Influence of Intertidal Aquaculture on Benthic Communities in Pacific Northwest Estuaries: Scales of Disturbance

CHARLES A. SIMENSTAD[1]
Wetland Ecosystem Team
School of Fisheries, WH-10
University of Washington
Seattle, Washington 98195

KURT L. FRESH
Fish Management Program
Washington Department of Fish and Wildlife, MS-43149
Olympia, Washington 98504-43149

ABSTRACT: We reviewed the scale and intensity of disturbance, and the response of benthic and epibenthic communities, to intertidal aquaculture activities in Pacific Northwest estuaries. Available data indicate a spectrum of influences on the ability of estuaries to sustain biota unrelated to the cultured species. Certain disturbances, such as adding gravel to mudflats and sandflats to enhance clam production, may subtly impact certain benthic and epibenthic invertebrates without changing the carrying capacity for estuarine-dependent taxa, such as juvenile Pacific salmon (*Oncorhynchus* spp.). However, habitat shifts might alter the relative suitability for different salmon species. In contrast, acute disturbances that produce large-scale changes in community dominants, such as manipulation of burrowing shrimp or eelgrass with pesticides or mechanical harvesting and manipulation of oyster grounds, strongly influence the carrying capacity for many fish and macroinvertebrates. Ensuring that estuarine ecosystems are sustainable for the breadth of processes and resources requires a comprehensive assessment of both natural and anthropogenic disturbance regimes, landscape influences, and the effects of local management for particular species on other resources.

Introduction

Through manipulation of estuarine habitats, many types of aquaculture disturb endemic communities (Pillay 1992); however, it is often unclear whether the degree of disturbance exceeds that to which the communities are naturally accommodated. Sousa (1984) defined disturbance as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established." This definition is descriptive of aquaculture because it encompasses physical as well as biological or chemical agents. Disturbance is not unidimensional; scales include: areal extent, intensity (magnitude), local and regional frequency, predictability, and rotation period (Sousa 1984). Correspondingly, adaptation to natural disturbance regimes implies that the disturbing agent is chronic, that is, occurs at sufficient frequency to encompass the lifetime of an individual (Thistle 1981). Lower-frequency events, which tend to be

acute (more intense), are termed disasters (Paine 1979). Although the nature and scales of disturbances and resultant community responses have been examined extensively in rocky intertidal habitats (Dayton 1971; Paine 1979; Sousa 1984) and coral reef (Connell 1978; Moran and Reaka-Kudla 1991; Woodley 1992), they have received little attention in estuarine intertidal soft-bottom communities, and especially relative to aquaculture as a disturbance factor. This is particularly true for Pacific Northwest estuaries, which are both prone to moderate levels of natural disturbance and are sites of intensive aquaculture. An examination of disturbance effects on estuarine and coastal marine ecosystems due to aquaculture is timely, both from the standpoint of increasing anthropogenic change and new scientific approaches (see, for example, Heip and Nienhuis 1992).

Estuarine communities have evolved to accommodate certain levels of physicochemical stress and disturbance. Benthic and epibenthic communities, in particular, have co-evolved in highly variable regimes of salinity, temperature, and substrate that vary on temporal scales from tidal cycles to geo-

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[1] Corresponding author.

logic trends in relative sea-level rise. The ability of estuarine communities to accommodate disturbance at low intensities but often high frequencies, and to rapidly recover from occasional disasters, implies that they are more resilient than communities that are more ecologically than physically regulated. Although extreme events such as hurricanes and prolonged freezing may devastate benthic communities over the short term, the rate of recovery can be quite rapid (e.g., within 1 yr) (Wolff 1973; Boesch et al. 1976; de Vlas 1982) as long as the perturbing factor does not persist; even then, recovery may not be entirely complete (Wolff 1990) and is dependent, in part, on the lifespan of community dominants. In part because of this resiliency to inherent environmental dynamism, estuaries are highly productive and often support higher standing stocks and secondary production of consumers than more stable terrestrial and oceanic ecosystems (Day et al. 1989).

Human civilizations have harvested fish and shellfish in estuaries for centuries. More recently, however, declining yields have been supplemented by culturing species of particular economic importance. Intense, single-species aquaculture has in some circumstances promoted conditions in estuaries indicative of stressed ecosystems (Lockwood 1991; Folke and Kautsky 1992). Alternatively, other aquaculture systems promote high biodiversity and production without deleterious effects to endemic communities (Pillay 1992). Aquaculturists also tend to be staunch advocates for maintaining or improving estuarine water quality in the face of increasing domestic and industrial waste discharge, wetland development, and water withdrawal (Cheney and Mumford 1986).

Aquaculture of estuarine organisms, principally molluscs, may disturb benthic-epibenthic habitats beyond natural intensities or frequencies, perhaps for years or decades. When scales of human disturbance exceed that of natural regimes (e.g., involves major changes in species composition, and components of primary and secondary production), effects can potentially cascade through the estuarine foodweb to affect production of other estuarine, marine, and anadromous populations. Intertidal habitats are important elements of estuarine ecosystems. They are highly productive, export organic matter to the estuary's detritus pool, and function as habitat for fish and wildlife during specific life-history stages (Peterson and Peterson 1979; Phillips 1984; Nichols and Pamatmat 1988; Barnhart et al. 1992). Thus, resource managers should consider effects of all types of unnatural (e.g., anthropogenic) disturbance, including aquaculture, at community and ecosystem levels.

Several types of aquaculture take advantage of

the unique structure and biological productivity of intertidal habitats in Pacific Northwest estuaries. Oyster culture, and to a lesser extent clam culture, are the dominant aquaculture activities that have persisted, often relatively unchanged, since their inception up to a century ago. Although not necessarily pervasive within these industries, some culture methods may disturb indigenous intertidal communities and thereby affect large segments of estuarine ecosystems where culture is concentrated.

Potential disturbance regimes of estuarine intertidal habitats by aquaculture must be considered within the context of the age and inherently dynamic nature of Pacific Northwest estuaries. Essentially all Pacific Northwest estuaries were formed as a result of 40,000 yr of Wisconsin glaciation and associated sea-level changes, and the climatology of the following 10,000 yr of the Pleistocene (Crandell 1965). Their young geologic age is further accentuated by periodic tectonic events that have often resulted in dramatic changes in intertidal elevation. For example, subsidences of 0.5–2.0 m along the outer coast have occurred at least six times in the last 7,000 yr (Atwater 1987). Superimposed on this geologic scale of regional disturbance, estuarine intertidal habitats in this region are subjected to smaller scales of climate-associated disturbance due to waves, currents, and freshwater discharge from major North Pacific storm events. This can produce wide salinity and temperature fluctuations, and comparatively dynamic sedimentation regimes. As a result, estuarine communities in this region are naturally shaped by broad extremes and frequencies of disturbance.

In this paper, we review practices of intertidal aquaculture in Pacific Northwest estuaries with respect to scales of disturbance on intertidal benthic and epibenthic communities. Our objectives are to examine development of intertidal oyster and clam culture in this region, to describe predominant culture methods, to describe scientific studies that evaluate intertidal community responses to various types and scales of disturbance imposed by intertidal aquaculture activities, and to assess ecological and management implications of the observed responses at the population, intertidal community, and estuarine ecosystem levels. Interpretations of benthic-epibenthic community responses to aquaculture disturbance are placed in the context of the level of natural disturbance to which the community has adapted, and the ability of the community to accommodate additional chronic disturbance. Although this approach is amenable to many tenets of ecological economics (Farber and Costanza 1987), we do not judge the economic value of aquaculture-altered intertidal communities

relative to indigenous communities. We recognize that the economics and job opportunities of aquaculture are often considered acceptable trade-offs for some ecological changes, especially if the changes are subtle and do not persist. It is our intent, however, to illustrate that some disturbances from intertidal aquaculture can deleteriously affect other natural resources dependent upon estuarine habitats and processes, and that the economic value of these resources should be considered when assessing such trade-offs.

Methods

Our summary of the history, technical development, and extent of intertidal oyster and clam culture in the Pacific Northwest is based on published literature, resource agency files, and consultation with estuarine resource managers. Data and observations on intertidal community responses were also assembled from diverse sources, often unpublished data familiar to us. Because these studies were limited in number, scope, and rigor, they represent only a qualitative mosaic of disturbance scales, time frames, and community responses. In particular, our quantitative assessments are restricted to density differences for a few prominent taxa of benthic infauna and epibenthic crustaceans and fishes. Where possible, we have also made qualitative estimates of habitat changes, such as in the density and standing stock of eelgrass (*Zostera* spp.). We emphasize that little of the following information has appeared in peer-reviewed scientific literature, and thus must be considered principally from the hypothesis-generating rather than the hypothesis-testing standpoint. Given the limitations of the available information, our major objective is to postulate aquaculture-related disturbances that warrant rigorous testing and consideration in future estuarine research and management.

TOPICAL AND GEOGRAPHIC SCOPE

We define disturbance as any physical modification of intertidal or shallow subtidal substrates that results from aquacultural practices (see Sousa 1984). In the case of intertidal aquaculture in the Pacific Northwest, most disturbance is the result of routine practices, but we acknowledge that different cultural practices in other regions may also produce disturbances by less frequent means. Disturbances included under this definition are addition of high densities of cultured animals to natural substrates and indigenous communities, altering sediment structure by mechanical modification of existing sediments or addition of different sediments, mechanically or chemically removing or reducing populations of certain indigenous plants or animals that are considered deleterious

to the efficient culture of the target species, and altering natural hydrologic and sedimentary regimes. We consider only direct disturbance to benthic-epibenthic communities and not secondary effects on water quality and nutrient cycling; these are addressed by other papers in this issue (Findlay et al. 1995; Levings 1995; Thompson 1995).

We focus on benthic infauna and epifauna, both macrofaunal and meiofaunal invertebrates, and epibenthic feeding fishes because other information is scarce. In a few cases, we have data for responses of benthic macroalgae and eelgrass (*Zostera* spp.). Our measure of response is an increase or decrease in density or standing stock. There were few data available on intertidal community changes. Consequently, community responses were interpreted as changes in important benthic and epibenthic taxa, principally community dominants.

In evaluating intertidal aquaculture, only the "on-bottom" intertidal culture of oysters (the introduced Pacific oyster, *Crassostrea gigas*, and to a very minor extent the native Olympia oysters, *Ostrea lurida*) and clams (predominantly littleneck clam, *Protothaca staminea*, and Manila clam, *Tapes philippinarum*) are considered. This includes principally ground, stake, long-line, and rack culture of oysters, and beach graveling and enclosures (e.g., netting) for hardshell clam production. In the case of oysters, this also includes practices used to remove (i.e., "harvest") bivalves from the intertidal. "Off-bottom" culture such as nori net culture, and suspended or float culture, are not considered. We also do not consider commercial or recreational harvest activities on natural bivalve populations, which involve extensive disturbance of intertidal communities in some estuaries (Cheney and Mumford 1986; Thompson and Cooke 1991).

We utilized almost exclusively data from estuaries in Washington State familiar to us. We focused on Willapa Bay, an extensive coastal estuary in southwestern Washington (Fig. 1), because of its extensive history and magnitude of intertidal oyster culture.

TYPES AND CHARACTERISTICS OF ESTUARINE INTERTIDAL HABITATS USED FOR AQUACULTURE

There are approximately 100 estuaries in Washington, ranging from large coastal estuaries (Willapa Bay and Grays Harbor) to the continuum of drowned river valley estuaries linked by transitional habitats that forms the inland sea of Puget Sound (Simenstad et al. 1982). The mosaic of habitats within an estuary depends largely on sediment dispersal and accumulation patterns, which in turn are determined by outflow dispersion and basinal
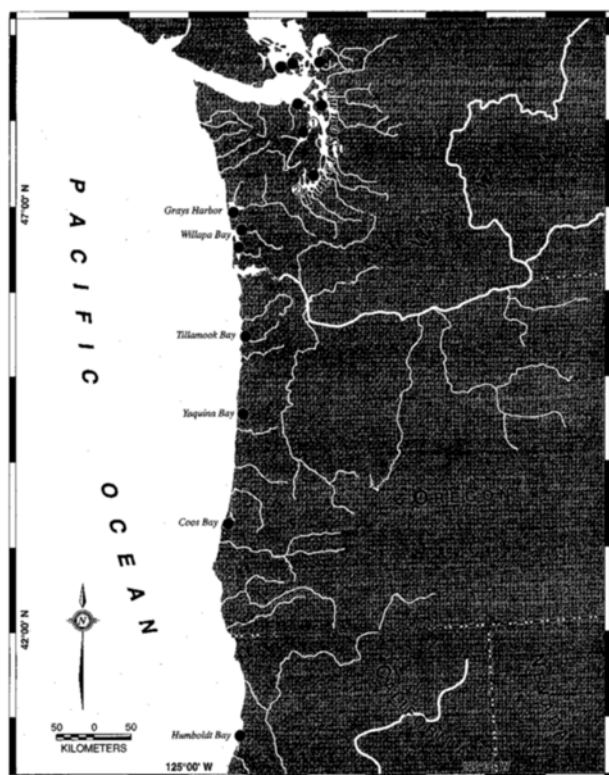
Fig. 1. Puget Sound and coastal estuaries of Pacific Northwest, with locations of the primary locations of intertidal aquaculture of oysters, clams, and mussels; specific sites mentioned in text include Bywater Bay = 1, and Oakland Bay = 2.

processes (Simenstad 1983). Although a diverse array of vegetated and unvegetated habitats are found in Washington's estuaries, only moderate gradient gravel-cobble beaches and low gradient mudflats and sandflats are significantly used for intertidal aquaculture.

Gravel-cobble habitats are common in more exposed regions of estuaries and along margins of the Puget Sound estuarine system (Downing 1983). Owing to waves and currents, these habitats seldom form as flats but rather as beaches. Although vegetation is often minimal, native eelgrass (*Zostera marina*) may occur in finer sediments while kelps (*Laminaria* spp., *Nereocystis leutkiana*) may attach to larger gravel and cobble at lower elevations. Most natural and cultured populations of hardshell clams are found on gravel beaches.

