



Review article

The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries

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ABSTRACT

Aquaculture is viewed as a potential mechanism to meet the growing demand for seafood around the world. The future of bivalve shellfish aquaculture in the U.S. hinges on sustainable practices on the part of industry and a more consistent regulatory regime. Bivalve shellfish aquaculture is a recent practice relative to its history in other countries, beginning in the late 1800s along the U.S. West Coast where it is now well established with farm raised product utilizing land-based hatcheries and grow-out directly in numerous estuaries. Bivalve shellfish aquaculture can be viewed as a disturbance which modifies the estuarine system in three ways: 1) changes in material processes – bivalves process food and produce wastes; 2) addition of physical structure – aquaculture introduces the cultured organisms and in some cases a physical anchoring structure; and 3) pulse disturbances like harvest and bed maintenance disturb sediments, remove species in addition to the cultured organisms themselves, and change resource or habitat availability. In U.S. West Coast estuaries, water column and sediment nutrient concentrations are relatively high and influenced by large tidal exchange and proximity to deeper nearshore ocean waters where upwelling controls production during summer months. Bivalves are unlikely to influence material processes except at local bed scales in these systems, although estuary-wide effects could appear as the fraction of cultured area rises or in poorly flushed bays. Bivalve culture clearly modifies estuarine habitat at local community and at landscape scales and effects are most often evaluated against existing structured habitat in the form of submerged aquatic vegetation. Individual activities act as pulse disturbances and the recovery of eelgrass (*Zostera marina*) to pre-disturbance levels is variable (<2 to >5 years). The extent of disturbance depends on the aquaculture practice and the distribution of eelgrass reflects a balance of space competition, pulse disturbance and recovery, and is therefore at dynamic equilibrium on aquaculture beds. Structure provided by aquaculture appears functionally similar to eelgrass for small benthic infauna and mobile epibenthic fauna while use of aquaculture as habitat by larger more mobile invertebrates and fish depends on mobility and varies with life-history stage and taxon being evaluated. Scale seems a very important management consideration and further research at estuarine landscape scales, especially for habitat use by important invertebrates and fish, may prove useful in designing and implementing best management practices. Though local and short term effects from aquaculture are clearly evident in U.S. West Coast estuaries, bivalve aquaculture does not remove area from the estuary or degrade water quality like other anthropogenic influences, and thus has not been implicated in shifts to alternate states or reduced adaptive capacity of the larger ecological system.

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1. Introduction

Aquaculture is increasingly viewed as a potential mechanism to meet the growing demand for food from the sea (Costa-Pierce, 2002), particularly as landings from world marine capture fisheries have plateaued (Brugere and Ridler, 2004; Muir, 2005). Although bivalve shellfish aquaculture represented only 10% of the world volume of fishery production in 2003, it represented 26% of world aquaculture production and 18% of world economic value (Lovatelli, 2006; Subasinghe, 2006). Bivalve shellfish production (both capture and aquaculture) has increased rapidly over the last 50 years from 1 million tonnes in 1950 to 13.2 million tonnes in 2003. However, 66% of that production is from China alone, whereas the U.S. produces less than 1% of the world's shellfish and leads the world in bivalve shellfish imports. Although domestic U.S. production is rising, concerns about environmental impacts currently constrain the U.S. industry, perhaps more substantially than in places like China, Japan and Southeast Asia where aquaculture has been a dominant and culturally accepted part of the coastal aesthetic for centuries (Kurokura, 2004; Costa-Pierce et al., 2005). The future of U.S. bivalve aquaculture hinges on sustainable mariculture practices on the part of industry and a more consistent regulatory regime, both of which were recently recognized as priorities by the U.S. Commission on Ocean Policy and the National Oceanic and Atmospheric Administration (USCOP, 2004; NOAA, 2006). Accomplishing these related goals will require an enhanced federal research program, however substantial research exists to help inform best practices and improve management decisions. In this review, we present an overview of the ecological issues associated with culture of clams and oysters in estuaries along the West Coast of North America.

Bivalve shellfish aquaculture in the U.S. is a recent practice relative to its history in other countries, beginning in the late 1800s with transfers of oysters (*Crassostrea virginica*) among East Coast estuaries and to West Coast estuaries as native populations were overfished (Baker, 1995; Lindsay and Simons, 1997; MacKenzie and Burrell, 1997). Today, farmed bivalves derive primarily from the West Coast; for instance, Washington state contributed 69% of U.S. production in 2002 (USDA, 2002 Census of Agriculture). However, the bulk of U.S. product still comes from capture fisheries along other coasts, where estuaries are larger, coastlines longer, and stocks of offshore clams newly accessible (Serchuk and Murawski, 1997). Contributions from these fisheries have declined recently, due in part to disease and overharvest in Chesapeake Bay, and a series of hurricanes along the U.S. Gulf Coast, yet the outlook for bivalve aquaculture is strong along all U.S. coastlines particularly given rising domestic demand and strong export markets in Asia (Harvey, 2006).

At the same time, bivalve shellfish aquaculture is experiencing increased regulatory scrutiny in the U.S. Human population density is rising along the coast, so more people are aware of aquaculture activities. Further, the cumulative effect of human activities now

threatens estuarine habitat, water quality and native species. On the East Coast, much of the concern focuses on anthropogenic nutrient inputs, eutrophication, and other industrial pollutants (Kemp et al., 2005; Paerl et al., 2006; Smith et al., 2006). West Coast estuaries have been impacted by fecal coliform contamination and eutrophication in areas of Puget Sound, but the smaller outer coast estuaries have experienced greater change from introduced species and freshwater diversion and impoundment (Emmett et al., 2000; Kareiva et al., 2000; Borde et al., 2003; Thompson, 2005). While a number of U.S. federal, state, and local regulations address aquaculture activities, the most recent nexus for federal action comes from the U.S. Army Corps of Engineers (ACOE), which asserts jurisdiction under the Clean Water Act (Section 404) and the Rivers and Harbors Act (Section 10). In March 2007, the ACOE issued a new nationwide permit for shellfish aquaculture which in turn requires consultation with the US Fish and Wildlife Service (USFWS) and the National Oceanic and Atmospheric Administration (NOAA) for their regulatory authority under the Endangered Species Act (ESA) and Essential Fish Habitat (EFH) provisions of the Magnuson Stevens Fishery Conservation and Management Act.

Because the “best available science” with which these agencies have chosen to address regulatory issues is limited, especially for aquaculture on the West Coast, the agencies have tended to be very cautious about perceived impacts to habitats and/or communities of estuarine organisms that have been studied in greater detail elsewhere. Perhaps the best example is simply not permitting or requiring mitigation for aquaculture activities in areas where submerged aquatic vegetation is present, due to its recognized importance to fish and invertebrates elsewhere and a federal goal of “no net loss of wetlands” that is generally applied to any activity in these environments. This “precautionary” approach has directly affected existing aquaculture operations in California and Oregon, where growers have been forced to abandon historic culture areas or switch to off-bottom culture, particularly in areas where seagrasses are present (Chew, 2001; Rumrill and Poulton, 2004). A federal review is currently underway by ACOE and NOAA to determine how the laws discussed above will be administered on a nationwide basis. Commercial shellfish growers have taken a pro-active role in this issue by developing their own environmental management system, codes of practice and a regional research plan (PCSGA, 2001; PSI, 2005). This scientific review is a response to the need for establishing a baseline of relevant scientific information to inform impending management decisions.

