economic values of food animals associated with eelgrass. Webb and Hourston (1979) found that in southern British Columbia alone, the value of the Pacific herring fishery for 1976-77 was $29.9 million (81,000 tons, $29 million for roe; 7,000 tons, $0.9 million for food fish). Helfferich and McRoy (1978) reported that the total 1976 catch of Pacific herring (20.2 million tons) was worth $10.7 million. It must be remembered that herring lay eggs on algae, pilings, and several types of hard substrates as well.

Dr. Robert Trumble, Washington State Department of Fisheries, related the values of the Pacific herring in Washington State for 1979-80 (Table 16). The combined value for 1979 was $4,468,122. In 1980 the combined value was $1,774,670. In 1981 the sport bait price was $0.30-$0.40/lb; commercial bait was $0.10/lb. This price was lower due to low crab stocks for which the commercial bait was sold. The last harvest of roe herring was in 1980, owing to low populations in Washington State.

In Washington State there are no records kept on the food fishery of herring, since the food use is localized. Eelgrass is the major substrate for egg deposition, but the herring also use algae. The largest single population of herring is in the Strait of Georgia. Large populations are also found at Port Orchard, Port Madison, Quartermaster Harbor, southern Hood Canal, Discovery Bay, Port Gamble, and lesser populations in the San Juan Islands, in Washington State (Dr. Robert Trumble, pers. comm. 1982). Herring lay eggs on eelgrass in February-March in Washington State and in mid-April to mid-May in the Strait of Georgia.

Dr. Lynn Goodwin, Washington State Department of Fisheries, applied the data on values of shellfish in Washington State (Table 16) (pers. comm. 1982). Eelgrass provides the cover for the juvenile spot shrimp to mature. This resource is primarily taken in Hood Canal. Dr. Ken Chew, University of Washington (pers. comm.) provided the current (1982) values of several of the shellfish species (Table 16).

Dr. Baumgartner, Washington State Department of Fisheries, related the harvest and price values for Dungeness crabs caught in Puget Sound and the coastal harvest. The number of crabs actually taken in eelgrass cannot be ascertained, since the crabs range from depths of 6 m (20 ft) to 72 m (240 ft). It is known that the crabs use eelgrass at certain times in their life cycle: in the juvenile stage, during spring molting, and at certain times of molting throughout the year. But the exact extent they depend on eelgrass or the exact role of eelgrass in their existence are yet to be discovered (pers. comm. 1982).

The Washington State Department of Game estimated the economic value to the State of Washington for black brant. In the 1981-82 season, each bird taken by hunting was worth $50 to $60/bird and $100/man/day. In the 1981-82 season there were 1,500 brant taken during the hunting season.

Finally, Stokes (1978) estimated the value of the various animal species which result in indirect or direct income to the State of Washington. It appears that income generated by the estuarine habitats and wetlands of the State comes to millions of dollars. Only those species listed by the Washington State Department of Fisheries are given in Table 16. The prices are based on 1975 values. Stokes (1978) listed the commercial, recreational, and

Table 16. Harvests and value of commercially important animals from eelgrass, Washington State (Personnel, Washington State Department of Fisheries; Stokes 1978).

Species	Year	Amount of harvest kg (lbs)	Value in $ (U.S.)
Pacific herring			
Roe	1979	1,744,185 (3,837,207)	3,510,157
Sport bait		1,035,050 (2,277,110)	804,267
Commercial bait		741,985 (1,632,367)	153,698
Roe	1980	1,437,472 (3,162,438)	1,055,656
Sport bait		768,552 (1,690,815)	532,630
Commercial bait		846,191 (1,861,620)	186,384
Spot prawn (*Pandalus platyceros*			
Commercial harvest	1979	14,766 (32,485)	$2.69/lb; Stokes (1978; 1975 prices)
	1980	12,967 (28,528)	
	1981	30,063 (66,140)	--
Sport harvest	1979	26,650 (58,630)	--
	1980	38,400 (84,481)	--
	1981	64,636 (142,200)	--
Hard shell clams			
Commercial harvest (wet wt)			
Butter clams	1979	457,811 (1,007,185	$0.10/lb; Stokes (1978; 1975 prices)
	1980	184,981 (406,960)	--
	1981	112,797 (248,154)	--
Horse clams	1979	21,947 (48,284)	$0.17/lb; (1978; 1975 prices)
	1980	27,683 (60,902)	--
	1981	45,584 (100,285)	--
Geoducks	1979	2,594,643 (5,708,215)	$0.25 to 0.30 each; $0.17/lb; Stokes (1978; 1975 prices)
	1980	1,777,360 (3,910,193)	--
	1981	1,950,058 (4,290,127)	--
Native little necks	1979	158,401 (348,482)	$1.10 to 1.20/lb;$0.21/lb; Stokes (1978; 1975 prices)
	1980	237,207 (521,855)	--
	1981	272,585 (599,688)	--
Manila	1979	670,680 (1,475,497)	--
	1980	666,414 (1,466,111)	--
	1981	675,640 (1,486,409)	--

continued

Table 16. (Concluded)