Much of the intertidal area of estuaries in Washington consists of low gradient mudflats and sandflats. Nearly all intertidal oyster culture in Washington occurs on this type of habitat. Mudflats typically occur in broad expanses of >1 km² between vegetated marsh areas and MLLW along channels and at delta foreshores of major rivers. Sandflats tend to occur along the more exposed

boundaries of mudflats in estuarine river deltas and in moderately exposed bays and beaches of Puget Sound.

Mid and lower tidal elevations of some mudflats and sandflats are colonized by seagrasses and macroalgae. Two species of seagrass occur, the native species, *Zostera marina,* and the exotic species, *Z. japonica. Z. marina* occurs predominantly between +1.0 m and −1.0 m, and *Z. japonica* between approximately +2.0 m and +1.0 m MLLW. The complex structure and invertebrate assemblages of eelgrass communities provide valuable habitat for fish and wildlife (Phillips 1984; Posey 1986a, 1987, 1988; Baldwin and Lovvorn 1994) and are a major source of detrital carbon for estuarine foodwebs in this region (Simenstad et al. 1979; Simenstad and Wissmar 1985). Numerous species of attached and unattached macroalgae are found in the more saline estuaries. For example, Thom (1984) identified 29 taxa in Grays Harbor, the most common of which included *Ulva* spp. and *Enteromorpha* spp.

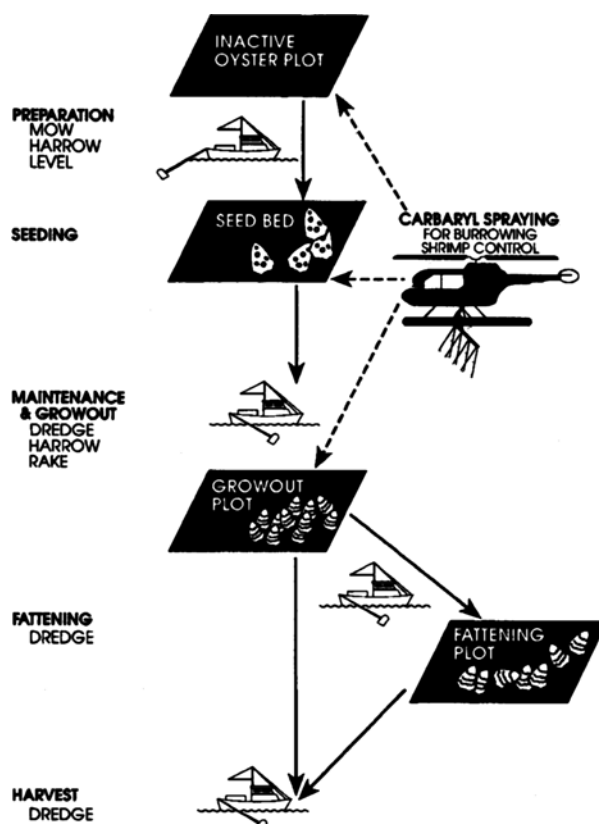## INTERTIDAL AQUACULTURE

Oysters

The most significant "on-bottom" type of aquaculture both economically and in terms of amount of benthic habitat affected is oyster culture. The oyster industry began in Washington in Willapa Bay in 1851 when native oysters were first harvested and shipped to markets in San Francisco (Armstrong 1857; Townsend 1893; Galtsoff 1929; Kincaid 1951; Minks 1971; Magoon and Vining 1981; Cheney and Mumford 1986). Native oyster populations crashed by the last 1800s (Galtsoff 1929; Kincaid 1951; Cheney and Mumford 1986). Subsequently, oyster producers focused their efforts on the culture of two non-native species: eastern (*Crassostrea virginica*) and Pacific oysters; these were introduced as early as 1895 in Willapa Bay and 1905 in Puget Sound (Galtsoff 1929; Minks 1971; Magoon and Vining 1981; Scholz et al. 1984; Cheney and Mumford 1986). A few Puget Sound oystermen cultivated native Olympia oysters using a diking system developed in France (Galtsoff 1929; Cheney and Mumford 1986), a practice that persists today. Culture of Pacific oysters was a commercial success, especially following the discovery that recently settled juveniles, or "seed," could be imported from Japan (Steele 1964; Scholz et al. 1984).

Since the early 1930s, Pacific oysters have been the dominant oyster grown in all areas of Washington, presently (1990 landings) accounting for over 98% of the landed value of cultured oysters in Washington (Washington Department of Fisheries [WDF] unpublished data). Today, oysters are cul-

tured on tidelands that are privately or publically owned or leased in many estuaries of Washington (Fig. 1). Total cultured oyster production is worth approximately $30 million, with approximately 4.5 million kg of meat harvested during the past year (K. Chew, Western Regional Aquaculture Center, University of Washington, Seattle, Washington, personal communication). Willapa Bay, alone, contributes more than 50% of the production. About 17,200 ha of tidelands in Willapa Bay are exposed at low tide but 10,500 ha are technically classified oyster lands (Doty 1990; Burrowing Shrimp Control Committee 1992). Currently, about 3,645 ha of Willapa Bay are managed for oysters (21% of the tidelands of the bay) with much of this currently under culture. In Grays Harbor, only about 2% of the intertidal habitat (365 ha) is used for oyster culture (Doty 1990; Burrowing Shrimp Control Committee 1992).

Most oyster culture, regardless of the method, occurs from −0.5 m to +1.1 m MLLW on varying combinations of mud, sand, and gravel, with predominance of mud. While many factors influence oyster production, bottom substrate, exposure, duration, temperature, and salinity are particularly important (Galtsoff 1929; Kincaid 1951; Shotwell 1977; Scholz et al. 1984; Cheney and Mumford 1986). Pacific oysters are grown either directly on the bottom ("ground culture"), on longlines suspended several feet off the bottom, or on racks. However, ground culture is by far the dominant technique used; one grower estimated that about 98% of the intertidal habitat cultivated in Willapa Bay is farmed using ground culture methods (R. Schuman, Shoalwater Bay Oysters, Bay Center, Washington, personal communication).

Detailed descriptions of how oysters are cultured in Washington, as represented generically in Fig. 2, can be found in Galtsoff (1929), Kincaid (1951), Magoon and Vining (1981), and Quayle (1988). Figure 2 represents the extreme disturbance case, however, because of the extent of mechanical and chemical manipulation of the oyster grounds; culture methods conducted by hand, which are still commonly employed, are much less disruptive. Ground culture of oysters can directly disturb the benthic community repeatedly, and to various intensities, over the approximately 3-yr harvest cycle. For example, to reduce density and improve growth, growers may transplant oysters several times. Harvesting oysters is frequently done with mechanical dredges, although some manual harvesting still occurs (Quayle 1988). In addition, mechanical harrowing, raking and leveling of intertidal flats can be used to improve the distribution of oysters on the plot (Sayce and Larson 1965). How any group of oysters or any extent

Fig. 2. A general depiction of the sequence and activities involved in the ground culture of Pacific oysters in Washington state. This model is based primarily on practices in Willapa Bay, where the use of carbaryl to control burrowing shrimp varies dramatically among oyster growers and specific plots.

of intertidal area under oyster culture is actually treated depends on many factors, such as oyster growth rates, which are influenced by environmental conditions, planting density, and plot location. Longline, stake, and rack culture generally tend to be used on ground that is marginal for bottom culture and are considered more expensive than bottom culture.

Beginning in 1963, growers in Willapa Bay and Grays Harbor, but infrequently in Puget Sound, have sprayed oyster grounds with the insecticide carbaryl (1-naphthyl-N-methylcarbamate; used principally as Sevin, tradename of Rhone Poulenc [formerly Union Carbide]). Carbaryl is sprayed directly on the intertidal substrate to kill populations of burrowing shrimp, including both ghost shrimp (*Neotrypaea* [*Callianassa*] *californiensis*) and mud shrimp (*Upogebia pugettensis*). Oyster growers in Willapa Bay and Grays Harbor contend that periodic control and elimination of burrowing shrimp is necessary for a healthy oyster industry because high densities of burrowing shrimp destabilize the

substrate. As a result, oysters placed directly on burrowing shrimp-dominated plots either sink into or are smothered by sediment redistributed by the bioturbation of shrimp. Burrowing shrimp are also considered a problem with other forms of culture, such as longlines, because oysters that fall onto the bottom are covered with sediment.

Some oyster growers claim that burrowing shrimp populations have recently exploded over historic levels, and that formerly productive oyster ground has become unusable because of high shrimp densities; we could find no quantitative data to test this assertion. Thallinassid shrimp appear to have been a pervasive problem as early as 1929, when Stevens (1929) reported that they hindered oyster culture in the region and infested some areas to such an extent that oysters were uneconomical to harvest. Eberhardt (1966) reported an "ever expanding population of soft shell shrimp." Early oyster growers often covered their plots with boards or placed a "dirt" layer over the mud to stabilize it for the oysters (Unpublished letter from Milo Moore, director, to Dr. V. L. Loosanoff, November 5, 1959. Washington Department of Fisheries files, Nahcotta Shellfish Laboratory, Nahcotta, Washington; Eberhardt 1966).

To our knowledge, the practice of applying insecticide to control borrowing shrimp is unique to this region and controversial (Buchanan et al. 1985; Washington Department of Fisheries/Washington Department of Ecology 1985, 1992). Spraying is permitted only in late spring or summer (generally August). Application rate has been quite variable but is generally 11.2 kg ha^{-1} (Washington Department of Fisheries/Washington Department of Ecology 1992). From 1976 to 1984 an average of 97.7 ha was treated, while an average of 171.9 ha was treated from 1984 to 1988 (Washington Department of Fisheries/Washington Department of Ecology 1985, 1992; Burrowing Shrimp Control Committee 1992). Land is treated on the average every 6 yr. Since 1963, approximately 890 ha of intertidal habitat in Willapa Bay have been treated with carbaryl at least once (Washington Department of Fisheries/Washington Department of Ecology 1985, 1992).

The most important intertidal habitats used for oyster production in Willapa Bay are the 1,000–1,200 ha used for "fattening" oysters (Shotwell 1977; Burrowing Shrimp Control Committee 1992). In general, oysters spread by the grower as "seed" over 3 ha can be moved onto 1 ha for the subsequent fattening (Shotwell 1977). Comparable data on the area of intertidal habitat under oyster culture in Puget Sound were not available, but Puget Sound (including Hood Canal) produces between 40% and 45% of the total state production,

the remainder of which is contributed by Willapa Bay and Grays Harbor (K. Chew, Western Regional Aquaculture Center, University of Washington, Seattle, WA; personal communication).

It was not possible to estimate the area actually utilized by culture operations in the state in any one year since it depends on many factors such as market forces and how often oysters are moved (e.g., use of growing and fattening plots). A minimum estimate can be obtained by dividing the total annual oyster landings by an estimate of the production in 1 ha [1] (920–1,226) obtained with bottom culture (Cheney and Mumford 1986). Furthermore, we assume each crop requires 3 ha of growing ground to 1 ha of fattening ground and that 3 year-classes are being farmed in any 1 year. These calculations suggest that from 1979 to 1989, 2,673 ha to 6,197 ha of estuarine intertidal habitat in Washington state were used for oyster culture.

Review of the few historic accounts and photographs of the region's estuaries suggest that culture practices have altered intertidal and shallow subtidal habitats from their historic composition. Early reports from Willapa Bay suggested that native oysters grew clustered in large groupings or "reefs" up to 1 m thick in the low intertidal and shallow subtidal channels (Armstrong 1857; Townsend 1893; Swan 1857; McDonald 1966). Some unmarketable native oysters were transplanted from subtidal and low intertidal areas to higher intertidal areas that were diked, where oysters were naturally less abundant. Oysters were collected after they had increased in size (Townsend 1893). Due to overharvest, as well as perhaps adverse climatic conditions and disease, populations of native oysters were drastically diminished. Normally, when native oysters were cultured, dikes were built in Willapa Bay to hold the oysters. The dikes were intended to retain water so that the native oysters, which are sensitive to heat and siltation, would have higher survival. However, mortality of transplanted oysters was high and the overall population diminished. Pacific oysters were eventually introduced to maintain the industry.

Once Pacific oysters became the focus of culturists, they were grown primarily on littoral flats above MLLW. Presently, ground-cultured oysters are distributed over broad intertidal flats in a relatively thin layer (at most one oyster thick) in order to maximize growth. Consequently, oyster culture appears to have changed the nature of oyster habitat from a thick reef-like structure to one that is analogous to fine sediments with a thin layer of large substrates (i.e., oysters) over it. As suggested by Fig. 3, some regions within the bay that were not heavily used by native oysters became more
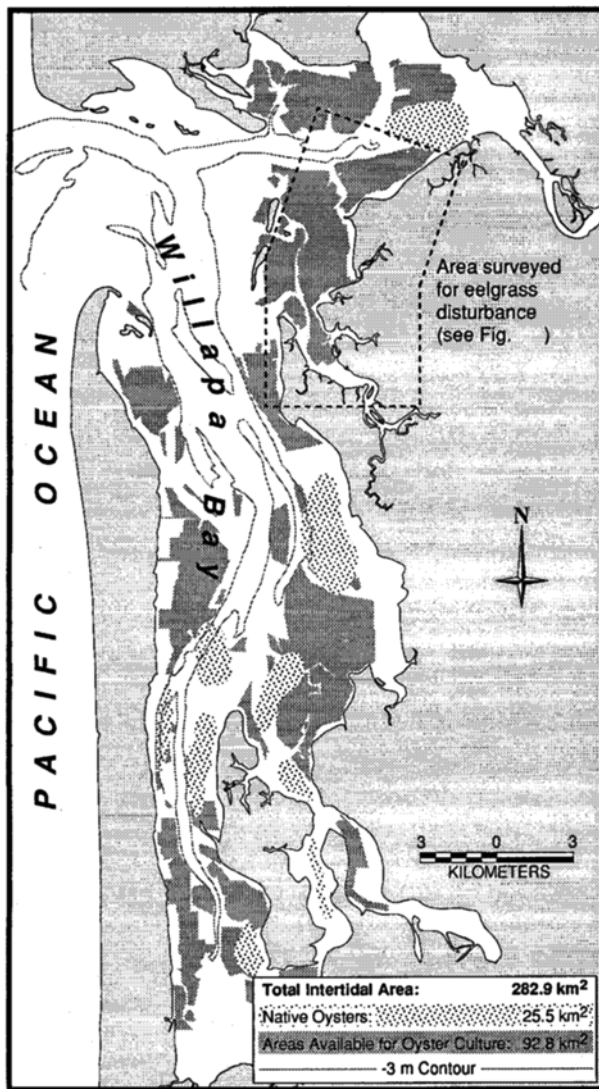
Fig. 3. Map of Willapa Bay, Washington, indicating historic distributions of native oysters (from Townsend 1893) and areas available for culture and harvest of Pacific oysters in the mid 1920s (Pacific County unpublished data).

suitable for Pacific oyster culture while other areas that were historically occupied by native oysters were not cultured.