In this review of the role of bivalve mariculture in estuarine ecosystems, we use an ecological framework that describes aquaculture practices as a disturbance (c.f. Simenstad and Fresh, 1995). We adopt the definition of disturbance used by Pickett and White (1985): “a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment”. In this context

disturbances vary in their spatial scale, frequency, and intensity, which are relevant, respectively, to bed size, crop cycle, and type of aquaculture activity. We qualitatively distinguish “pulse” (short discrete events) from “press” disturbances (longer-lasting chronic events), despite their subjective definitions that imply a difference in the pace of the response (Glasby and Underwood, 1996). Nevertheless, the distinction is useful in considering, for instance, the effects of the farmed organisms, which are regularly present (press disturbance), and the effects of harvest operations, which occur periodically in the crop cycle (pulse disturbance). Disturbance has been viewed as a key process influencing marine benthic community dynamics for several decades (Sousa, 2001). Indeed, natural disturbances are essential components in the maintenance of community structure in some ecosystems (e.g. fire in many terrestrial ecosystems), even though they can have immediate negative effects on the abundance of some species. Anthropogenic disturbances may mimic such natural disturbances, although multiple, novel perturbations can exceed a system’s capacity to maintain its characteristic state (Sousa, 1984; Paine et al., 1998). This capacity to recover, or resilience (Holling, 1973), depends on such factors as the extent of the disturbance relative to the mobility of key species, and the frequency of disturbance relative to generation time (Paine et al., 1998; Peterson et al., 1998). Recent ecological literature suggests that the likelihood of regime shifts to alternate states can increase when anthropogenic disturbance causes reduced “ecological” resilience (Gunderson, 2000; Folke et al., 2004; Scheffer et al., 2005; Groffman et al., 2006; Walker et al., 2006; Levin and Lubchenco, 2008). Using “disturbance” as a descriptor in a management context may involve a perception that disturbances are “negative”. This is true only if the species of interest has “positive” value to the manager and the disturbance causes loss. Here, we describe aquaculture disturbance effects on species and ecosystems, but leave positive or negative value judgments to readers and managers.

Bivalve shellfish aquaculture influences the system in three primary ways: 1) material processes – bivalves process food and

produce wastes; 2) physical structure – aquaculture introduces the cultured organisms themselves and in many cases a physical anchoring structure; and 3) pulse disturbances – harvest activities, in addition to some bed maintenance practices, can remove species in addition to the cultured organisms themselves, and change resource or habitat availability (Fig. 1). These influences occur on the time scale of the crop cycle (1–6 years, depending on area, method, and species) and do not include such longer-term changes as the introduction of non-native organisms during imports for aquaculture. Introduction of non-native species is an important management issue, particularly when they become invasive, but aquaculture and other vectors for marine invasions have been reviewed elsewhere (Gruet et al., 1976; Carlton and Mann, 1996; McKindsey et al., 2007; Minchin, 2007), and regulations and practices have changed to reduce the role of aquaculture imports in homogenizing biota (e.g. ICES Code of Practice on the Introductions and Transfers of Marine Organisms, ICES, 2005).

Our focus is on the intertidal culture of bivalve mollusks in estuaries along the West Coast of North America, particularly oysters because of the great spatial extent of estuarine area devoted to their culture and relatively large amount of research conducted to date. Although a similar review was conducted by Simenstad and Fresh (1995), substantial progress has been made toward quantifying the role of bivalve aquaculture in the estuarine environment since that time. Our intent is not to repeat their earlier effort, nor provide an exhaustive bibliography, but instead to update with new results and place in context with recent ecological literature from outside the U.S. West Coast. We begin with sections highlighting why these West Coast estuaries are distinct and how bivalves have been and are currently cultured there. Material processing, physical structure, and pulse disturbance associated with some aquaculture practices represent three interrelated aspects of the ecological role of shellfish aquaculture. Each topic is considered in its own section, first with generalizations from research worldwide, and then a summary of

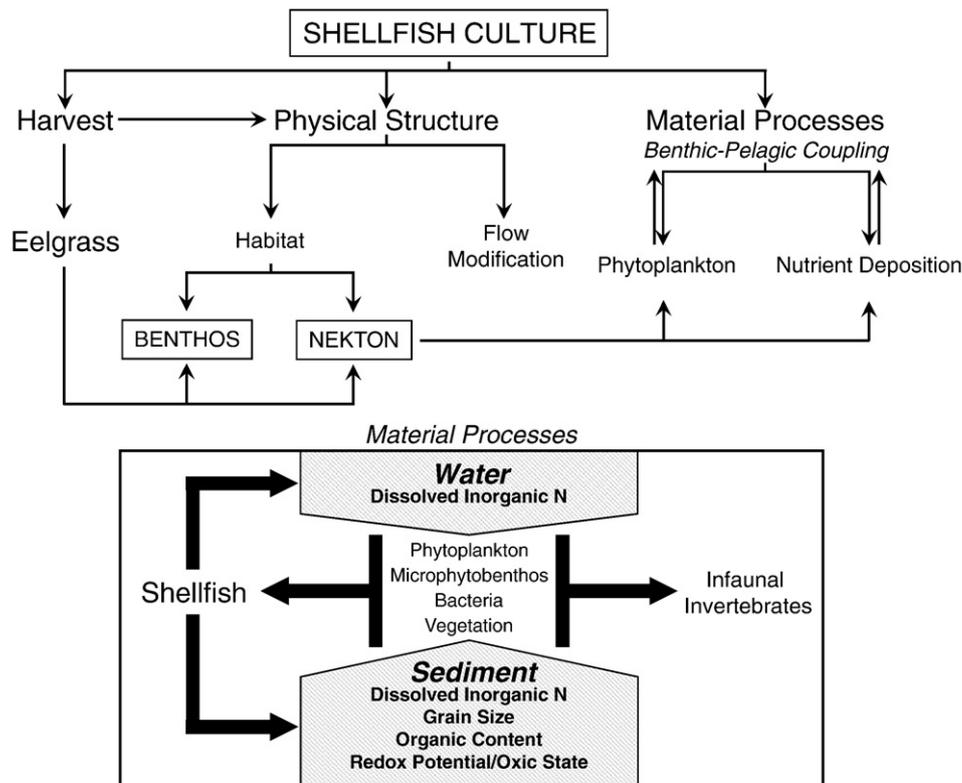


Fig. 1. Conceptual diagram of 3 pathways of shellfish aquaculture interaction with the environment. This simplistic view is of course more complex when broken down into component parts such as those for material processes including both benthic pelagic coupling and biodeposition (inset).

results from studies on the West Coast of North America in particular. In many cases, the evidence from West Coast estuaries aligns well with international perspectives; in some cases, the characteristics of West Coast estuaries lead to different ecological roles of shellfish aquaculture than have been demonstrated elsewhere; and finally, in most cases, the relatively nascent area of research on environmental impacts means that the picture for West Coast estuaries remains incomplete. In the final section, we address important research gaps, particularly at the landscape level that remain to be filled in order to make sound management decisions, though we recognize that such decisions clearly involve social and economic criteria as well.

2. Characteristics of West Coast estuaries

The major shellfish-growing areas on the West Coast of the U.S. include small coastal estuaries in California, Oregon, and Washington, as well as Puget Sound, which is a deep fjord extending several hundred km inland. Similarly, in British Columbia, Canada, bivalve aquaculture occurs both in small sounds on the west side of Vancouver Island and within the Strait of Georgia. Alaska's shellfish aquaculture industry is in its infancy but has grown markedly and oyster culture occurs primarily in remote geographic locations within areas like Kachemak Bay and Prince William Sound (Harrington, 2005; Oliveira et al., 2006). Four bivalve species contribute 99% of production from aquaculture in this region with Pacific oysters (*Crassostrea gigas*) representing 89%, and Washington leads production on a per-state basis, with production split about evenly between outer coast estuaries and Puget Sound (Table 1). West Coast estuaries have three general characteristics that set the context for aquaculture: they are geologically young and small; they have substantial oceanic influence; and they harbor distinct and relatively species-poor ecological communities. We treat each of these issues in turn.