Species	Year	Amount of Harvest kg (lbs)	Value in $ (U.S.)
Mussels	1979	13,703 (30,148)	--
	1980	18,082 (39,780)	--
	1981	42,871 (94,317)	$1.30/lb
Sport harvest			
All hardshell clams (wet wt)	1979	444,682 (978,300)	--
	1980	692,273 (1,523,000)	--
	1981	621,364 (1,367,000)	--
Oysters			
Sport harvest (meats)	1979	19,364 (42,600)	--
	1980	20,409 (44,900)	--
	1981	18,818 (41,400)	$1.26/lb; Stokes (1978; 1975 prices)
Dungeness crabs			
Commerical harvest (Puget Sound)	1979	833,266 (1,833,186)	$0.703/lb (ex vessel)
	1980	789,777 (1,737,509)	$0.638/lb (ex vessel)
	1981	683,091 (1,502,800)	$0.836/lb (ex vessel)
Commerical harvest (Coastal)	1979	3,873,551 (8,521,812)	$0.769/lb (ex vessel, Westport)
	1980	2,710,491 (5,963,081)	$0.664/lb (ex vessel, Westport)
	1981	1,111,749 (2,445,847)	$0.918/lb (ex vessel, Westport)
Sport harvest	1980	225,593 (496,305)	$5.30/lb; Stokes (1978; 1975 prices)
	1981	184,818 (406,600)	--
Red rock crabs	1980	16,995 (37,390)	$2.65/lb; Stokes (1978; 1975 prices)
	1981	10,678 (23,492)	

replacement costs of most of the animals that result in income from the marine environment, many of which spend a part of their life cycle in eelgrass meadows in the Pacific Northwest. The amount of income generated from the harvests of these animals is staggering.

Thus, as the harvest data for commercial and sport fisheries and game continue to be collected and evaluated, it appears that the seagrass system has not only scientific value, but an enormous economic value as well. This aspect appears not to be well understood by the general public, who continue to place great demands upon the various agencies to diversify its use.

Transplanting Programs

It is possible that transplantation of seagrasses will adequately mitigate direct and/or indirect inadvertent disturbances to the system. Recent work done by Fonseca et al. (1982b), using eelgrass on

a variety of substrates including dredged spoils in North Carolina, appears cost effective and may very well be successful in selected Pacific Northwest estuaries. The only work done in Puget Sound thus far (Phillips 1972; Backman 1983) involved only small experimental plots. Boone and Hoeppel (1976) prepared an appraisal and recommendation for an eelgrass transplantation and restoration program in south San Diego Bay, California. In the absence of any available large-scale projects in which to assess transplant success and costs, they recommend that since transplantation has been shown to be feasible, a pilot study should be made on the 8-acre Delta Beach site using a variety of techniques. Goforth and Peeling (1979) conducted the pilot project at the site. They established an initial sublittoral plot of 46 m^2 to test the relative success of three plug sizes with the plants placed in biodegradable fiber pots. A second transplant was conducted to establish 1.62 ha (4 acres) of eelgrass in the intertidal and sublittoral zones. Survival of the potted plants was relatively high. After 30 mo there was 35%-46% survival of the plugs in the initial transplant. In the second transplant only 10% of the plugs survived in the subtidal after one growing season, while in the intertidal, plug survival ranged between 50%-75%.

No one has had any success using eelgrass seeds in transplants (Phillips 1972; Churchill et al. 1978). The seeds have a very low rate of germination at ambient seawater salinities, at least in the middle portions of its distribution, including locations on both coastlines where human-related impacts are the greatest; and field mortalities of seedlings are extremely high (Phillips 1972). Fonseca et al. (1982b) found very high survival and spread of eelgrass in North Carolina on fine sediments of dredge spoils. However, I would exercise caution in extrapolating their success in North Carolina to areas throughout the range of eelgrass on both coastlines in North America. In order to state that eelgrass can be successfully transplanted in a large mitigation project in the Pacific Northwest (>0.4 ha; 1.0 acre), at least one large-scale pilot project is needed. Phillips and Backman completed a large experimental transplanting project in Puget Sound, reported by Backman (1983). Although almost 200 small plots of eelgrass were monitored quarterly for over 2 yr for survival, growth, and phenology, their results cannot be used to determine possible success of a mitigation project.

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16. Abstract (Limit: 200 words)

This document synthesizes the extant literature pertinent to the ecology of eelgrass beds of the Pacific Northwest: that part of the coast extending from Cape Flattery, WA, to Cape Mendocino, CA. This report describes the physiographic setting of the eelgrass community, the distribution of the grass beds, autecology of the eelgrass in terms of growth and reproductive strategies and physiological requirements and functions. The ecological and functional attributes of the eelgrass system or community are also described. This approach encompasses both detailed site descriptions and a broader overview of the eelgrass community and its ecological role within the estuarine complex. The final section discusses management considerations and takes into account local issues and impact scenarios.

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