In summary, oyster plots undergo chronic disturbance that is of various levels of intensity. They may be harrowed, dredged, raked, leveled, and treated with carbaryl. Some cultural activities can be repeated on a plot several times in a year. Moreover, activities on the most intensively cultivated intertidal plots have been repeated annually for decades. These activities impose some level of disturbance on the benthic substrate and associated community.

Clams

Washington is the only state in the western United States where commercial quantities of hardshell clams are regularly farmed (Cheney and Mumford 1986). Clam aquaculture in Washington is a much more recent industry than the oyster industry, having developed mostly over the last 30–40 yr (Magoon and Vining 1981). Some 50 species of clams occur in Washington, including hardshell and softshell varieties and subtidal and intertidal populations (Magoon and Vining 1981); eight are actively farmed. Manila and littleneck clams are most relevant to this paper since they involve culturing activities that result in direct impacts to benthic habitats, and moreover account for nearly 100% of the total cultured hardshell clam landings in Washington (Washington Department of Fisheries unpublished data). Nearly all clam aquaculture occurs in Puget Sound, with Cheney and Mumford (1986) reporting at least 21 clam farmers who owned or leased 270 ha in Puget Sound.

Manila clams grow and survive optimally on intertidal beaches that are protected from heavy wave action where the substrate has a high ratio of gravel to fines (Magoon and Vining 1981; Anderson et al. 1982; Toba et al. 1992). They occur naturally and grow best in the high intertidal zone between +0.6 m and +2.0 m tidal elevation. Conversely, littleneck clams survive and grow best below +0.6 m MLLW in substrate with higher proportions of gravel. Although litteneck clams are found in intertidal and subtidal areas, only intertidal populations are presently farmed. Manila clams are found closer to the surface than native littlenecks (Magoon and Vining 1981).

Two types of culturing activities are utilized by growers in Washington State, either separately or in combination: manipulation of clam seed on natural substrates, and habitat modification (Magoon and Vining 1981; Anderson et al. 1982; Thompson and Cooke 1991; Toba et al. 1992). Clam seed manipulation, involving the distribution, form (e.g., individual, bagged), and timing of seeding, does not directly impact benthic habitats unless clams are placed in bags on the substrate, and thus will not be considered further.

Habitat modification techniques involve placing gravel on beaches and using protective netting. Since the 1950s, some growers have placed gravel or gravel mixed with crushed oyster shell over mud and sand beaches to create a more productive clam habitat (Washington Department of Fisheries 1988; Thompson and Cooke 1991; Toba et al. 1992). Best results have been obtained with gravel 0.9–1.9 cm in diameter that is placed in layers 10–

20 cm thick (Washington Department of Fisheries 1988; Thompson and Cooke 1991).

On some beaches, including those that have been graveled, protective netting is used to hold clams in place and reduce losses from predation (Toba et al. 1992). Best results have been obtained with netting with a mesh size of 1.27 cm. The frequency with which habitat alterations are employed in culture operations is quite variable and depends on such factors as location of plot, market forces, and the grower's preferences.

Intertidal Community Responses to Aquaculture Disturbance

PHYSICAL DISTURBANCE

Modification of Substrate Structure

Evaluations of immediate responses by benthic communities to substrate modification from aquaculture activities do not exist. Data are restricted to *post facto* situations in which sites under oyster or clam culture are compared to adjacent "reference" sites presumed to be under natural disturbance regimes. In some cases, this comparison may be invalid because habitat utilized as a reference site may have been cultured and thus not representative of natural communities (see discussion of carbaryl studies, following). We must also acknowledge that some reference sites may be inherently different, as selection of oyster or clam culture sites is often not random; however, we have no way of determining the existence of such pre-existing differences.

In addition to obvious shifts in substrate composition, other physicochemical characteristics and processes may be altered that are important to intertidal biota. Thompson (1995) and Thom et al. (1994) indicate that substrate modification for enhanced clam production can significantly depress cover of macroalgae, enhance chlorophyll *a* concentrations, increase benthic respiration, and increase nutrient fluxes (particularly PO_4^3, total inorganic N, NO_2^-, NH_4^+). The magnitude of these community responses, however, tend to be very site-specific.

Benthic Infauna in Graveled Clam Plots

The Washington Department of Fisheries has investigated differences in benthic infauna composition and densities at sites that have been graveled to enhance clam production. Infauna were sampled with a 78.5-cm^2 diameter core inserted 10–15

cm deep, with the extracted material sieved through 1.0-mm screen. Their results (Washington Department of Fisheries 1988; Thompson and Cooke 1991; Thompson, 1995; Washington Department of Fisheries and Fisheries Research Institute, University of Washington unpublished data) indicated a shift away from communities numerically dominated by glycerid, sabellid, and nereid polychaetes to ones dominated by bivalve molluscs and nemerteans.

Epibenthic Meiofauna in Graveled Clam Plots

In 1989, Simenstad et al. (1991) investigated epibenthic meiofauna at two intertidal sites in Puget Sound that had been treated with gravel to enhance clam production. At one site, Bywater Bay (a broad sandflat with median grain size of 0.42–0.56 mm), a layer of coarse-screened gravel 1.7 cm thick was placed over 0.56 ha at a tidal elevation of approximately MLLW in 1979. The other graveled site, Oakland Bay, is a low-gradient mudflat. At a tidal elevation of MLLW, gravel (6 mm to 19 mm diameter) in a layer approximately 10 cm thick was added in 1974. Sampling was conducted utilizing a 0.018-m^2 epibenthic suction pump with retention of organisms on 125-μm screens. Twenty-five replicate samples, which were sufficient to detect a 100% change in density with 95% confidence, were distributed haphazardly along a 100-m sampling transect located along the MLLW contour; sampling occurred five times biweekly from late March through late May. In the laboratory, samples were re-sieved through 253-μm screens to concentrate large taxa documented to be important prey of nearshore fishes such as juvenile Pacific salmon. Epibenthos taxa and total densities were $log_{10}(x + 1)$ transformed before statistical comparisons using one-way analysis of variance. Taxa richness (S) and diversity (Shannon-Weiner H') were based on both taxonomic and life-history stages applied consistently across all samples.

Epibenthos assemblages on graveled plots were different at the two sites, suggesting the importance of local, site-specific conditions, including level of natural disturbance (Fig. 4). The graveled treatment at Bywater Bay had consistently more taxa but lower diversity for four of the five sampling dates, while tax richness and diversity tended to be higher at Oakland Bay. Changes in densities of important fish prey, however, were both taxa-specific and site-specific (Table 1). For instance,

Fig. 4. Temporal changes in the density (number m^{-2}) of epibenthic organisms on natural (control) and graveled (treatment) intertidal sandflats and mudflats at Bywater and Oakland bays, Washington, March 26–May 22, 1989.
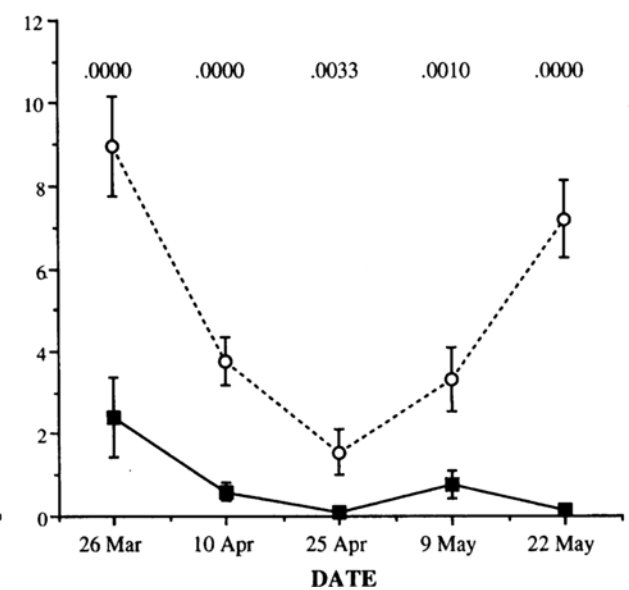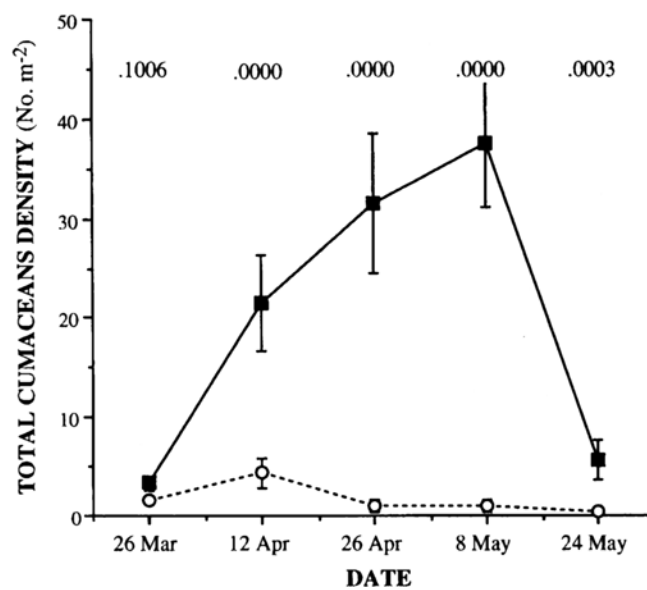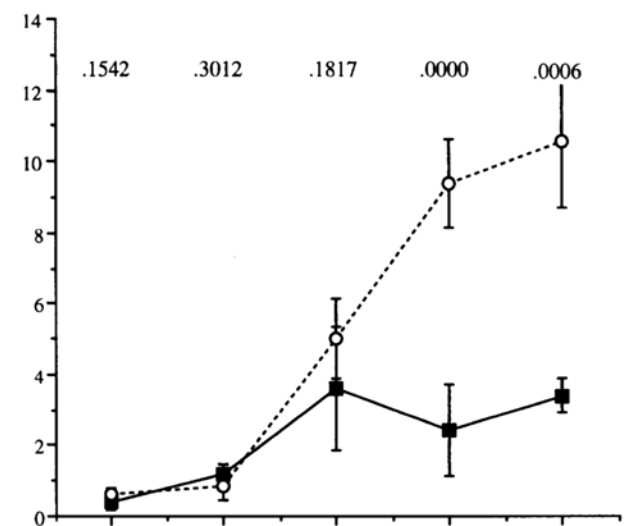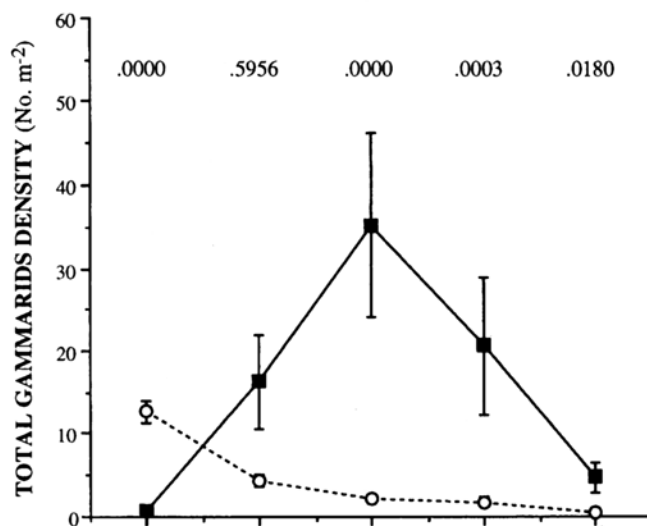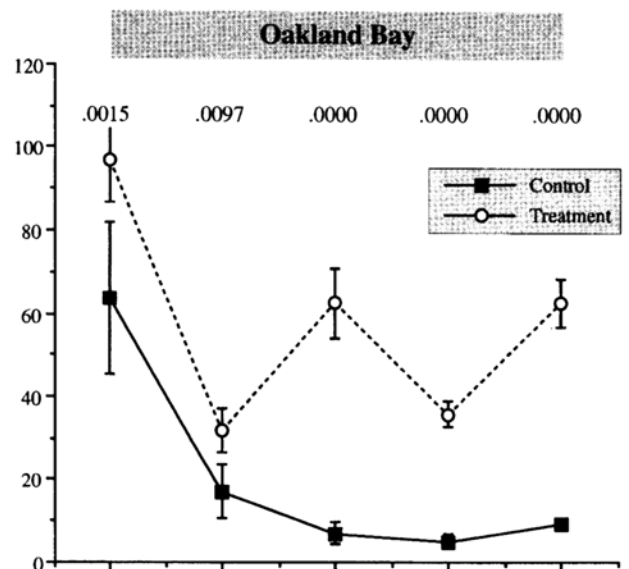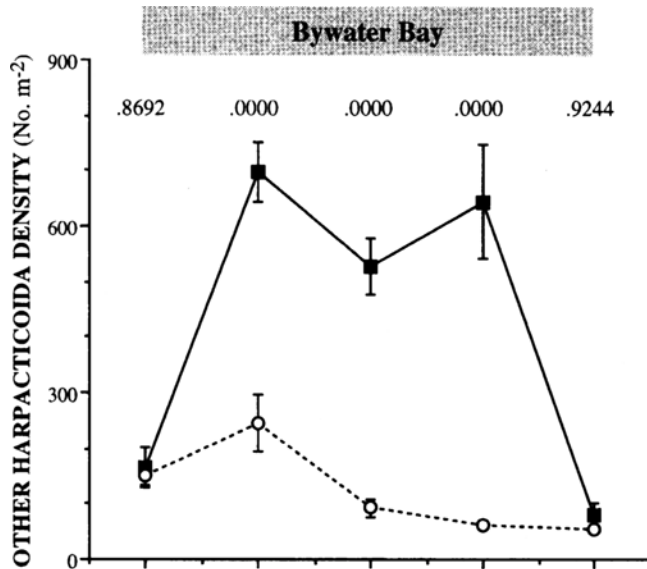
TABLE 1. Statistical significance levels of one-way analyses of variance for differences in the log-transformed densities of epibenthic crustaceans on natural (control) and treatment (gravel additions) littoral flats at Bywater Bay, Hood Canal, and Oakland Bar, Puget Sound, Washington, between March 26 and May 24, 1989. Values in boldface type denote enhancement, and underlined values indicate depression, of epibenthos densities at the graveled site relative to the control; — indicates insufficient densities to test.