Estuaries on the West Coast of North America are geologically young and relatively small compared to other well studied estuarine systems like Chesapeake Bay, but comparable in size to other shellfish-growing areas (Table 2). Only small remnants of the larger estuaries once present along the U.S. Pacific Coast in the Miocene and Pliocene epochs remain, due to subsequent uplift of the nearby landmass and estuarine infill (Jacobs et al., 2004). Further disturbances and oscillations due to glaciation and sea level change have subjected these estuaries to frequent flooding and emptying due to their small size (e.g. subsidences of 0.5 to 2 m have occurred multiple times with tectonic events in the last 7000 years (Atwater, 1987; Hagstrum et al., 2004). Combined with a relatively steep elevation gradient nearby, this causes these estuaries to provide much more spatially restricted and less stable environments than their larger counterparts on the Atlantic and Gulf Coasts. On the other hand, it would be incorrect to consider all of the region's estuaries as identical in abiotic features: substantial variation occurs in climate, mesoscale oceanographic features, and bathymetry, especially along the wide latitudinal range stretching from Alaska to California. Mesoscale oceanographic features establish faunal discontinuities (e.g. Cape Mendocino, Point Conception, Columbia River plume). Bathymetry varies because

estuaries have formed at drowned river valleys (small coastal estuaries) and in deep fjords (especially Puget Sound and the Strait of Georgia; Emmett et al., 2000). Human impacts also vary regionally, for instance San Francisco estuary in California experienced substantial shoreline development, urbanization, and tidelflat "reclamation", which caused severe water quality impairment and abandonment by the oyster industry in 1939 (Barrett, 1963) as have other smaller estuaries in Southern California (Pitman, 1995). Smaller coastal estuaries of Northern California, Washington and Oregon generally have lower human population densities than does the Puget Sound trough, where water quality problems have also been more pervasive (Glasoe and Christy, 2004).

West Coast estuaries experience pronounced effects of the nearshore coastal ocean (Hickey and Banas, 2003). Coastal estuaries lie along an upwelling coast, and mesotidal conditions, combined with small size and extensive intertidal flats, contribute to substantial tidal exchange with the ocean (Table 2). For instance, Willapa Bay, Washington can exchange nearly half its volume during a single spring tide and the tidal exchange is about 40% in Coos Bay, Oregon. Even Puget Sound, due to the influx of ocean water at depth, shows signs (salinity, carbon) of ocean influence throughout its length (Babson et al., 2006; Ruesink et al., in prep). In addition, freshwater input is restricted during summer due to a Mediterranean climate pattern of winter rain and summer drought to the extent that smaller estuaries in California are hypersaline lagoons (Largier et al., 1997). Thus terrestrial inputs are generally less important for food webs than in other estuaries, because winter inputs coincide with low temperatures that limit productivity. Nevertheless local effects of rivers and small streams have been demonstrated in the riverine region of both Willapa Bay and smaller coastal estuaries in summer (Ruesink et al., 2003; Rumrill and Sowers, 2008). Winter inputs have been studied in San Francisco Bay where the North Bay shows evidence of terrestrially driven production despite anthropogenic water diversion (Thompson, 2005). Overall, oceanic conditions greatly influence both primary and secondary production within these systems (Roegner et al., 2002; Ruesink et al., 2003). Although the Mediterranean climate pattern ameliorates two types of natural disturbances with strong effects elsewhere in the U.S (winter ice in Northeast estuaries and hurricanes on the Southeast and Gulf Coasts), shallow intertidal flats in West Coast estuaries and extreme tidal exchange may nevertheless result in severe pulse disturbances from winter storms.

Although the continental shelf fauna along the West Coast is diverse, estuaries are relatively species-poor in a number of functional groups, possibly as a result of their comparatively short geologic history. We suspect that this short list of native species contributes to: 1) the availability of few native bivalves suitable for aquaculture, and therefore the adoption of primarily non-native species, 2) small numbers of estuarine-dependent fishes, and 3) "empty niches" for high-impact invasions. Cultured species in West Coast estuaries are predominantly non-native and have developed self-sustaining feral populations in some areas. This dependence on non-native bivalve species makes the U.S. West Coast similar to Europe (where Pacific oysters and Manila clams are also introduced and cultured), and different from the rest

Table 1

Yields (thousand pounds) by bivalve species from the West Coast of North America aquaculture in 2005 (from PCSGA, 2006; BC Ministry of Environment, 2006).

	Alaska	British Columbia	Washington	Oregon	California
Major growing areas	Kachemak Bay, Prince William Sound, Southeast Coast	Baynes Sound, Sunshine Coast, Cortez Isl., W. Vancouver	Willapa Bay, Grays Harbor, North Puget Sound, south Puget Sound	Coos Bay, Tillamook Bay	Humboldt Bay, Tomales Bay, Drakes Estero
<i>Crassostrea gigas</i> (Pacific oyster)	920	17,638	77,000	6290	10,000
<i>Ruditapes philippinarum</i> (Manila clam)	41	4188	8500		14
<i>Mytilus galloprovincialis</i> (Mediterranean mussel)	3		2100		600
<i>Panopea abrupta</i> (geoduck clam)			850		

Table 2

Comparison of system characteristics of several estuaries in Europe where aquaculture has been studied in detail, Chesapeake Bay, and U.S. West Coast estuaries.

Estuary	Type and ave. depth	Physical conditions	Residence time	Development and anthropogenic disturbance	Bivalves	Area total/ intertidal	Biomass, aquaculture area	References
Thau Lagoon, France	Lagoon with two small openings 4.5 m	Low wind, small tidal amplitude <1 m	5 months	Two towns	Oysters on longlines (80%), mussels (20%)	75 km ² / <1 km ²	12,000 t harvested, 14–20,000 t present, 15 km ²	De-Casabianca et al. (1997), Souchu et al. (2001), Gangnery et al. (2003), Mazouni (2004), Mesnage et al. (2007), Metzger et al. (2007)
Sacco di Gorro, Italy	Lagoon with two 900 m openings 1.5 m	FW flow regulated	1–25 days	Towns, flow highly managed with dredging	Clams, mussels	26 km ² / 0 km	15,000 t clams 1000 t mussels harvested, 8 km ²	Viaroli et al. (2003), Melia and Gatto (2005), Nizzoli et al. (2006), Marinov et al. (2007)
Marennes Oleron, France	Bay w/ Charente and Gironde Rivers 5m	3 m tidal range, low river flow, wind important	<10 days	Town, riverine nutrient influence	Oysters on trestles	136 km ² / 82 km ²	30,000 t harvested 100,000 t present, 32 km ²	Raillard et al. (1993), Bacher et al. (1998), Gouleau et al. (2000), Leguerrier et al. (2004)
Chesapeake Bay, VA and MD	Drowned river valley, 8 m	Very large rivers (e.g. Susquehana) small tidal amplitude (0.7 m)	22 days	Large cities and towns, dredging	Clams, native oyster fishery	9900 km ²	940,000 t oysters in their heyday	Newell (1988), Gerritsen et al. (1994), Cerco and Noel, 2007 Brooks (2000)
Totten Inlet, Puget Sound, WA	Portion of fjord 10 to >100 m	6 m tidal range, limited FW input	10 to 11 days	Rural, many waterfront residences	Clams, oysters, mussels and geoducks	24.7 km ² / 0.85 km ²	1136 t oysters, clams and mussels	Hedgepeth and Obrebski (1981), Hickey and Banas (2003), Ruesink et al. (2006), Banas et al. (2007)
Willapa Bay, WA	Bay w/ relatively small rivers, 3.2 m	Low river flow, tides and wind most important, 1.9 m tidal range, Columbia River influence	6–54 days at upper end	Towns, diked tidelands	Oysters on bottom and longlines	358/ 227 km ²	1468 t harvest, 46 km ²	Hickey and Banas (2003), Ruesink et al. (2006), Banas et al. (2007)
Coos Bay, OR	Bay w/ relatively small rivers, 4 m	Low river flow, tides and wind important, 1.7 m tidal range	10–40 days	Small cities, lumber mills, diked tidelands, dredging	Oysters on bottom and longlines	34 km ² / 3.8 km ²	17 t	Hickey and Banas (2003), Rumrill (2006)
Humboldt Bay, CA	Bay w/ very small creeks, almost lagoonal, 3.5 m	Very low river flow, tides and wind important,	5 months in North Bay	Small Cities, dredging	Oysters on longlines	67/21 km ²	454 t, 260 ha	Barnhart et al. (1992), Rumrill and Poulton, 2004
Baynes Sound, British Columbia	Coastal portion of fjord, w/ Courtenay River and small creeks entering small embayments	Vertical stratification, of water column due to freshwater input and protection from wind and surface mixing	2 months for bottom water	Small towns	Oysters on bottom and deepwater rafts, clams with netting, wild clam harvest	87 km ²	850 t clams, 2510 t oysters, 458 ha	Jamieson et al. (2001), Carswell et al. (2006)