Taxa	Date				
	Mar 26	April 10–12	April 25–26	May 8–9	May 22–24
Bywater Bay					
Tisbe spp.	**0.0164**	**0.0006**	**0.0000**	**0.0000**	**0.0825**
Zaus spp.	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**
Harpacticus spp.	0.0431	0.0000	0.0000	0.0000	**0.4410**
Dactylopusia sp.	0.5978	0.3223	—	—	—
Other Harpacticoida	0.8692	0.0000	0.0000	0.0000	**0.9244**
Corophium spp.	—	—	—	—	—
Paracalliopiella pratti	**0.0000**	**0.2056**	**0.1628**	—	—
Anisogammarus pugettensis	**0.0030**	0.4186	0.0000	0.0021	0.0180
Total Gammaridea	**0.0000**	0.5956	0.0000	0.0003	0.0180
Cumella vulgaris	0.1006	0.0000	0.0000	0.0000	0.0003
Lamprops quadriplicata	0.0000	0.0397	0.1551	0.3702	0.3223
Total Cumacea	0.0000	0.0000	0.0000	0.0000	0.0003
Oakland Bay					
Tisbe spp.	**0.0000**	**0.0000**	**0.0000**	**0.0160**	**0.0013**
Zaus spp.	—	—	—	—	**0.3223**
Harpacticus spp.	**0.0000**	**0.0000**	**0.0000**	**0.2610**	—
Dactylopodia sp.	—	—	—	—	—
Other Harpacticoida	**0.0015**	**0.0097**	**0.0000**	**0.0000**	**0.0000**
Corophium spp.	**0.7097**	**0.3012**	**0.0588**	**0.0000**	**0.0006**
Paracalliopiella pratti	—	—	—	—	—
Anisogammarus pugettensis	—	—	**1.000**	—	—
Total Gammaridea	**0.1542**	**0.3012**	**0.1817**	**0.0000**	**0.0006**
Cumella vulgaris	**0.0000**	**0.0000**	**0.0033**	**0.0010**	**0.0000**
Lamprops quadriplicata	—	—	—	—	—
Total Cumacea	**0.0000**	**0.0000**	**0.0033**	**0.0010**	**0.0000**

harpacticoid copepods (e.g., *Tisbe* spp.) that are important prey of some species of juvenile salmon (e.g., *Oncorhynchus keta*; Simenstad et al. 1982) were significantly enhanced at both Bywater and Oakland bays, while *Harpacticus uniremis* populations were enhanced at Oakland Bay and depressed at Bywater Bay. Similarly, densities of other harpacticoid taxa, such as *Harpacticus spinulosus*, that constitute prey for recently metamorphosed pleuronectids and invertebrate predators were significantly depressed at Bywater Bay and enhanced at Oakland Bay. Densities of gammarid amphipods and cumaceans (predominantly *Cumella vulgaris*), which are also important prey of different species of juvenile salmon (e.g., *O. tshawytscha* and *O. kisutch*), generally increased at Oakland Bay but declined at Bywater Bay.

Overall, the net differences between the gravel-treated and control beaches (Table 2) indicated that some taxa's abundances were depressed by graveling at Bywater Bay but their abundances did not change or were actually enhanced at Oakland Bay. Simenstad et al. (1991) concluded that these results were a function of the almost total replacement of natural sand substrate with gravel at Bywater Bay, as compared to a net increase in sedi-

ment diversity, but not total loss of mud and silt, by addition of gravel at Oakland Bay.

Epibenthic Meiofauna Associated with Predator Exclusion Nets

Simenstad et al. (1993) continued investigations of intertidal clam culture influences on epibenthic meiofauna by examining effects of plastic nets placed over beach areas to exclude predators of juvenile clams. As in the study of beach graveling by Simenstad et al. (1991), the influence of predator exclusion nets was tested with pair-wise comparisons of covered plots to adjacent natural beach substrates. Plots were tested that had been netted for at least a year and thus had stabilized after the immediate disturbance of installing the nets. The same key prey organisms of intertidal-foraging fishes and sampling technique (epibenthic pump) were used as in the graveling study. Study plots were also located at Bywater and Oakland bays. Plots for the predator exclusion net study were characterized by more gravel substrate and were located higher in the intertidal ($+1.1$ m to $+1.2$ m MLLW). The null hypotheses tested were that there were no significant differences in densities of selected prey of juvenile salmon and other ma-

TABLE 2. Summary of effects on epibenthic fish prey of graveling and placement of predator exclusion nets on intertidal habitats at Bywater Bay, Hood Canal, and Oakland Bay, southern Puget Sound, Washington, March 25–May 24, 1989, as inferred from difference between natural and graveled or netted treatments; summarized from Simenstad et al. (1991) and Simenstad et al. (1993). ++ = strongly enhanced densities, + = moderately increased densities, * = no detectable effect; − = moderate decrease in densities, and −− = strongly decreased densities; blank indicates insufficient densities to conduct tests.

| | Graveling | | Predator Exclusion | | | |
| | | | Bywater | | Oakland | |
Prey Taxa	Bywater	Oakland	Treatment	Block	Treatment	Block
Harpacticoid copepods						
Tisbe spp.	++	++	−	*	+	+
Zaus sp.	++	+?				
Harpacticus spp.						
(*H. uniremis* and *H.* sp. *uniremis* group)	−	+	++	++	−	+
(*H. spinulosus, H. arcticus*)	−−	++	−		+	+
Dactylopusia sp.	*	*	−		++	*
Other Harpacticoida	−−	++				
Gammarid amphipods						
Corophium spp. (*C. salmonis, C. spinicorne*)	−?	+	−	−	−	−
Paracalliopiella pratti	+	*				
Anisogammarus pugettensis	−−	−?				
Total Gammaridea	...	+				
Tanaids						
Tanais sp.			−	...	+	−
Cumaceans						
Cumella vulgaris	−−	++	−−			
Lamprops quadriplicata	...	*			*	
Total Cumacea	−−	++				

rine fishes, and sediment structure between plots with predator exclusion nets (treatment) and adjacent natural (control) plots. Statistical analysis was conducted on log-transformed densities in a randomized block ANOVA, where nine pairs (one netted, one control) of sampling plots were arranged perpendicular along the beach contour. This constitutes the statistical block indicating an independent source of variation due to linear position along the beach. Sampling occurred in 1991 at approximately monthly intervals from April to June to encompass the period when intertidal hab-

TABLE 3. Statistical significance levels of analyses of variance, using a randomized block design within month, for differences in log-transformed densities of selected epibenthic crustaceans on natural (control) and treatment (predator exclusion nets) littoral flats at Bywater Bay, Hood Canal, and Oakland Bay, Puget Sound, Washington, between April 2 and June 5, 1991. Values in boldface type denote enhancement, and underlined indicates depression, of epibenthos densities at the netted site relative to the control; neither bold nor underlining indicate not determinable (i.e., nearly identical or densities were too low to determine).

| | Date | | | | | |
| | April 2–3 | | May 6–7 | | June 4–5 | |
Taxa	Treatment	Block	Treatment	Block	Treatment	Block
Bywater Bay						
Tisbe spp.	<u>≤0.05</u>	0.816	**0.751**	0.270	<u>0.846</u>	0.350
Harpacticus uniremis						
Copepodites	<0.05	<0.05	<0.05	0.270	<u>0.656</u>	0.350
Adults	<0.05	<0.05	<0.05	<0.05	**0.198**	<0.05
Tanais sp.	<u>0.798</u>	0.464	<u>≤0.05</u>	<0.05	<u>0.501</u>	<0.05
Corophium spp.	<u>0.860</u>	0.083	<u>≤0.05</u>	0.094	<u>0.161</u>	<0.05
Cumella vulgaris	<u>≤0.05</u>	<0.05	<u>≤0.05</u>	<0.05	**0.085**	<0.05
Oakland Bay						
Tisbe spp.	**<0.05**	<0.05	<0.05	<0.05	**0.940**	<0.05
Harpacticus uniremis						
Copepodites	<0.05	<0.05	**0.855**	<0.05	**0.788**	<0.05
Adults	<u>0.673</u>	<0.05	<u>≤0.05</u>	0.070	<u>0.627</u>	0.203
Dactylopusia sp.	**<0.05**	0.446	**<0.05**	0.386	<u>0.134</u>	0.105

itats are most extensively used by juvenile epibenthic-feeding marine fishes.

Sediment structure, as measured by Folk's (1965) methodology of dry-sieving and pipette analysis, indicated that at both study sites, mean grain size was consistently finer in netted plots than on the natural beach, but only significantly so for one of three months. Basic sediment structure was different at the two study sites; Bywater Bay had higher proportions of fine sand and very fine sand and silt compared with higher proportions of granules to pebbles at Oakland Bay. However, the increase in sediments <1–2 mm in treatment plots at both sites implied that nets decreased near-bed resuspension and trapped more material transported alongshore, thus promoting a comparatively more stable and muddier substrate than in control plots.

Results were similar to what was reported for beach graveling by Simenstad et al. (1991). Epibenthos responses to netting were site-specific, and probably depended on the inherent level of natural disturbance. In general, most epibenthic crustaceans at Bywater Bay were depressed in predator exclusion net (treatment) plots compared to the unnetted (control) plots. Densities of adult harpacticoid copepods, such as *Dactylopusia* spp., *Harpacticus spinulosus*, *Amphiascus* sp., *Robertsonia* sp. cf *knoxi*, and the cumacean *Cumella vulgaris* were consistently higher in control plots. However, differences were not statistically significant compared to the high block effects (Table 3). An exception was adult and copepodite *Harpacticus uniremis,* which were strongly enhanced on the netted plots in April and May but not in June (when densities had generally declined). Block effects were also strongly significant in all months for adults, and during one month for copepodites. Predator exclusion nets at Oakland Bay, in contrast, often resulted in enhanced total epibenthos densities, especially in April (Table 3). Densities of *Tisbe* sp., *Dactylopusia* sp., and *Harpacticus uniremis* copepodites were all enhanced except in June, when densities declined compared to the uncovered plots.

Epibenthic Meiofauna on Oyster Plots

Epibenthic community structure on two oyster plots in Willapa Bay was sampled by Simenstad and Cordell (1989) during their evaluation of carbaryl effects but were not reported therein. One actively cultured plot was composed of dense 3-yr-old oysters on silty sand substrate, included some mud shrimp burrows, and had attached macroalgae (*Ulva* and *Enteromorpha*) covering much of the substrate and oysters. The second plot was an inactive oyster culture plot with patchy coverage of mixed eelgrass (*Z. marina*) and oyster shell over silty sand

sediment; it also included mud shrimp burrows and minor amounts of macroalgal cover. To our knowledge, both plots had been undisturbed for at least 3 yr. All methodology followed the design and protocols of the carbaryl spray effects experiment (see below), in which 10, randomly selected replicate samples were taken with a 0.018-m² epibenthic suction pump over a 100 m × 100 m sampling area on one plot.

Although structure, density, and taxa diversity of the epibenthos assemblages on the two plots were generally similar, several major differences were noted (Table 4). First, harpacticoid taxa diversity was higher in the active oyster plot, and second, prey taxa (e.g., *Harpacticus spinulosus, Tisbe* sp., *Paralaophonte congenera, Corophium* sp., *Pontogeneia* sp. and Crangonidae) of some epibenthic-feeding fishes, such as juvenile salmon, tended to be more dense on the inactive oyster plot. Third, prey taxa (e.g., Ectinosomatidae, *Microarthridion littorale,* and *Tachidius triangularis*) of other fishes, such as juvenile flatfishes, were more dense on the active oyster plot. It is possible that interstitial harpacticoids (including those specifically listed in the previous sentence) were more prevalent and dense on the active oyster plot because of the dense oyster pseudofeces and finer, more organic sediments that accumulated. The higher density of nematodes further suggests that surface sediments may have contributed more fauna in samples obtained from the active oyster plot.

Reduction or Removal of Attached Vegetation

Since the 1800s, oyster growers in Willapa Bay have generally regarded eelgrass as a nuisance. In some cases, eelgrass is moved on oyster plots in order to maximize water flow over the plots and increase ease of harvest by dredging (Townsend 1893; Eberhardt 1966; McDonald 1966). We could find no documentation on how pervasive this practice is today. Eelgrass may also be impacted by dredging, harrowing, and leveling, all of which extensively disrupt surface sediments and potentially destroy aboveground eelgrass shoots and leaves, and perhaps belowground roots and rhizomes as well. Data describing quantitative changes in either shoot density or aboveground or belowground biomass of eelgrass on oyster culture sites, or for adjacent, undisturbed intertidal habitats, does not exist in the Pacific Northwest. However, effects of oyster culture (primarily dredging) were studied in 1962 and 1963 by Waddell (1964) in Arcata Bay, a part of Humboldt Bay in northern California. Comparing paired plots (one cultured plot and one uncultured), he concluded that oyster culture impacted eelgrass shoot density, plant size (i.e., shoot length), and biomass. Impacts depended on

TABLE 4. Taxa composition, mean densities (± 1 standard deviation), and diversity of epibenthic meiofauna and small macrofauna from an active oyster culture plot and an inactive oyster plot in Willapa Bay, Washington, June 1988. See text for description of plots and sampling methodology.