of the U.S. and Asia (Ruesink et al., 2005). West Coast estuaries contain fewer species of estuarine-dependent fish and invertebrates, particularly those that use estuaries as nurseries, than their U.S. East and Gulf Coast counterparts and display latitudinal trends in both abundance and diversity (Percy and Myers, 1974; Horn and Allen, 1976; Haedrich, 1983; Monaco et al., 1992; Nelson and Monaco, 2000). This could simply be due to small estuary size, but also the relatively large proportion of intertidal area, lack of significant freshwater input and their short geologic history. Similar latitudinal differences between estuaries and less diverse fish communities in small shallow estuaries have also been found in European, Tasmanian, South American, Australian and South African estuaries (Potter and Hyndes, 1999; Edgar et al., 2000; Araujo and de Azevedo, 2001; Pihl et al., 2002; Harrison and Whitfield, 2006). The mid- to high intertidal flats of West Coast estuaries are typically unstructured. High marsh occurs only above mean higher high water in West Coast estuaries, and seagrass (native eelgrass, *Zostera marina*) occurs around mean lower low water (Borde et al., 2003; Thom et al., 2003). With the exception of some relatively steep gravel and cobble beaches in fjords from Puget Sound, Washington north to Alaska, nearly all intertidal aquaculture activities take place on low gradient mud and sandflats, habitats that naturally have little structure in the region, except where aquaculture overlaps with native eelgrass. However some unwanted species have also entered this zone, forming structure in what is essentially an “empty niche”. These include several species of cordgrass (*Spartina* spp.) which have prompted multi-million dollar control efforts and, from British Columbia to northern California, an introduced seagrass, *Zostera japonica* (Daehler and Strong, 1996; Feist and Simenstad, 2000; Bando, 2006; Ruesink et al., 2006; Rumrill, 2006). Although species-poor in general, West Coast estuaries harbor several species of Pacific salmon (*Oncorhynchus* spp.), anadromous fish that spend variable amounts of their early life history in estuaries. Due to their cultural importance and longstanding fisheries, salmon drive substantial management activity and many subpopulations of salmon are extinct or listed as threatened or endangered under the US Endangered Species Act. Although the declines are likely from a variety of causes extending from freshwater to the ocean (Kareiva et al., 2000; Ruckelshaus et al., 2002; Good et al., 2007), loss and/or substantial modification of estuarine habitat may not be compatible with salmon recovery.

3. Historical fisheries and current farming practices

The most widely cultured bivalves in the United States are oysters, clams and mussels. Because of the presence of shells in middens, it is clear that bivalves have been harvested from North American estuaries for thousands of years (Trigger, 1986; Cannon, 2000). Coincident with European colonialism, extensive harvest of native oysters (*Ostrea lurida*) on the West Coast began in the mid-1800s (Baker, 1995), slightly after similar activity (for eastern oysters, *C. virginica*) along the Atlantic and Gulf Coasts in the 17th and 18th centuries (Kirby, 2004). Initial harvest implements included sailing vessels, poled bateaux, and a variety of hand tools (e.g. tongs), followed by dredges. Natural beds were gradually depleted on both U.S. coasts, in part due to the lack of return of shell material for natural recruitment (Kirby, 2004; Ruesink et al., 2005). When the native Pacific Coast oyster declined due to overharvest in the late 1800's, eastern oysters (*C. virginica*) and later Pacific or Japanese oysters (*C. gigas*) were transplanted to estuaries along the U.S. West Coast (Collins, 1892; Townsend, 1896; Steele, 1964; Sayce, 1976; Lindsay and Simons, 1997; Robinson, 1997; Shaw, 1997). From at least 1928 until 1977 (except during WWII), “seed” oysters were shipped from Japan to the U.S. West Coast annually for transplant. Additionally, after Pacific oysters established naturally-reproducing populations, some local production was possible. Waters were warm enough for “natural” spawning and

setting to take place in Pendrell Sound and Ladysmith Harbor in British Columbia, and Dabob Bay and Willapa Bay, Washington (Scholz et al., 1984; Quayle, 1988).

With the advent of hatchery technology in the early 1980's (Nosho and Chew, 1991), oyster aquaculture along the West Coast of the U.S. became a completely integrated farming operation (see Conte et al., 1994 for a detailed description). Hatcheries are now essential to oyster aquaculture in Alaska, Oregon, and California, and contribute substantially in Washington and British Columbia, although naturally-set oysters continue to be incorporated when they are available. Most production involves *C. gigas*, but several other oyster species are also cultivated: *C. virginica*, *C. sikamea*, *C. ariakensis*, *Ostrea edulis*, and the native oyster *O. lurida*. In hatcheries, adult broodstock are conditioned and induced to spawn. Larval oysters are fed cultured phytoplankton until they are competent to settle and attach to a substrate (Muller-Feuga, 2000). This substrate is either pieces of shell (cultch) or ground shell or sand (cultchless). When the oysters are moved into estuaries, they are grown utilizing a variety of methods including bottom culture, floating bags, rack and bag systems, long lines and trays. In bottom culture, cultch with attached oysters is placed directly on intertidal (generally <0.6 m MLLW) and shallow subtidal bottom where it is left until the oysters reach market size, usually in one to three years depending on location and temperature. In Willapa Bay, where oyster growth varies substantially by area, oysters may be seeded to one area, allowed to grow for a period of one to two years and then transplanted to a second area called a fattening bed for final growth. Beds may also be harrowed with implements fashioned after the English pasture harrow (Sayce and Larson, 1966) to bring oysters back to the surface and break up clusters. Oysters are harvested (or collected for re-laying) from bottom culture by hand or with mechanical or suction dredges. In long line culture, seeded cultch is strung on lines or ropes that are suspended from stakes or rails and harvest is usually by hand. Cultchless oysters are often grown in high-density polyethylene (HDPE) or polypropylene mesh bags placed on the bottom, suspended off the bottom on racks, or placed in floating bags attached to longlines (Conte et al., 1994). Although not a focus of this review, suspended culture is typically used in areas that are relatively deep such as Puget Sound and especially British Columbia, Canada: seeded cultch is strung on lines or cultchless oysters are placed in trays or lantern nets, and these are suspended from floats. After harvest, single oysters are generally destined for the half shell market, and oyster clusters are either separated into singles, or processed at a shucking plant where the meats are packaged in containers for sale.

Oyster aquaculture contends with several pest species, most of which are predators or competitors and controlled by hand removal (Buhle et al., 2005). However, one species deserves special attention because its control involves the application of a chemical pesticide. Burrowing shrimp (*Neotrypaea californiensis*) are native deposit-feeders that bioturbate sediments up to 1 m in depth. At high densities, they preclude on-bottom oyster culture because the oysters are smothered or sink due to disturbance of the sediment by the shrimp. Since the 1960s, shrimp have been removed from oyster beds through the application of carbaryl (Sevin™), a general arthropocide (Feldman et al., 2000). Its use is now only legal in Willapa Bay and Grays Harbor, Washington where about 170 ha and 60 ha respectively (4% of the cultivated area and less than 1% of the tidelflat in Willapa Bay) are treated by aerial application from a helicopter each year. Many species in addition to shrimp are killed by the pesticide, but the longer-term changes, including appearance of eelgrass, derive from the removal of shrimp and addition of oysters (Dumbauld et al., 2001; Dumbauld and Wyllie-Echeverria, 2003; Dumbauld et al., 2004). This pesticide is scheduled to be phased out of use in these estuaries by 2012, but the most effective alternative method of shrimp control discovered to date may also be chemical.