		Plot			
		Active Oyster		Inactive Oyster	
Taxa	Dominant Life-History Stages	Mean Density (number m^{-2})	%	Mean Density (number m^{-2})	%
Turbellaria	all	5.6 (17.6)	0.06	18.5 (39.3)	0.29
Nematoda	all	1,322.2 (1,657.1)	14.54	450.6 (444.0)	7.12
Polychaeta	all	227.8 (307.0)	2.50	135.8 (152.4)	2.14
Oligochaeta	all			24.7 (40.4)	0.39
Mesogastropoda	juvenile			12.3 (24.5)	0.19
Bivalvia	juvenile	188.9 (114.8)	2.08	49.4 (70.5)	0.78
Halacaridae	all	88.9 (187.4)	0.98	55.6 (78.6)	0.88
Ostracoda					
Podon leuckarti	adult	577.8 (344.7)	6.35	6.2 (18.5)	0.10
Myodocopa	juvenile	5.6 (17.6)	0.06		
Podocopida	all	122.2 (90.0)	1.34	117.3 (122.5)	1.85
Copepoda	nauplii	122.2 (205.9)	1.34		
Calanoida	copepodite	5.6 (17.6)	0.06	6.2 (18.5)	0.10
Paracalanus sp.	copepodite	5.6 (17.6)	0.06		
Centropages abdominalis	copepodite			6.2 (18.5)	0.10
Eurytemora americana	copepodite	122.2 (82.0)	1.34	166.7 (138.9)	2.63
Acartia sp.	copepodite	1,483.3 (1,314.2)	16.31	870.4 (731.8)	2.63
Harpacticoida	copepodite	244.4 (307.9)	2.69	61.7 (128.6)	0.97
Tegastidae	adult	5.6 (17.6)	0.06		
Longipedia sp.	copepodite	411.1 (502.5)	0.06	197.5 (326.4)	3.12
Scottolana canadensis	copepodite	5.6 (17.6)	0.06		
Ectinsomatidae	all	583.3 (524.6)	6.41	123.5 (126.6)	1.95
Harpacticus spinulosus	adult	11.1 (23.4)	0.12	148.1 (162.0)	2.34
Zaus spp.	mating pair	12.3 (37.0)	0.19		
Tisbe spp.	all	222.2 (216.0)	2.44	469.1 (659.8)	7.41
Microarthridion littorale	adult	561.1 (775.8)	6.17	49.4 (128.6)	0.78
Tachidius triangularis	adult	688.9 (666.8)	7.57	80.2 (68.7)	1.27
Danielssenia sp.	adult	44.4 (86.1)	0.49		
Laophontidae	copepodite	188.9 (174.1)	2.08	74.1 (103.9)	1.17
Paralaophonte congenera	adult	516.7 (449.1)	5.68	1,284.0 (1,454.9)	20.27
Heterolaophonte longisetigera	adult			74.1 (92.1)	1.17
Heterolaophonte hamondi	gravid female			6.2 (18.5)	0.10
Heterolaophonte sp.	adult	5.6 (17.6)	0.06		
Ameiridae	adult			24.7 (74.1)	0.39
Ameira longipes	adult	92.6 (196.4)	1.46		
Ameira sp.	adult	43.2 (54.0)	0.68		
Cletodidae	adult	27.8 (60.0)	0.31		
Huntemannia jadensis	adult	16.7 (37.5)	0.18	43.2 (60.7)	0.68
Nannopus palustris	adult	6.2 (18.5)	0.10		
Acrenhydrosoma karlingi	adult	33.3 (38.8)	0.37		
Amonardia normani	copepodite	11.1 (23.4)	0.12	6.2 (18.5)	0:10
Amphiascus sp.	adult	67.9 (77.5)	1.07		
Stenhelia peniculata	adult	55.6 (86.9)	0.61	6.2 (18.5)	0.10
Stenhelia sp.	adult	44.4 (73.1)	0.49	43.2 (110.3)	0.68
Stenhelia sp. A	mating pair	11.1 (35.1)	0.12		
Typhlamphiascus pectinifer	adult	50.0 (80.5)	0.55	30.9 (56.3)	0.49
Amphiascoides sp. A	adult	83.3 (87.8)	0.92	117.3 (89.8)	1.85
Robertsonia sp. cf knoxi	adult	38.9 (87.1)	0.43	160.5 (189.3)	2.53
Bryocamptus sp.	copepodite	38.9 (123.0)	0.43	74.1 (169.0)	1.17
Mesochra sp.	adult	27.8 (60.0)	0.31	30.9 (62.8)	0.49
Dactylopusia vulgaris	adult	11.1 (23.4)	0.12		
Diarthrodes sp.	adult	44.4 (51.1)	0.49	530.9 (542.3)	8.38
Poecilostomadoida	all	16.7 (26.8)	0.18	6.2 (18.5)	0.10
Clausidiidae	copepodite	238.9 (173.8)	2.63	86.4 (92.6)	1.36
Oithona helgolandica	adult	5.6 (17.6)	0.06		
Balanomorpha	larvae	33.3 (46.8)	0.37	80.2 (74.1)	1.27
Cumacea					
Leucon sp.	all	166.7 (196.0)	1.83	37.0 (92.1)	0.58
Cumella vulgaris	all	333.3 (238.6)	3.67	246.9 (269.5)	3.90

TABLE 4. Continued.

Taxa	Dominant Life-History Stages	Plot			
		Active Oyster		Inactive Oyster	
		Mean Density (number m⁻²)	%	Mean Density (number m⁻²)	%
Tanaidacea-Dikonophora	juvenile			12.3 (24.5)	0.19
Leptochelia savignyi	all	16.7 (37.5)	0.18	6.2 (18.5)	0.10
Epicaridea	unidentified	5.6 (17.6)	0.06		
Amphipoda-Gammaridae					
Corophium sp.	juvenile	11.1 (35.1)	0.12	24.7 (29.3)	0.39
Pontogeneia sp.	juvenile			6.2 (18.5)	0.10
Amphipoda-Caprellidea	juvenile			18.5 (27.8)	0.29
Caprella laeviuscula	mating pair			6.2 (18.5)	0.10
Decapoda-Caridea					
Crangonidae	larvae			6.2 (18.5)	0.10
Diptera					
Chironomidae	larvae	5.6 (17.6)	0.06		
Unidentified egg				18.5 (55.6)	0.29
Total		9,094.44 (4,217.35)		6,333.33 (3,978.34)	
Total number of taxa categories		50		53	
Numerical diversity; Shannon-Weiner H'		4.29		4.36	
Brillouin		4.29		4.35	

the length of time each area had been cultured, with effects increasing as the length of time the plot had been under culture increased. For example, the mean reduction in eelgrass biomass ranged from 30% after one season under culture to 96% after four seasons and appeared to persist for up to two additional years after culture (Waddell 1964).

Although we could find no comparable information in Washington estuaries, we developed an approximate, qualitative estimate for one intensely cultured area of Willapa Bay in the vicinity of Stony Point. We examined this area using infrared aerial photographs to assess effects of apparent dredging and other oyster culture activities (Fig. 5). The photographs were 1:2,000 scale and encompassed a 66.4 km² area in the region of Stony Point (33.4 km² of which was intertidal) taken in June 1986; from these photographs we delineated polygons of apparent habitat disruption. Based on colorimetric differences with adjacent plots known to have considerable eelgrass coverage, we classified disturbance as (1) moderate to intense or (2) minor to moderate. These polygons presumably reflected sediment disruption and lower coverage of eelgrass and macroalgae, but these interpretations could not be verified by ground-truthing. Based on computer-generated estimates of the total area of the polygons, we estimated that 2.53 km² (12.6%) of the 20.07 km² available for oyster culture within our survey area was moderately to intensely disturbed and 1.03 km² (5.1%) was minimally to moderately disturbed.

Even though this analysis indicated disturbance

to eelgrass habitat, we could not document the extent or standing stock of eelgrass that was there before oyster culture activities occurred, or what remained thereafter. However, Doty (1990) presented qualitative data on percent coverage of eelgrass in the same general area of oyster culture plots near Stony Point after carbaryl spray application in 1986–1988. All sites had historically been under oyster cultivation. At the time of carbaryl application, none of the five oyster culture plots in the Stony Point-Palix River region had more than ~25% "light" eelgrass (i.e., 21 ± 18 shoots m⁻²) and ~45% "heavy" eelgrass coverage (i.e., 80 ± 34 shoots m⁻²). "Light" shell (10–50% coverage) was prevalent (e.g., >50%) in three of the five sites and "open habitat" (<10% shell or eelgrass) occupied between almost 15% and 85% of the plots' areas. Although this composition may be representative of sites under long-term cultivation, there are no comparable data from an "undisturbed" eelgrass site (i.e., one that has not been cultured). Reexamination of two of these plots over the next 3 yr indicated an overall increase in "heavy" shell (e.g., >50% shell cover), with either a small increase or decline in eelgrass coverage. While interpretation of these data is hampered by a lack of a natural control, it indicates a variable effect of oyster culture on eelgrass in the area we examined by photographic analyses. Brooks (1993) also attributed generally higher abundances of most invertebrate taxa on control sites compared to carbaryl treatment sites in the same vicinity to be the result of "significantly more eel grass (sic) cover." Such
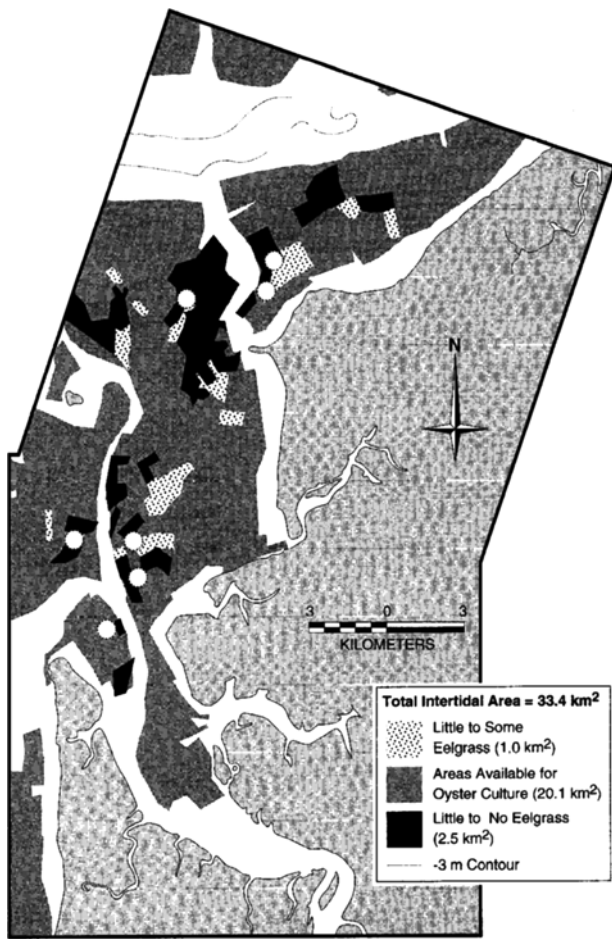
Fig. 5. Insert map of Stony Point region of Willapa Bay in which areas of extreme and moderate disturbance of intertidal flats was estimated from infrared aerial photographs; white dots represent oyster culture plots examined by Doty (1990) for eelgrass and oyster coverage.

differences were presumably due to oyster culture activities on the treatment plots in the same year.

Disturbance of eelgrass habitats may not be confined to ground culture methods for oysters. Carlton et al. (1991) and Pregnall (1993) documented modifications or significant reductions in eelgrass habitat and biota as a result of stake and rack culture in the South Slough National Estuarine Research Reserve, Coos Bay, Oregon. Carleton et al. (1991) found at least a 75% reduction in eelgrass shoots commensurate with decreased recruitment and survivorship of tellinid clams where stake and rack cultured oysters were harvested manually. Pregnall (1993) found almost an equivalent reduction in eelgrass shoots in an area of stake culture, associated with significant reductions in the densities of Dungeness crab (*Cancer magister*), macrofauna burrows, total infauna species, and small individuals of the bivalve *Cryptomya californica*. On

the other hand, significantly increased biomass of macroalgae and densities of mobile species such as *Cancer productus, Hemigrapsus* spp., sculpins (Cottidae), and blennies (Pholidae, Stichaeidae) were associated with the oyster beds. Pregnall's (1993) work was also one of few studies to examine community shifts that occur with removal of oysters. She described an influx of bivalve recruits and virtual disappearance of large mobile epibenthic organisms. Moreover, the number of eelgrass shoots in oyster plots had not recovered to control levels 5 mo after removal of oysters. Pregnall's overall conclusion was that oyster culture should not be allowed in areas of eelgrass meadows.

We must stress that the relationship between oyster culture and eelgrass is complex because other intertidal oyster culture activities may enhance eelgrass. In particular, it has been argued that carbaryl application may benefit eelgrass by permitting it to recruit and grow in areas where it has been eliminated by dense populations of burrowing shrimp (see below; Washington Department of Fisheries/Washington Department of Ecology 1992). Other than Doty's (1990) qualitative descriptions, we are currently unaware of other data on eelgrass density or standing stock on any one oyster plot over time, much less over broader areas of the estuary influenced by oyster culture. Furthermore, benthic disturbance to eelgrass habitats by oyster ground culture certainly does not approach that of escalator hydraulic dredging or clam "kicking" (i.e., suspending sediments and clams in a propeller wash) fisheries for soft-shell and hard-shell clams in other regions (Godcharles 1971; Peterson et al. 1987); these activities are often prohibited in eelgrass habitats.