The West Coast harbors several native clams of historical importance to subsistence and commercial fisheries. These include: butter clams (*Saxidomus giganteus*), littlenecks (*Protothaca staminea*), horse clams or gapers (*Tresus capax* and *T. nutalli*), and geoducks (*Panopea abrupta*). On outer coast sandy beaches, razor clams (*Siliqua patula*) are fished commercially and recreationally (Lindsay and Simons, 1997). Eastern softshell clams (*Mya arenaria*) provided a small commercial fishery after their introduction from the East Coast in the late 1800's, but only during an initial post-invasion "boom" (Palacios et al., 2000) and more recently in Puget Sound. Clam aquaculture currently focuses on two species, one introduced (*Ruditapes philippinarum*, Manila clam) and one native (*P. abrupta*). Manila clams apparently arrived from Asia in the 1930s as a hitchhiker with oyster seed (Quayle, 1941; Chew, 1990). Growth in production occurred when growers were able to "seed" areas with small clams produced in hatcheries, at about the same time (1970s–80s) that such techniques were developed for oysters. Farmed Manila clams produced in hatcheries are held in trays or upwellers during a nursery period before being planted in a growout area or placed in mesh bags for growout (Toba et al., 1992). Several techniques are employed to enhance ground for clam production. Growers sometimes add gravel or oyster shell (Toba et al., 1992; Thompson, 1995), which provides substrate for the attachment of naturally-settled clams and likely makes feeding more difficult by some predators. Plastic or nylon netting of varying mesh is also often placed over clam beds to reduce predation. Manila clam aquaculture tends to occur higher (0.6–1.2 m MLLW) in the intertidal than does oyster culture. Harvest of planted tideflats is generally with a hand operated rake to collect clams, which grow close to the surface, but some mechanized harvest methods have also been developed (B. Dewey, pers. comm.). Worldwide, Manila clams are grown in China and Korea where they are native (Zhang and Yan, 2006), and in Europe from Italy to Great Britain, where they are introduced (Chew, 1990; Spencer et al., 1997).

A second clam species, the geoduck (*P. abrupta*) has recently become important for aquaculture in Washington and British Columbia. Geoducks are very large clams (up to 3.25 kg whole weight, Goodwin and Pease, 1991; Hoffmann et al., 2000) that have provided a valuable subtidal fishery for several decades. As a fishery, clams are not planted, and "recovery" of harvest tracts depends on recruitment which has only recently been assessed over appropriate temporal and spatial scales (Orensanz et al., 2004). Aquaculture techniques have been applied primarily to intertidal flats and have achieved crop cycles of ca. 5–6 years since growth is fast during initial years and then slows (clams can grow to be well over 100 years old; Goodwin, 1976; Shaul and Goodwin, 1982; Hoffmann et al., 2000). Geoduck culture techniques continue to evolve with survival in the hatchery and growout phases being highly variable. Protecting the hatchery produced geoduck "seed" from predation and drying out at low tide is essential. To date growers have largely used nursery tubes made by cutting 4–6 inch diameter PVC pipe into foot long sections and partially embedding them in the sediment. Several small (1 cm) geoducks are added, and mesh is placed over the top to exclude crabs and predatory snails (Beattie, 1992). This mesh may cover tubes individually or extend over an array of many tubes, anchored only at the edges (more like anti-predator nets used for Manila clams). The tubes are removed after 1–2 years, at which point the geoducks have reached a size and depth that avoids most predators and precludes desiccation at low tide. The geoducks continue to grow for several more years before reaching market size (15 cm shell length, approx. 1 kg whole weight). Harvest methods have been borrowed from the capture fishery and involve loosening the sediment around each geoduck with low pressure but high volume seawater forced through narrow tubes (stingers); geoducks are then removed by hand.

4. Shellfish as filter feeders and material processors

When abundant, suspension feeding bivalve mollusks can serve as important links between benthic and pelagic processes (benthic

pelagic coupling) because they filter large volumes of suspended particles from the water column and eject them as both uningested pseudofeces and unassimilated feces which sink to the bottom (Newell, 2004). Bivalve aquaculture differs importantly from the culture of most finfish and crustaceans (Pohle et al., 2001; Crawford et al., 2003) in that cultured bivalves exploit naturally occurring phytoplankton at the base of the estuarine food chain, thus obviating the need for external feed inputs. For this reason, shellfish aquaculture does not result in additional nutrient loading, but rather, a transfer of nutrients from water column particles to benthic sediments in biodeposits, rapid nutrient cycling when dissolved inorganic nutrients are released into the overlying water, and a net removal of a portion of those nutrients when shellfish are harvested.

Particles filtered by bivalves range in size from bacterioplankton to less mobile zooplankton and include both living and non-living material, but most species are generally efficient at retaining material down to 3–5 μm (LeGall et al., 1997; Ward and Shumway, 2004; Prins and Escaravage, 2005; Lehane and Davenport, 2006; Lonsdale et al., 2007; Trotter et al., 2007). Bivalves can influence the community of plankton present via selective feeding favoring removal of picoplankton and phototrophic nanoflagellates over heterotrophic flagellates and diatoms in summer months at some locations (Bougrier et al., 1997; Wetz et al., 2002) but also feed on re-suspended microphytobenthos (Malet et al., 2007). Bivalves actively pump water through the gills and the particles are sorted on the ctenidia and labial palps. Capture efficiency increases non-linearly with particle diameter (Ward et al., 1998a). Captured particles are actively sorted by both size and quality (though the mechanism for the latter is not well studied; Shumway et al., 1985), and rejected particles become pseudofeces (Beninger et al., 1999). Oysters transport smaller phytoplankton to the dorsal ctenidial tract and detritus and larger particles to the ventral groove for sorting by the labial palps (Cognie et al., 2003). In contrast, particle sorting by mussels occurs primarily at the labial palps (Ward et al., 1997, 1998b). Oysters also tend to be able to cope with high seston loads by augmenting pseudofeces production, whereas clams and scallops lower their clearance rates as particle concentrations increase (Newell and Langdon, 1996; Defosse and Hawkins, 1997; Hawkins et al., 1998; Chauvaud et al., 2000). Finally some post-ingestive particle selection occurs in the stomach as the particle slurry moves across ridged sorting areas and pouches to the digestive diverticula (Cognie et al., 2001; Brillant and MacDonald, 2002, 2003). Assimilation efficiency varies with food source and how susceptible the particles are to enzymatic breakdown (Langdon and Newell, 1996). Some of the absorbed nitrogen is excreted as urine (primarily as NH_4). Both feces and pseudofeces are excreted by bivalves as mucous-bound aggregates with higher sinking velocity (up to 40 \times) than the ingested particles (Widdows et al., 1998). The particles gradually undergo a de-watering process and are incorporated into the sediment adding to the nitrogen and phosphorous pools (Deslous-Paoli et al., 1992; Hatcher et al., 1994). The feeding activities described here potentially allow bivalve shellfish aquaculture to alter larger material processes in the estuary in the following ways: water quality, sediment properties, and resources for primary producers indirectly through the release of inorganic nutrients. We treat each of these in turn.

4.1. Alteration of water quality

Measurable effects on water properties hinge on the filtration capacity of bivalves relative to the residence time of water in the estuary (Prins et al., 1998; Prins and Escaravage, 2005) – simplistically, longer residence times give suspension-feeders more opportunity to remove particles. This relationship is complicated however, not only by estuarine hydrography, but also because phytoplankton population growth, not just grazing, influences density, particularly if phytoplankton are supplied with readily available nutrients released

by the grazers themselves or by anthropogenic sources (Dame, 1996; Prins et al., 1998; Chapelle et al., 2000; Souchu et al., 2001; Mazouni, 2004; Asmus and Asmus, 2005). Also, clearance rates are difficult to estimate in the field (Riisgard, 2001), sensitive to seasonal variation, and only relevant to the volume of water accessible to the benthos which can be modulated by structure created by the bivalves themselves (Lenihan et al., 1996). The contribution of cultured bivalves to clearance is further obscured when they represent an unknown fraction of all suspension-feeders (Heip et al., 1995; Leguerrier et al., 2004; Pomeroy et al., 2006; Dubois et al., 2007; Putland and Iverson, 2007), though this has also been measured and models developed to quantify it in some places (Sauriau et al., 1989; Leguerrier et al., 2004; Grizzle et al., 2008; Sequeira et al., 2008). Although it represents a relatively small contribution (1% of the meat weight), nitrogen is also removed from the system when actively growing shellfish are harvested (Lindahl et al. 2005). Finally, even if one is able to assess and detect alterations in water quality due to the presence of farmed bivalves, questions regarding scale and relevance such as whether they “improve water quality” or “exceed the system’s carrying capacity” remain. We suggest that water clarity improvement will be more important in areas experiencing cultural eutrophication, and carrying capacity concerns will be informed by considering current relative to historic bivalve and other filter feeder densities.

Substantial work has been carried out worldwide on bivalve carrying capacity, especially via coupled biological–physical models (Dame and Prins, 1998; Gangnery et al., 2001; Sara and Mazzola, 2004; Duarte et al., 2005; McKindsey et al., 2006; Ferreira et al., 2007; Grant et al. 2008; Wang et al., 2008) because experimental work at the scale of whole estuaries is daunting. Several reports exist of bivalve growth rates declining as aquaculture densities increase over time, consistent with reduced phytoplankton densities available as food, particularly in areas such as lagoons with long water residence periods and/or shallow water column and high bivalve density often in three-dimensional culture systems (Rodhouse and Roden, 1987; Heral, 1993; Comeau et al., 2008). One recent monitoring effort documented the effects of removal of extensive oyster aquaculture from a eutrophic bay in Taiwan with mean chlorophyll levels and phytoplankton production being enhanced 4-fold in a less flushed portion of the bay (Huang et al., 2008). Invasive bivalves such as *Potamocorbula amurensis* in San Francisco Bay (Thompson, 2005), *Corbicula fluminea*

in the Potomac River (Cohen et al., 1984), and dreissenids in the Hudson River and Great Lakes (Strayer et al., 1999) also provide evidence of top-down control of phytoplankton. Finally, depletion has been documented at spatial scales of individual aquaculture operations, and sophisticated models have been developed to explore the effects of hydrography and bivalve configuration on seston depletion at this scale (Newell et al., 1998; Drapeau et al., 2006; Grant et al., 2007). The results of these models align well with actual measurements of particle concentrations, but they generally indicate little impact on water properties beyond the immediate “footprint” of the aquaculture operation (but see Grant et al. 2008).

Many aquaculture areas on the West Coast of North America remain relatively pristine, that is, they have experienced low levels of cultural eutrophication. Consequently, carrying capacity concerns may be more relevant than the ability of cultured organisms to ameliorate water quality in these areas, although aquaculturists themselves can clearly be beneficial as an effective lobby for continued low-impact shoreline development (Steele, 1964; Glasoe and Christy, 2004). The calculation of present relative to historic bivalve densities has not been carried out for many locations, but in Willapa Bay, Washington, *C. gigas* occurs at >2.5 times historic biomass of *O. lurida* (Ruesink et al., 2005); the difference in filtration rate is probably less because the smaller native oyster should have higher mass-specific filtration. Willapa Bay shows a gradient in phytoplankton concentration from the mouth to upper estuary, and three competing hypotheses involve physical mixing of rich ocean and poor river water along the estuarine gradient, longer residence time of water in the upper estuary, and grazing by oysters that are farmed, especially near the mouth of the bay. Overlaying oyster filtration on a circulation model indicates that phytoplankton concentration declines into the bay more than would be expected from simple mixing, and the extra loss is consistent with the capacity of cultured oysters to filter it out (Banas et al., 2007). Interestingly, this result is achieved even though a large fraction of the bay’s water (>80%) never moves over a shallow tidal flat and is not susceptible to filtration (Banas et al., 2007). Empirically, however, the water that moves across Willapa Bay’s tidal flats is measurably affected by cultured oysters growing there. Wheat et al. (in prep.) documented declines of about 10%/100 m in phytoplankton when tracking parcels of water across oyster beds on flood tides (Fig. 2), whereas water flowing across newly-planted beds or other habitat types showed no

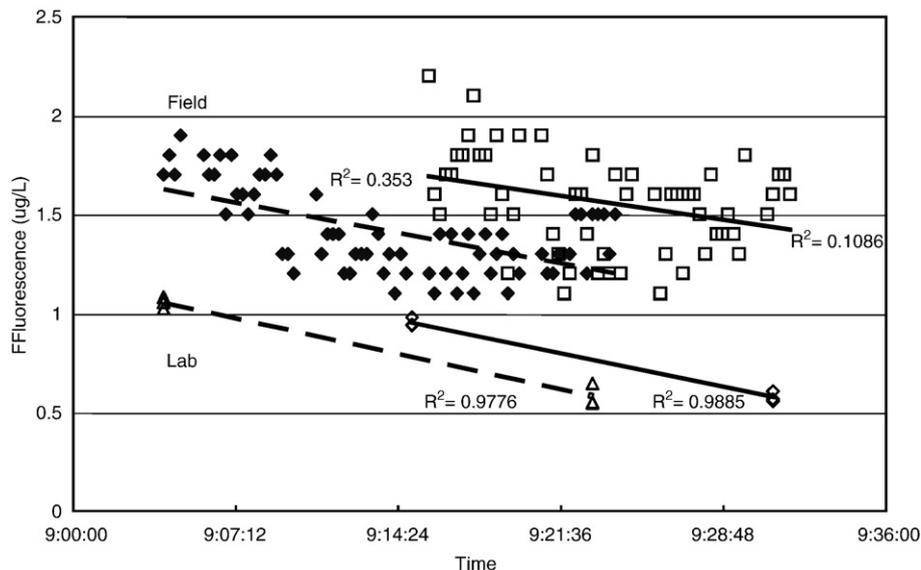


Fig. 2. Preliminary results from field surveys in Willapa Bay, Washington using drifting sensors (YSI® instruments) which moved over long-line oyster aquaculture areas and displayed a negative slope indicating phytoplankton (measured as chlorophyll *a* fluorescence) was being removed from the water column. Two separate drifts with instruments in the field are shown (top) and separate instrument calibration measurements taken with water bottles at start and end of drifts and measured on laboratory fluorometer (bottom).

such change. One West Coast area where public concern has been raised about aquaculture exceeding carrying capacity is in the southern end of Puget Sound, Washington. Interestingly, this is also one area where excessive nutrients from upland sources and some eutrophication have also been documented. However, the area of most extensive aquaculture (Tottem Inlet) maintains higher bivalve growth than elsewhere in Puget Sound (Ruesink et al., in prep.), and only local phytoplankton depletion around raft structures has been documented (Cheney, pers. comm). Overall, existing evidence from the West Coast confirms that cultured bivalves affect water properties, but the effect is largely evident at small spatial scales (except see Banas et al., 2007). While water quality is certainly impaired in some West Coast shellfish-growing areas, this is most often due to the presence of fecal coliforms which do not affect water clarity and eutrophication has not yet been described as a significant problem in most areas.