CHEMICAL DISTURBANCE

As described previously, intertidal plots under oyster culture in Grays Harbor and Willapa Bay (accounting for >50% of the oysters produced in the state) are treated with the insecticide carbaryl in order to control populations of burrowing shrimp (primarily *Neotrypaea* and *Upogebia*). Extensive laboratory toxicity studies have shown that carbaryl kills the target species of burrowing shrimp (e.g., Stewart et al. 1967; Chambers 1970) but is nonspecific and can have lethal and sublethal impacts on nontarget vertebrate and invertebrate species (Lindsay 1961; Stewart et al. 1967; Armstrong and Milleman 1974; Tagatz et al. 1979; Mount and Oehme 1981; Buchanan et al. 1985). These studies also demonstrated that mortality depends upon such factors as taxa, concentration of carbaryl applied, and duration of exposure, with crustaceans particularly sensitive (Stewart et al. 1967). Despite decades of use, there has been relatively limited

research on the effect of carbaryl on natural estuarine communities. In this section, we review relevant field studies on impacts of carbaryl on benthic infauna, epibenthic meiofauna, and fish in Willapa Bay and Grays Harbor.

Benthic Infauna

In general, field studies of the effects of carbaryl on burrowing shrimp show that mortality is variable, ranging up to 100%, and depends on species of shrimp, time of application, concentration of carbaryl applied, and other factors. Snow and Stewart (1963, cited by Buchanan et al. 1985) reported a 82–94% reduction in burrowing shrimp following carbaryl treatment in Tillamook Bay, Oregon. In Willapa Bay, Dumbauld et al. (1989) used 40-cm core samples of shrimp densities to assess mortality as a function of carbaryl application rate on replicated, 16-m² plots in 1988 and 1989 and 100-m² plots in 1989. Shrimp mortality immediately following treatment was variable, ranging up to 100% (Fig. 6). In one experiment, mud shrimp mortality was consistently greater, while in the others ghost shrimp mortality was greater. in 1989, the highest application rate tested (0.9 kg ha⁻¹), which is one-half that preferred by oyster growers, resulted in ~80% shrimp mortality (Washington Department of Fisheries/Washington Department of Ecology 1992).

Because shrimp burrow counts are generally correlated with shrimp density, they can be used as an index of shrimp density (Posey 1986a; Posey et al. 1991; B. Dumbauld, Washington Department of Fisheries, Nahcotta, Washington, personal communication). Tufts (1990) estimated percent reduction in burrow counts shortly after several oyster plots were treated in 1987. Burrow counts declined an average of 98.7% on seven plots with an application rate of 0.82 kg ha ¹ of carbaryl, and an average of 97.5% on six plots treated at 1.22 kg ha ¹. On 10 plots treated at rates from 0.82 kg ha⁻¹ to 1.64 kg ha⁻¹ in 1986, the percent reduction in burrow counts averaged 94.4% (Tufts 1989).

There are few field studies examining mortality of macroinfauna after carbaryl application. One study in Tillamook Bay, Oregon, where effects of carbaryl application on benthic infauna were evaluated on small experimental plots (Armstrong and Milleman 1974), is relevant. Significant reductions in the densities of some clam species were found while there were no apparent affects on nemerteans and polychaetes.

Impacts on the benthos in Willapa Bay in 1984 were evaluated in a study by Hurlbert (1986). Hurlbert sampled one 2.03-ha bed immediately prior to treatment in July 1984, on the low tide following treatment, and 60 d post-treatment; six cores (182
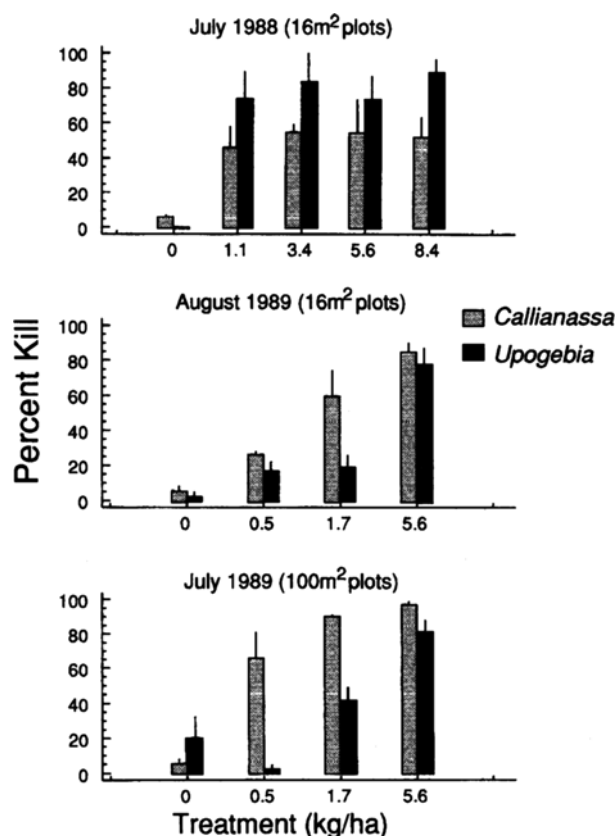

Fig. 6. Changes in density of burrowing shrimp following experimental application of carbaryl on small plots in July and August 1988 and 1989 (from Dumbauld et al. 1989). Percent mortality was determined by taking cores 24–48 h following treatment while burrows were counted 1 mo following application.

cm²) were taken on each sampling date and no control was examined. Densities of several infauna taxa declined significantly, including *Macoma balthica*, *Nephtys caecoides*, and *Pectinaria granulata*, while other taxa exhibited little or no change or increase in density.

Hueckel et al. (1988) counted dead macroinvertebrates on seven 100 m × 2 m transects on three oyster plots immediately following carbaryl application in summer 1987. Carbaryl killed burrowing shrimp, nereid worms, crangonid shrimp, scale worms, Dungeness crab, and nemerteans (Table 5). Estimates of the number of invertebrates killed were highly variable, as evidenced by the broad confidence intervals, and are conservative since they only include animals observed on the surface of sediments.

Several on-going evaluations of carbaryl's impacts on benthic infauna indicate that there are variable short-term effects on some taxa. Dumbauld (Washington Department of Fisheries, Nah-

TABLE 5. Densities of dead invertebrates (A: number m ^{2}) and fish (B: number ha ^{1}) on three plots sprayed with carbaryl in 1987 (from Hueckel et al. 1988); values are means and 95% CI (value in table) from seven transects sampled on three plots.

A. Invertebrates

Taxa	Density	
	Number m $^{-2}$	95% CI
Burrowing shrimp	1.39	5.76
Nereid worms	0.35	0.64
Crangon shrimp	0.09	0.06
Scale worms	0.03	0.08
Dungeness crab	0.01	0.04
Nemertina	0.01	0.01

B. Fish Taxa

Taxa	Density	
	Number ha $^{-1}$	95% CI
Saddleback gunnel	489	620
Staghorn sculpin	361	790
Bay goby	309	630
Three-spined stickleback	40	141
Starry flounder	10	40

cotta, Washington, personal communication), for example, found variable responses in densities of dominant benthic infaunal taxa on sprayed plots compared to unsprayed plots within 24 hr, 1 d, 2 d, 3 mo, and 1 yr after carbaryl treatment. Marked depressions occurred in densities of the amphipod *Corophium acherusicum* and the cumacean *Hemilucon comes* in mud shrimp-dominated plots, the amphipod *Eohaustorius estuarius* in ghost shrimp-dominated plots, and in oligochaetes in both communities. In contrast, densities of the tanaid *Leptochelia savignyi*, the polychaetes *Capitella capitata*, *Mediomastus californiensis*, *Hemipodus borealis*, and the bivalves *Cryptomya californica* and *Macoma*

balthica either showed no apparent change or measurably increased.

Brooks' (1993) study in the Palix River-Wilson Point region of Willapa Bay in 1992 showed differential responses by sympatric infaunal taxa, and both short-term and persistent long-term effects (summarized in Table 6). He used a 0.1-m ^{2} modified van Veen grab to sample (n = 9) two carbaryl treatment sites and one control site 2 d before and 2 d, 14 d, and 51 d after application of 1.4 kg ha $^{-1}$ of carbaryl on July 14, 1992. Densities of two tubicolous crustaceans, the amphipod *Corophium acherusicum* and the tanaid *Leptochelia savignyi*, were both reduced within 2 d after carbaryl application. While *C. acherusicum* densities were reduced by an average of 97%, *L. savignyi* densities declined only ~10%, and populations of both species had recovered to densities comparable to the controls by 51 d post-treatment. Significant (ANOVA) differences in density were found for six of 10 taxa 2 d prior to treatment compared to 2 d following carbaryl spraying. However, site effects were also significant in all but one (*Cryptomya californica*) of the six cases, indicating that natural variation among sites was large or larger than the response to carbaryl. Spray effects were evident in five of the same 10 taxa between 2 d and 51 d after carbaryl application, but site effects were evident for four of the five; only the cockle, *Clinocardium nuttalli*, showed a significant spray effect without a site effect. The effect of time was generally more significant as the amount of time elapsed following treatment increased.

Long-term effects of carbaryl on benthic infauna are poorly documented. Dumbauld et al. (1992)

TABLE 6. Summary of benthic infauna and epibenthos responses to application of carbaryl in Willapa Bay, Washington, in July 1992; short-term refers to abundances changes between 2 d prior and 2 d after spraying, and long-term refers to changes between 2 d after and 51 d after spraying; confounding factors are significant site and time effects based on analysis of variance (modified from Brooks 1993).

Taxa	Short-term (S-T)	Long-term (L-T)	Confounding Factors			
			Site		Time	
			S-T	L-T	S-T	L-T
Sensitive taxa						
Amphipoda[1]	nearly eliminated	rebounded dramatically	X			X
Leptochelia savignyi	reduced	rebounded dramatically	X	X		X
Burrowing shrimp[2]	nearly eliminated	increased	X	X		X
Cumacea[3]	nearly eliminated	slow recovery	X	X		X
Harpacticoida	small reduction	variable	—	—		X
Clinocardium nuttalli	small reduction	substantial reduction				X
Cryptomya californica	small reduction	slow recovery		X		X
Insensitive taxa						
Ostracoda						
Macoma balthica						

[1] Primarily *Corophium acherusicum*.

[2] *Upogebia pugettensis* and *Neotrypaea californiensis* combined.

[3] Primarily *Cumella vulgaris* and *Leucon* sp.

indicated that densities of some taxa, such as the amphipod *Eohaustorius*, may remain depressed for up to 1 yr, and some taxa, such as *Cryptomya* and the phoronid *Phoronopsis hermeri*, show delayed responses. However, it is clear that the new community that develops on sprayed plots will be different than what existed before because shrimp are largely eliminated from the plots and oyster are added. Through bioturbation, burrowing shrimp strongly influence benthic community composition, especially sedentary macrofauna such as spionid polychaetes, bivalves (especially *Cryptomya californica*, a commensal clam living in shrimp burrows), gammarid amphipods (e.g., *Corophium* spp.), and the tanaid *Leptochelia dubia* (Peterson 1977, 1984; Brenchley 1981; Bird 1982; Murphy 1985; Washington Department of Fisheries/Washington Department of Ecology 1985; Posey 1986a; Posey et al. 1991). However, despite over 100 yr of oyster culturing and minor scientific research on Willapa Bay, there is no information on the type of community that will develop on oyster plots treated with carbaryl. It is likely that a reduction in shrimp density and conversion to oysters enhances densities of some infaunal taxa and reduces densities of others. Although Bird (1982) indicated reduced benthic biodiversity with increased shrimp densities, Posey (1986a) found species richness basically unchanged, which he attributed to the differences in scale of the two studies. (Posey sampled at much finer spatial resolution.) Posey et al. (1991) speculated that the long-term effect is one of changing relative abundances rather than reducing faunal densities. Of course, the communities colonizing oyster plots will probably be comparatively dynamic on the scale of oyster culture cycles because regular culture activities will continue to disturb plots. Oysters will eventually be harvested and shrimp will reinvade until the next cycle of preparing the plot for re-seeding. This is a critical point to consider when evaluating comparisons with so-called "natural" reference plots because these plots are probably still at early or intermediate stages in development from an intensively cultivated plot. No one has documented that their reference sites actually originated from plots that had not been under prior oyster cultivation.

Although most studies of carbaryl impacts have focused on the sprayed plots, some burrowing shrimp (and other animals such as crabs; see Doty 1990) may be killed adjacent to sprayed plots. Tufts (1989), for example, reported that there were reductions in burrow counts in areas adjacent to treated plots that generally correlated with carbaryl concentrations in water samples.
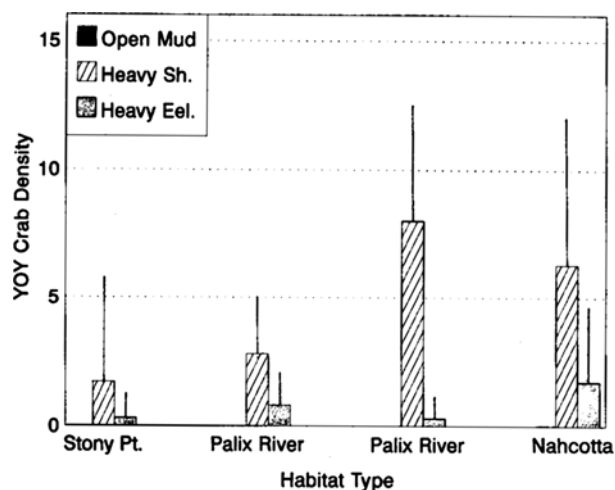

Fig. 7. A comparison of young-of-year (YOY) crab settlement (numbers of YOY crab m $^{-2}$) in oyster shell habitats, eelgrass, and bare mud in Willapa Bay. Means (± 1 SD) are presented for four sites sampled in late June and early July 1986–1987 either prior to carbaryl treatment or at least 1 yr after treatment. The three habitats compared are open mud, heavy eelgrass cover (>50% eelgrass and <10% oyster shell), and heavy shell (>50% oyster shell) (from Doty 1990).