4.2. Alteration of sediment properties

As with water quality, measurable effects of bivalves on sediment properties hinge on the density of shellfish relative to water flow. In the case of sediment alteration, however, the effects of bivalves are expected to be quite local, and flow enters into consideration because of its role in dispersing biodeposits (Callier et al., 2006). Much of the work on sediment effects has been carried out in the context of suspended culture. The buildup of biodeposits under or within culture operations reduces grain size and increases organic content, which can reduce oxygen content (Rodhouse and Roden, 1987; Christensen et al., 2003; Nizzoli et al., 2006; Mesnage et al., 2007; Richard et al., 2007; Hargrave et al., 2008). Nitrogen content in sediments (porewater) is often also elevated (Kautsky and Evans, 1987; Deslous-Paoli et al., 1992; Hatcher et al., 1994; Giles and Pilditch, 2006), but the more important consequence is for nitrogen cycling. Rates of NH_4^+ flux from bivalve communities can be fairly high ($1\text{--}5 \text{ mmol N m}^{-2} \text{ h}^{-1}$, Dame et al., 1992; Giles and Pilditch, 2006), however burial of N and P and removal of N from the system via denitrification (Fig. 1) are also enhanced by deposition from bivalves (Kaspar et al., 1985; Kautsky and Evans, 1987; Hatcher et al., 1994). Denitrification requires adjacent layers of oxygenated sediments supporting nitrifying bacteria and anaerobic conditions that support denitrifying anaerobes (Newell et al., 2002; Newell et al., 2005). Further feedback comes from microphytobenthos, which can intercept dissolved organic nitrogen being regenerated from the sediments and produce oxygen which further alters sediment chemistry and/or can be used by bacteria at the sediment–water interface to maintain nitrification (Rysgaard et al., 1995). These biochemical pathways are challenging to measure and quantify at larger scales in the field, for instance due to the presence of other nutrient regenerators like nekton in salt marsh creeks (Haertel-Borer et al., 2004). Laboratory studies are hampered by inappropriate boundary layer flows which were shown to greatly influence microphytobenthos and thus nutrient regeneration in mesocosm studies (Porter et al., 2004). A difference in nutrient cycling has also been observed across species. For instance on-bottom farming of clams stimulates transfer of both organic matter and oxygen to the sediment due to bioturbation by these animals whereas suspended mussel culture results in only the former and thus reduced oxygen (Nizzoli et al., 2006). Thus clam farming results in more balanced benthic metabolism with net losses of nitrogen from the sediment. The multitude of factors and number of ecosystem processes influenced by shellfish and complexity of the interactions make modeling efforts attractive tools for examining ecosystem effects on nutrient cycling (Cranford et al., 2007).

In general, there do not seem to be any characteristics of West Coast estuaries that would cause expectations of sediment effects to differ from those reported elsewhere, however sediment chemistry and chemical fluxes are largely unexplored there. When oyster aquaculture and natural habitat types were surveyed in Willapa Bay,

the metabolic activity of aerobic microbes was lower in on-bottom oyster aquaculture, consistent with a larger contribution from anaerobes (Richardson et al., 2008), however no differences were found in sediment grain size, organic content, or oxidation–reduction potential. While these results may initially suggest weaker effects of cultured bivalves on sediment properties than have been observed in other systems, it is more likely that their effects were obscured in this comparative study by underlying sediment heterogeneity or the influence of local hydrodynamics. Indeed Rumrill and Poulton (2004) measured small-scale topographical alteration of sediment profiles directly beneath suspended long-line cultures of *C. gigas* in Humboldt Bay, California, and changes in sediment dynamics were most evident in experimental plots with high densities of oysters. Similarly experimental manipulation of oysters in Willapa Bay has produced sediment changes more consistent with those measured elsewhere: the addition of high-density oysters to small ($2 \text{ m} \times 2 \text{ m}$) plots in eelgrass reduced grain size and increased organic content relative to nearby controls (E. L. Wagner, unpubl. data). There was also evidence that oysters actually lowered ammonium concentrations in sediment porewater with one possible mechanism being rapid denitrification that occurs at the interface of organic and inorganic sediment layers created by biodeposition. In contrast, a similar experiment adding geoduck clams to small plots with eelgrass in Puget Sound resulted in slightly raised porewater ammonium concentrations, but grain size and organic content were apparently affected primarily by eelgrass and not the clams (Ruesink and Rowell, in prep).

4.3. Feedbacks to primary producers

The previous sections have addressed how bivalve feeding removes particles from the water and releases nutrients in two forms: packaged in biodeposits or dissolved into the water column and sediment porewater. These dissolved nutrients may stimulate the population growth of phytoplankton and benthic microphytobenthos (Kaspar et al., 1985; Swanberg, 1991; Mazouni, 2004; Asmus and Asmus, 2005; Sara, 2007). Microphytobenthos may be directly fertilized via biodeposition whereas phytoplankton may be either directly fertilized via ammonia release into the water or indirectly fertilized via re-suspension of biodeposits and/or stimulated nutrient recycling in the sediments (Fig. 1). Submerged aquatic vegetation and microphytobenthos may also benefit from improved light penetration if bivalves exert top-down control on phytoplankton (Phelps, 1994; Newell and Koch, 2004; Wall et al., 2008). Nutrients released by bivalves into sediment porewater can stimulate production of seagrasses, as documented for mussels growing with seagrass in Europe, Florida, and southern California (Reusch et al., 1994; Reusch and Williams, 1998; Peterson and Heck, 1999, 2001). In general an increase in sediment porewater ammonium toward optimal levels ($\sim 100 \mu\text{M}$) should enhance plant biomass and growth (Dennison et al., 1987; Hughes et al., 2004), although high levels of biodeposits could lead to toxic sulfide concentrations especially in already eutrophic areas (Sorokin et al., 1999; Stenton-Dozey et al., 2001; Holmer et al., 2005; Vinther and Holmer, 2008; Vinther et al., 2008). Aquaculture also has the potential to stimulate competitors with seagrass, for instance providing attachment sites for epiphytic macroalgae and enriching nutrients used by algae (De Casabianca et al., 1997; Thomsen and McGlathery, 2006; Vinther and Holmer, 2008; Vinther et al., 2008). Seagrasses tend to be negatively affected by both epiphytic algal growth and macroalgal blooms (Hauxwell et al., 2001; McGlathery, 2001; Hauxwell et al., 2003).

What evidence exists for West Coast bivalve aquaculture to affect primary producers through nutrient or light pathways? In studies unrelated to aquaculture, eelgrass shoot growth and depth distribution have been shown to be light limited in Pacific Northwest estuaries (Thom et al., 2008). The addition of fertilizer to sediments around eelgrass growing in Padilla Bay resulted in NH_4 in excess of $1000 \mu\text{mol l}^{-1}$ and

higher eelgrass shoot growth (approximately 0.5 cm/shoot/d; Williams and Ruckelshaus, 1993). Thus, to the extent that bivalves improve light availability or augment nutrient concentrations in sediment porewater, aquaculture could improve conditions for eelgrass growth. However total production of eelgrass was lower in aquaculture than in nearby eelgrass beds in Willapa Bay, due to a combination of reduced shoot density and smaller shoot size (Tallis et al., in press). The interaction has been explored experimentally in two additions of bivalves to eelgrass. On a per-shoot basis, eelgrass with geoducks grew faster than without (due to larger shoot size). The mechanism could be from a 20% enhancement of porewater ammonium, or from reduced intraspecific competition because eelgrass occurred at lower density in the presence of clams (Ruesink and Rowell, in prep.). In contrast, eelgrass with oysters grew slower than without (due to smaller shoot size). The plants may have been responding to an unexpected reduction in porewater ammonium associated with high-density oysters, but more likely were “clipped” by sharp shells (E.L. Wagner, unpubl. data). So far, the interaction between bivalves and eelgrass on the West Coast appears weak in terms of light or nutrient pathways (as opposed to strong effects via competition; see Section 5 below). Eelgrass growth responses to direct manipulations of light and nutrients have involved large changes in these drivers, whereas bivalves may not change the ambient levels so substantially. In any case, documented ambient porewater ammonium is close to the optimum for eelgrass growth in many of the region's estuaries, especially during summer months: Willapa Bay, Washington (80 μM , J.L. Ruesink, unpubl. data), Yaquina Bay, Oregon (60–170 μM and 750–2500 μM ; Larned, 2003; Kaldy, 2006, respectively), San Diego Bay, California (20–120 μM ; Reusch and Williams, 1998), south Puget Sound, Washington (50–90 μM ; Ruesink and Rowell, in prep.), and Padilla Bay, Washington (30–137 μM ; Williams and Ruckelshaus, 1993). Eelgrass growth appears consistently depressed below maximum when ammonium concentrations are below 40 μM (Dennison et al., 1987).