Epibenthos

Field evaluations of carbaryl's effects on epifauna have focused primarily on Dungeness crab, because of its commercial importance, and to a lesser extent on epibenthic meiofauna. Willapa Bay and Grays Harbor are important nursery areas for Dungeness crab (Armstrong and Gunderson 1985; Gunderson et al. 1990). Crab larvae are released into coastal waters and settle onto benthic habitats beginning in early spring (Gunderson et al. 1990), with the highest juvenile settlement occurring in the coastal estuaries in oyster shell habitats followed by eelgrass (Armstrong and Gunderson 1985; Doty 1990) (Fig. 7). Doty concluded that shell is of primary importance for survival of newly settled YOY (young-of-year) crab and that oysters planted in commercial quantities provide a substantial amount of cover for newly recruited crabs. The importance of some type of structure to YOY crab settlement has also been documented in Puget Sound (McMillan 1991).

All YOY crab on intertidal areas sprayed with carbaryl are killed shortly after spraying, as are a portion of the YOY crab in adjacent intertidal areas (Doty 1990). A small number of older crab may also be killed, primarily on sprayed plots. Some recolonization occurs within 1 mo of the carbaryl application.

Crab mortality depends on type and extent of habitat in an area and timing of the carbaryl application. In general, the number of crabs killed is directly correlated with the amount and distribu-

tion of shell on a plot. Doty (1990) developed a "worst case" model to estimate the impact of the carbaryl application on Dungeness crabs in Willapa Bay from 1985 to 1987. He estimated that between 1986 and 1988, 3–4% of the YOY crabs in Willapa Bay would be killed by carbaryl application, assuming 2,400 ha are under ground culture and the acreage treated with carbaryl was 111–145 ha annually. The replacement of burrowing shrimp with oysters provides high quality rearing habitat for crabs, thereby increasing the probability that more crabs will survive than if shell were not there. Thus, by improving the habitat structure, the oyster industry might, to an unknown degree, mitigate impacts of carbaryl on crabs by increasing crab production.

Impacts of carbaryl application on epibenthic meiofauna were examined by Simenstad and Cordell (1989) by sampling a sprayed plot and reference plot that had not been treated for several years. Both plots were low-gradient flats of fine sand and mud with a moderate, patchy cover of eelgrass, and were located at approximately −0.2 m MLLW. Densities of meiofauna were sampled using a 0.018-m^2 epibenthic pump at 10 randomly selected points over a 100 m × 100 m sampling grid located in the middle of treatment and reference plots. Plots were sampled soon after being inundated by the flood tide on three occasions: 1 d before carbaryl treatment, immediately after carbaryl application (which occurred at low tide, with the intertidal flat exposed), and 12 d post treatment.

One-way analysis of variance using $\log_{10}(x + 1)$-transformed density (no. m^{-2}) data indicated that carbaryl did not kill all or most epibenthos on treated tracts (Table 7), in contrast to its effects on other animals such as Dungeness crabs, where mortality is usually 100% (e.g., Doty 1990). Judging by the numbers of certain species that were on a treated area 24 h after spraying, some animals either were left alive following the spraying or recruited by migrating from adjacent intertidal areas. Given the mobile nature of many epibenthos (e.g., Hicks and Coull 1983), we suspect that rapid colonization explains in part the numbers of epibenthos on the plot after treatment. Percent change (%) in density depended on taxa and time period (Table 7). Densities of the cumacean *Cumella* spp. and gammarid amphipods *Corophium* spp. did not decline immediately following spraying, but did so within 12 d. In addition, densities of the epibenthic harpacticoid *Tisbe* spp. declined immediately (one tidal cycle-one tidal day) after treatment but had recovered 2 wk later.

Using a similar epibenthic pump sampler, Brooks (1993) found some evidence that carbaryl

TABLE 7. Density (number m^{-2}) of epibenthic taxa on one site treated with carbaryl and one control site. Carbaryl treatment occurred on July 1, 1988. Samples were taken 2 d before application (June 29, 1988), on the flood tide following treatment, (July 1, 1988), and 12 d after treatment (July 12, 1988) (from Simenstad and Cordell 1989). Taxa presented are those that are important food items of economically important fish, such as juvenile salmon.

Taxa	Sampling Period		
	June 29, 1988	July 1, 1988	July 12, 1988
Total harpacticoids			
Treatment			
Number	3,339.2	5,450.2	11,878.2
SD	6,594.1	6,835.9	12,654.9
Control			
Number	1,095.1	2,570.8	8,301.8
SD	2,253.2	3,027.4	8,235.7
Longipedia sp.			
Treatment			
Number	66.7	266.7	405.5
SD	122.3	307.5	301.1
Control			
Number	83.3	105.6	855.6
SD	160.8	155.9	490.5
Tisbe spp.			
Treatment			
Number	305.6	122.2	894.5
SD	443.1	116.5	1,272.1
Control			
Number	166.7	366.7	777.7
SD	202.9	461.5	821.1
Corophium spp.			
Treatment			
Number	27.8	188.9	5.6
SD	47.2	448.7	17.6
Control			
Number	5.6	16.7	61.1
SD	17.6	52.7	92.4
Cumella vulgaris			
Treatment			
Number	57.8	933.3	88.8
SD	131.9	1,402.9	140.8
Control			
Number	105.6	272.2	1,116.7
SD	222.9	604.1	861.7

impacted epibenthic ostracods and copepods, although species-specific or genera-specific differences in densities were not tested. Only ostracods and copepod copepodite larvae illustrated significant spray effects (declines) between 2 d prior and 2 d after spray application, but the time effect was also highly significant for controls in both cases (a significance level was not reported for a site effect). Harpacticoid copepod densities declined at both treatment and control sites, such that neither

spray nor time effects were significant. Long-term changes, between 2 d and 51 d after spraying, were significant only for harpacticoid and calanoid copepods. Harpacticoids actually increased on both sites, resulting in significant spray, site, and time effects; calanoids showed an initial post-spray increase and then a broader decline at the treatment site compared to the control site, resulting in only a significant spray effect. A complicating factor in interpreting Brooks' (1993) results was that the taxonomic level reported did not allow differentiation of taxa that were associated with substrate (i.e., "true" epibenthos) from those that were more pelagic or tidally advected.

Demersal and Benthic/Epibenthic-feeding Fishes

At low tide, when carbaryl is applied, some fish may remain on oyster plots in pools and shallow channels. Fish species that have been found in these habitats include saddleback gunnels (*Pholis laeta*), Pacific staghorn sculpin (*Leptocottus armatus*), bay goby (*Lepidogobius lepidus*), starry flounder (*Platichthys stellatus*), English sole (*Pleuronectes* [*Parophrys*] *vetulus*), and shiner perch (*Cymatogaster aggregata*) (Washington Department of Fisheries/Washington Department of Ecology 1992). As observed for benthic infauna, fish on oyster plots treated with carbaryl are killed. Hueckel et al. (1988) estimated the number of fish killed on the same three plots where they surveyed the number of macroinfauna killed. Mortality averaged 1,209 fish ha^{-1} for all species combined, ranging from 10 fish ha^{-1} for starry flounder to 489 fish ha^{-1} for gunnels (Table 5). Tufts (1989, 1990) counted the number of fish killed in single 33.3 m × 3.3 m plots on each of 26 plots sprayed with carbaryl in 1986 and 1987. For all species combined, the average numbers killed were 92.8 fish ha^{-1} in 1986 and 45.8 fish ha^{-1} in 1987. The number of fish killed varied considerably between tracts and depended mostly on the amount of wetted fish habitat (defined as the amount of water >5 cm in depth). This ranged from 0% to 100% depending on the plot and when it was sprayed following the low tide.

Discussion

The influence of an anthropogenic disturbance on established communities depends strongly on the temporal, spatial, and intensity scales over which it occurs; thus, an evaluation of the community responses should occur over the same scales. In assessing potential effects of aquaculture activities, we used a comparatively short-term approach using "natural" disturbance regimes of control or "reference" sites as the standard, although we acknowledge that these sites may have

been influenced by previous aquaculture activities. Where we found a major shift in taxa densities or distributions, primarily through reduction or exclusion of selected taxa, we considered disturbance to be significantly higher compared to natural variation exhibited by the indigenous community. None of our examples tested disturbance frequencies much beyond several years or considered frequencies and intensities of natural disturbance, such as 100-yr flood cycles, which the community perhaps cannot withstand. Thus, our evaluation of the significance of aquaculture-associated disturbance is relevant only to chronic, local scales rather than ecosystem-level spatial scales and disaster-level temporal scales.

ECOLOGICAL REPERCUSSIONS OF AQUACULTURE-ASSOCIATED DISTURBANCE

On a community scale, responses to chronic, low intensity or infrequent, intermediate intensity disturbances tend to be within the scope of behavioral or ecological adaptability of the flora and fauna. For instance, on a plot-specific basis, effects of carbaryl spraying on epibenthic meiofauna appears to be extremely short-term, if not inconsequential (Brooks 1993). This is because dispersal of most epibenthic populations is often continuous and dynamic as a function of tidal advection and resuspension (Palmer 1984, 1988; Kern and Taghon 1986; Hicks 1988; Simenstad et al. 1988) and food resource exploitation (Decho and Fleeger 1988). Also, meiofaunal animals tend to have high, multivoltine turnover rates (Hicks and Coull 1983) that facilitate rapid recolonization. The question then becomes one of the spatial scale of processes that affect repopulation and how changing the extent, timing, and frequency of carbaryl spraying might induce a threshold response in intertidal biota. If such a threshold response was attained, recolonization could be inhibited over broad spatial and temporal scales. However, at present there are no data on the potential change in recruitment success and rate that might occur if spraying occurred over spatial scales of square kilometers rather than hectares, involved more than a single application per year, or occurred at times other than mid summer.

In addition, it should be recognized that, with the existing data, the effects of carbaryl cannot be separated from effects of other oyster culture practices, or of the oysters themselves (e.g., as substrate for algal attachment, habitat for predators, producers of pseudofeces, and filtering the water column). How these chemical, physical and biological influences are interrelated is unknown.

Similarly, intertidal graveling or predator exclusion nets in some habitats (e.g., low energy, fine

sediment) may enhance average epibenthos diversity and standing stock by increasing complexity of the sediment structure. Moreover, introduction of substrates suitably large for macroalgal attachment might mediate disturbance. In this case, seemingly subtle differences in the intensity of disturbance (e.g., amount of gravel added), the natural disturbance regime (e.g., tidal or wave resuspension and resorting of sediments), and other factors important to intertidal community structure (e.g., sedimentation rate) define taxon-specific responses. In this case, the intertidal community will likely be altered for as long as the gravel or net persists (e.g., years).

Changes in the composition of intertidal soft-bottom communities can affect growth and survival of fish and wildlife that forage in these habitats. This is particularly germane in Pacific Northwest estuaries, where a number of economically-important fishes feed preferentially on specific taxa of intertidal soft-bottom meiofauna and small macrofauna. Of prime interest are juvenile chum, chinook, and coho salmon that exhibit a high fidelity for shallow estuarine habitats. These fish feed on a restricted suite of epibenthic harpacticoid copepods, gammarid amphipods, cumaceans, and emergent insects produced in estuarine habitats. Fish growth and survival to the adult stage may depend upon this early life-history period (Levy and Northcote 1982; Simenstad et al. 1982; Pearcy 1992). When feeding in estuarine habitats, particularly in eelgrass meadows and mudflats, juvenile chum salmon prey extensively on only a few taxa of harpacticoid copepods such as *Harpacticus uniremis*, *Tisbe* spp., and *Zaus* sp. (Healey 1979; Simenstad et al. 1982, 1988; D'Amours 1987, 1988). A number of other species, including smelts (Osmeridae), sand lances (Ammodytidae), and sticklebacks (Gasterosteidae) also prey heavily on these same prey taxa in estuarine habitats early in their life histories (Simenstad et al. 1988). Similarly, amphipods such as *Corophium salmonis* and *C. spinicorne* and cumaceans are preyed upon extensively by juvenile chinook salmon (Dunford 1975; Northcote et al. 1979; Levy and Northcote 1982; Simenstad et al. 1982) and by migratory waterfowl and shorebirds such as sandpipers and dunlin (*Caladris alpina*) in mudflats and marshes (Albright and Armstrong 1982; Baldwin and Lovvorn 1994).

Overall, many estuarine fishes utilize specific prey resources that are associated with unique habitats, or perhaps even microhabitats (e.g., discrete levels in a highly epiphytized eelgrass "canopy," Simenstad et al. 1988). Their use of these areas may be linked to taxon-specific productivity of prey at these sites (e.g., Coull and Feller 1988). If prey required for growth and reproduction of the fish

are limiting, and there are no data to either validate or reject this hypothesis, significant declines in populations of these prey as a result of habitat modifications could reduce the carrying capacity for their predators. In some cases, the prey of one predator might be enhanced while that of another depressed. An example of this occurred on the beach graveled at Bywater Bay, where densities of *Tisbe* spp. (a major prey of juvenile chum salmon) were depressed and densities of *Cumella vulgaris* (prey of chinook) were enhanced. Such shifts suggest that there are costs and benefits of disturbance to natural resources and points out the type of information needed by estuarine habitat managers.

We can only speculate on large-scale community shifts over entire estuarine ecosystems, as there have been no evaluations of either cumulative or overall effects of aquaculture-associated disturbance at this scale. For instance, it is not unreasonable to postulate that disturbance from aquaculture in Willapa Bay may have promoted shifts between soft-bottom intertidal communities dominated by eelgrass and burrowing shrimp. Burrowing shrimp strongly influence the structure of the benthic/epibenthic community in which they dominate. They essentially function as "disturbance equivalents" to keystone predators by reducing the prominence of less mobile species (Peterson 1977, 1984; Posey et al. 1991; Dumbauld et al. 1992) and often smothering seagrasses (Suchanek 1983). In addition, burrowing shrimp influence nutrient cycling through release of dissolved nutrients from their burrows and modification of community metabolism (Murphy and Kremer 1992). Alternatively, estuarine eelgrass communities are speciose, productive and important as habitat for a myriad of economically-important fishes and their prey resources (Phillips 1984).

In most cases, ghost shrimp and eelgrass do not overlap, but mud shrimp and eelgrass do overlap (B. Dumbauld, Washington Department of Fisheries, Nahcotta, Washington, personal communication; the authors' personal observations). Therefore, given the potential of amensalistic interactions between burrowing shrimp and eelgrass (Brenchley 1981), large-scale disturbance from oyster culture may have historically mediated the ability of ghost shrimp to extensively colonize intertidal flats in estuaries such as Willapa Bay. Several Nineteenth Century accounts suggest that there was a considerable amount of dense eelgrass and reduced natural oyster (*Ostrea lurida*) populations on the tideflats (Swan 1857; Townsend 1893). This suggests that during some periods, or in certain areas, one or the other alternate community states dominated, perhaps as a function of natural

disturbance or biological (e.g., recruitment) cycles. However, persistent disturbance of eelgrass habitat by dredging, harrowing, and leveling for oyster culture may have more recently promoted expansion of burrowing shrimp by allowing these disturbance-oriented species to colonize stressed eelgrass habitats, and arresting successional development of the eelgrass community in favor of repeated invasions and dominance by burrowing shrimp. Such a disturbance-induced "release" of habitat for subsequent colonization by burrowing shrimp has been shown experimentally by Harrison (1987). He found that removal of all eelgrass shoots allowed adult shrimp and tube worms to dominate the sediment and inhibit survival of eelgrass (*Z. japonica*) transplants.

A major question yet to be resolved is whether, in the absence of anthropogenic disturbances, burrowing shrimp can invade and degrade a fully developed eelgrass bed, or if spreading eelgrass can displace burrowing shrimp. Harrison (1987) proposes that, under natural disturbance regimes, the cycles of activity of the eelgrasses and of the shrimp are sufficiently out of phase to allow eelgrass to expand and colonize new habitat at the expense of the adult animals, which do not reach peak activity until summer. Under this model, continued disturbance of eelgrass by intensive oyster culture, however, could shift dominance to burrowing shrimp. Peterson (1977, 1984) provided similar evidence of such multiple stable points in intertidal soft-bottom estuarine communities protected from or impacted by harvesting (digging) burrowing shrimp for bait. He found that over 3 yr *N. californiensis* could not reestablish dominance in an estuarine sandflat once the bivalve *Sanquinolaria nuttallii* had recruited to a plot from which the ghost shrimp had been removed. Whether such large-scale shifts to burrowing shrimp–dominated communities has occurred and has resulted in a net reduction of eelgrass habitat for important fish and macroinvertebrates (e.g., Dungeness crab) is indeterminable because there are no data on the persistence, standing stock, and structure of eelgrass under various levels and activities of oyster culture.

Initial recovery of eelgrass from potentially similar disturbances, however, may be slow. Peterson et al. (1987) found that eelgrass biomass did not recover from the disturbance of mechanical clam harvesting in Back Sound, South Carolina, until at least 4 yr, longer than the normal rotation period of oyster culture in the Pacific Northwest.

Burrowing shrimp densities and distributions may also be controlled by predation, which may be variable according to natural ecosystem cycles (e.g., El Niño) and disturbance events as well as anthropogenic factors. Intertidal benthic predators such as the staghorn sculpin, *Leptocottus armatus* (Posey 1986b), or gray whale, *Eschrichtius robustus* (Weitkamp et al. 1992), feed extensively on *N. californiensis*. However, only gray whale populations have probably been historically reduced enough to alter the balance in community dominants. Gray whale foraging can decimate intertidal *N. californiensis* populations, potentially removing 55–79% of the ghost shrimp standing stock. Although it is very likely that gray whale foraging in Pacific Northwest estuaries was reduced dramatically during the period of whaling, it is probably increasing as their populations again approach pre-whaling levels (Reilly 1981); Weitkamp et al. (1992) reported the presence of gray whale feeding pits in Willapa Bay in 1991.

When evaluating cumulative influences of a disturbance at the ecosystem scale, we should not ignore potentially overwhelming landscape influences. In the Pacific Northwest, forest harvest and other rural and urban alterations of shoreline, riparian, and upland habitats in the surrounding landscape can significantly change inflows of sediments and fresh water to estuaries (Simenstad et al. 1992; Jay and Simenstad 1994). Clearly, factors other than burrowing shrimp and aquaculture can contribute to changes in eelgrass in Willapa Bay. For instance, logging in the watersheds of the Bay may have increased turbidity levels to the point that some eelgrass photosynthesis is affected. Similarly, the proliferation of shoreline armoring (e.g., bulkheads and rip-rap embankments) in Puget Sound has severely reduced the input of fine sediments to beach habitats (Downing 1983). Thus, beaches throughout Puget Sound have likely experienced historic shifts in intertidal communities much greater than what has resulted from beach graveling and predator exclusion nets for clam culture.

In other estuaries, nutrient loading from watersheds and shoreline developments have resulted in eutrophication, hypoxia, and other system responses that have resulted in large-scale community changes (Nixon et al. 1986). Although ecosystem effects of such physical and geochemical changes upon entire estuaries are not common in this region, increased toxic plankton blooms ("red tides") have resulted in frequent closures of oyster, clam, and mussel harvesting in several bays and beaches. Fecal coliform has also become a more pronounced problem (Nishitani et al. 1988; Pepe and Plews 1991). The long-term challenge will be discriminating the relative importance of these various exogenous factors in the estuary (i.e., to gather information to manage at the ecosystem scale).

MANAGING FOR SUSTAINABILITY ON THE ESTUARINE ECOSYSTEM LEVEL

To a large extent, the prevailing attitude is that estuaries are relatively robust and self-maintaining, such that only extreme anthropogenic influences usually enter into management decisions (Wolff 1990). Complex physicochemical and ecological linkages among estuarine organisms and communities can be altered over the long-term by persistent disturbances that exceed natural regimes. Management strategies that fail to consider the tolerance of estuaries to anthropogenic disturbance, such as that posed by intensive aquaculture, may well threaten the sustainability of estuarine resources and ecosystem processes upon which coastal economies depend.

Thus, we suggest that aquaculture should be managed not only as an economic asset, as it has been historically, but as an ecological force as well because it influences important estuarine processes (e.g., productivity of other estuarine resources) that support other "free" resources (Schiewer and Arndt 1990; Lockwood 1991). Estuaries have a critical role in the life histories of many economically and ecologically important animals. Salmon, herring, smelt, crab, and flatfish feed in Pacific Northwest estuaries (Simenstad et al. 1982; Simenstad et al. 1988; Gunderson et al. 1990) and several species of migratory waterfowl and shorebirds feed on the large invertebrate production that occurs on the mudflats of several estuaries (Baldwin and Lovvorn 1994). Growth and survival of animals in estuaries not only depends on specific habitats but on linkages between habitats and areas within the estuary. The detritus utilized as food by a detritivorous amphipod in one site can originate from another location in the estuary. Linkages are not only provided by physical processes but by the organisms as well. Many estuarine organisms are highly mobile, such as juvenile salmon which use many areas within one estuary and may also use other estuaries as well. Thus, they can transfer energy and other material throughout an estuary or even between estuaries.

The influences of aquaculture on highly interdependent ecological processes across whole estuarine ecosystems have historically received little attention (Folke and Kautsky 1989), although the European Common Community, through the International Council for the Exploration of the Sea (ICES), is a notable exception (Lockwood 1991). Benthic aquaculture in the Pacific Northwest has not historically been evaluated and managed as a disturbance, but rather has been treated largely as a natural resource, comparable to organisms such as Dungeness crab or salmon. Thus, estuarine

management issues have tended to focus on effects of activities such as water pollution and navigation channel dredging on aquaculture rather than considering environmental effects of aquaculture on other estuarine resources. Typically, environmental effects of certain aquaculture practices have only been questioned or investigated when another important species, such as Dungeness crab, is at risk.

Large-scale disturbances by aquaculture can pose complex ecological as well as socioeconomic management dilemmas. Estuarine ecosystems should be able to sustain both aquaculture and critical habitat of estuarine-dependent resources, such as salmon and Dungeness crab. However, for this to be true, resource managers need to evaluate interactions and competing demands at the scale of both watershed and estuary. All aspects of intensive aquaculture practices should be considered at these scales in evaluating cumulative and cascading effects through trophic, nutrient recycling, and other ecosystem processes. For instance, oyster plots generally support a much higher diversity of benthic and epibenthic flora and fauna associated with the complex oyster shell substrate compared to the bioturbated habitat dominated by burrowing shrimp (e.g., Table 4). Dense cultures of suspension-feeding bivalves can also filter considerable phytoplankton and particulate material from the water column and deposit it on the benthos. This can improve water quality in some cases, but high densities of bivalves, and particularly cultured populations, can also effectively deplete food particles to the point of depressing growth of indigenous suspension feeders (Peterson and Black 1987; Héral 1991).

A key part of managing aquaculture within an ecological context is to minimize impacts. "Best management practices" can be designed in some cases to minimize adverse consequences of disturbance, such as efforts under way to define alternatives to carbaryl (Burrowing Shrimp Control Committee 1992). Best management practices may also be able to address species-specific or population-specific issues. For instance, effects of beach graveling and predator exclusion nets on epibenthic crustaceans on Puget Sound beaches differ according to the salmon species. In some cases, such as beach graveling in estuaries like Oakland Bay, an activity may be beneficial for all epibenthic-feeding fishes of concern. Impacts of graveling could be minimized by using thin layers of gravel and reducing the frequency of graveling. Best management practices may not be able to deal with some, notably larger scale, disturbances, suggesting the need to investigate potential mitigative options. Examples of this include loss of *Corophium* due to carbaryl application and impacts to eelgrass.

INFORMATION NEEDS

Estuarine management would greatly benefit from improved documentation of the type, scale, and magnitude of aquaculture's effects on estuarine communities relative to natural disturbance regimes. Many basic issues have yet to be resolved, such as: competitive or other amensalistic interactions between eelgrass and burrowing shrimp; postdisturbance successional patterns in intertidal communities exposed to both natural and anthropogenic disturbances; long-term responses to both natural disturbance and that induced by aquaculture; threshold responses by fish and wildlife to cumulative shifts in ecosystem habitat composition, the roles of rapidly expanding exotic species (including *Zostera japonica* and *Spartina alterniflora*) in modifying natural estuarine processes and disturbance regimes; and changes in community structure and basic benthic processes associated with densely cultivated bivalves. While some of these questions will require long-term study, understanding resilience to natural disturbance will enable us to better manage anthropogenic disturbance.

We think significant and rapid improvements in our assessment of the scope and scale of impacts is both possible and essential, and requires understanding inherent processes and mechanisms. We found it difficult to answer such basic questions as the intensity, frequency, and extent of intertidal habitat under various aquaculture regimes. For instance, while some oyster growers mow eelgrass because it is a nuisance, we were not able to determine the aerial extent, timing, and location of mowing. It is difficult to imagine a responsible assessment of cumulative effects in the absence of this type of information. An increased understanding of aquaculture as a disturbance within a mechanistic, multispecies, multifactor "ecosystem" context (Peterson 1993) would benefit estuarine management by allowing full consideration of ecological costs and benefits. Furthermore, aquaculture offers an approach to estuarine management that is very amenable to ecological experimentation (Peterson 1990, 1993), in which basic and applied science can be merged to provide the ecological information necessary to manage estuaries as sustainable ecosystems (Lubchenco et al. 1991). Rather than management by regulation, this approach is more likely to foster more socially-acceptable and economically-acceptable strategies (e.g., best management practices). The necessary goal is to obtain the scientific knowledge required for estuarine management on an ecosystem level before major community shifts or the collapse of exploitable populations occur, as has often been

the case with single-species fisheries management (Ludwig et al. 1993).

CONCLUSIONS

Based upon the limited information available for the Pacific Northwest, we found many potential disturbances resulting from aquaculture to be within the scale of natural variation. In addition, other changes in invertebrate assemblages involved species substitutions within the same general taxa. In terms of mobility-mode functional-group hypotheses (Brenchley 1981; Posey 1986a, 1987), the anthropogenic disturbance regimes are normally insufficient to modify interactions among functionally similar organisms. This is particularly the case with smaller epibenthic crustaceans; clam culture and oyster culture slightly modified habitat structure but not functional group or community diversity. If consequential at all, the management implication of these changes involve issues of the cumulative impacts as a function of the spatial and temporal scales of the aquaculture activity, and the costs and benefits to potentially impacted resources.

Large-scale disturbances, such as those associated with some intensive oyster practices, may induce chronic shifts in the benthic community by removing or reducing the influence of community dominants such as eelgrass or burrowing shrimp, and altering the apparent amensalistic relationship between them. However, disturbance to the larger ecosystem cannot be assessed without: a much greater understanding of habitat associations and disturbance tolerance of noncultured species; the cumulative response of the system at the actual scale of aquaculture disturbance rather than the scale of small experimental plots; and the trade-offs between benthic communities being modified and those impacted by aquaculture activities, both of which have valid ecological, economic, and cultural value. At present, we are not equipped with the essential tools required to understand these complex interactions, particularly at the ecosystem level. We suggest that an important initial step toward resolving this predicament would be development of conceptual models of ecosystem interactions among important estuarine processes and communities that can both incorporate natural and anthropogenic disturbance and be scaled across an estuarine ecosystem.

Conflicts among resource-dependent industries and other socioeconomic concerns such as tourism require management of environmental effects at the ecosystem rather than the site level (Folke and Kautsky 1989). In most cases, understanding the disturbance nature of intertidal aquaculture is no different than assessing the impact of increased

loading of organic wastes and other chemicals (e.g., antibiotics) from net pen and pond culture. Information from baseline or reference conditions, relevant physicochemical processes (e.g., flushing rates, source and sink processes), and temporal and spatial variation are critical to predicting the scope of impacts and the ecosystem response (Pillay 1992).

ACKNOWLEDGMENTS

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