5. Press disturbance – shellfish aquaculture as structured habitat

Bivalve shellfish act as ecosystem engineers or foundation species by influencing habitat and resources available for other species (Jones et al., 1997; Bruno and Bertness, 2001). While engineering roles, such as the provision of complex hard substrate, are most obvious for oysters and mussels living above the substrate, all shell-producers including infaunal clams alter solute concentrations and their shells may contribute to surface structure after they perish (Palacios et al., 2000; Lehnert and Allen, 2002; Gutierrez et al., 2003). Ecosystem engineers have both positive and negative effects on ecological communities – they provide habitat and resources for some species, whereas other species may be displaced. Thus the effect of aquaculture involves both its “footprint” locally (for instance, percent physical cover within a small area) and regionally (for instance, density of farms), and its value for other species. Habitat “value” is not easily measured, as is evident in recent debates about “essential fish habitat” and “nursery habitat” (Able, 1999; Beck et al., 2001). Ideally, one is interested in how such habitats influence production of other species, but in practice lower-level indicators are generally measured: reproduction and survival, distribution and abundance, or simply presence and absence (Able, 1999). In this section, we first address the press disturbance resulting from ecosystem engineering by cultured organisms themselves, followed by structures added as part of aquaculture methods (e.g. stakes, tubes, racks, and nets).

The paradigm for soft-sediment tideflat communities is that they are structured by predation, which keeps prey densities at such low levels that larval recruitment and competition are relatively unimportant (Posey, 1990; Olafsson et al., 1994; Lenihan and Micheli, 2001). However, larger bioengineering species are an exception to this rule including large bioturbators (burrowing shrimp in West Coast

estuaries; Posey, 1986; Posey et al., 1991; Dumbauld et al., 2001) and structure forming species like bivalve shellfish and eelgrass. Competition between cultured bivalves and eelgrass has been studied more thoroughly on this coast than in other locations, perhaps because aquaculture is so important and the two habitat types often co-occur or are adjacent. The relevance of eelgrass is two-fold: first, seagrasses in general are declining worldwide (Orth et al., 2006), and second, they form structured habitats and have consequently served as a benchmark for habitat provided by shellfish (Jackson et al., 2001; Heck et al., 2003; Bostrom et al., 2006). Because both shellfish and eelgrass shoots occupy space, it is no surprise that competition occurs. The focus of research has been to document the mechanism and strength of this competition. In terms of mechanism, oysters may influence eelgrass through both their “footprint” and abrasion or drying of leaves when exposed at low tide (Simenstad and Fresh, 1995; Schreffler and Griffen, 2000; Boese et al., 2003). Repeated damage is a possible explanation for smaller shoot sizes on aquaculture beds relative to nearby eelgrass (Tallis et al., in press). Living within the sediment, clams are not expected to cause leaf damage but may nevertheless compete for space. Geoduck clams at aquaculture densities (10 m^{-2}) reduced eelgrass density by ~30% in south Puget Sound during summer months; this difference disappeared during winter when shoot densities naturally thinned in control plots (Ruesink and Rowell, in prep.).

The strength of competition between shellfish and eelgrass can usefully be explored by examining how each species performs by itself and in combination (Fig. 3A, see example below). Some combinations generate overyielding, in which total production is larger than expected from averaging the 2 species. Overyielding can occur because individuals perform better in combination with another species than on their own. Other combinations result in underyielding, in which total production is lower than expected from the average of 2 species, often a result of strong interspecific competition. Thus, a key issue has been to elucidate the relationship between cultured bivalve density and eelgrass – does eelgrass do better or worse than expected from the percentage of area transformed to hard substrate? As a thought experiment, imagine that light limitation in the eelgrass canopy sets up low shoot density, and oysters at low densities simply insert themselves into unoccupied space. This may be the case, for instance, in an experimental addition of oysters at 10–20% cover in Willapa Bay, where eelgrass densities were not distinguishable from controls (shoot density = 25–50 m^{-2} ; B.R. Dumbauld, unpubl. data). This would constitute a case of overyielding, because shoot density was apparently not reduced by the amount of oyster cover. On the other hand, to the extent that oysters damage nearby eelgrass shoots, it is possible to imagine eelgrass declining by more than the percent cover of oysters. At a site in the South Slough estuary (Coos Bay, Oregon) experimental addition of low densities of oysters (ca. 13 shells m^{-2} or 10% cover) resulted in a decline in eelgrass cover relative to an adjacent control plot (Rumrill and Christy, 1996), particularly at a higher tidal elevation (from 10% cover at deployment to 3% cover after 75 days versus an increase from 8% cover at deployment to 10% cover measured on the control plot). In Tillamook Bay, Oregon eelgrass shoot survival was only 1% in 3×3 m plots where oyster clusters (4–50 individuals) and eelgrass were transplanted compared to 59% survival in adjacent plots where only eelgrass was transplanted (Schreffler and Griffen, 2000). Both eelgrass and oyster cover may vary over time as demonstrated two years after clumps of oysters were added to 2×2 m plots in Willapa Bay, when eelgrass entirely disappeared from plots that had >20% oyster cover (Fig. 3B; E.L. Wagner, unpubl. data). Interestingly, however, a year later these plots showed a simple 1:1 tradeoff between oysters and eelgrass (Fig. 3C). At a still larger scale, on cobble shores in British Columbia, density of eelgrass transplanted down-slope from oysters declined more than density of similar transplants to areas not below oysters (Kelly and Volpe, 2007). If this spatial relationship was indeed causal, the competitive effects of

oysters extended for several meters beyond their immediate location. Based on available evidence, eelgrass can coexist with bivalves at low densities used in on-bottom aquaculture on soft sediments, but more research needs to be directed at best management practices that could raise the likelihood of overyielding.

Introduced Pacific oysters are cultivated in many of the same West Coast estuaries once occupied by extensive beds of native oysters, *O. lurida*, raising the possibility of negative competitive effects between these oyster species. Despite relaxed fishing pressure, *O. lurida* has mostly failed to recover since it was overexploited in the late 1800's. Native oysters persist at very low abundance at many West coast locations and many factors likely contribute to their scarcity; however, one unexpected consequence of presence of cultured *C. gigas* in the intertidal is the development of a "recruitment sink" (Trimble et al., in press). Given a standardized recruitment surface (a stack of 11 Pacific oyster shells), native oysters disproportionately recruited to reefs of *C. gigas*, rather than eelgrass or unstructured tideflat in Willapa Bay, Washington. This gregarious settlement was an advantageous strategy when beds of native oysters were primarily found subtidally, but the modern shell distribution has shifted to be more intertidal due to *C. gigas* culture. Since *O. lurida* is sensitive to desiccation and temperature extremes, showing <5% annual survival at tidal elevations emerging from the water just 2–10% of the time, compared to >20% survival when continually submerged (Trimble et al., in press), native oyster recruits to intertidal shell habitat provided by *C. gigas* cannot persist.

Numerous studies have been conducted on the role of bivalves as habitat for fish and invertebrates in both estuarine and marine

systems (Zimmerman et al., 1989; Jones et al., 1997; Breitberg, 1999; Coen et al., 1999; Posey et al., 1999; Bruno and Bertness, 2001; Coen and Grizzle, 2007; see discussion in Section 5.3 below), but most have concentrated on natural assemblages where these animals are considered to be foundation species or ecological engineers rather than aquaculture settings. Mussel and oyster reefs modulate water flow and transport, allow attachment of algae and invertebrates, and provide cover and refugia from predation (Bahr and Lanier, 1981; Zimmerman et al., 1989; Tokeshi and Romero, 1995; Lenihan, 1999; Ragnarsson and Raffaelli, 1999; Gutierrez et al., 2003; Rodney and Paynter, 2006). With the exception of restoration activities however, oysters and mussels in aquaculture settings are not generally allowed to form reef structures, but instead are either suspended on structures or spread out on the substrate to grow as individuals or small clusters and intentionally kept from forming three-dimensional reefs to positively influence valve shape and growth for market. Thus the ecological role of cultured bivalves as habitat, particularly when non-native, needs to be studied separately and not inferred from studies of bivalve reefs.

5.1. Benthic infauna

When suspended culture occurs over soft sediments, organic enrichment via biodeposition can transform a diverse benthic community dominated by suspension feeders (bivalves, crustaceans, and some polychaetes) into one dominated by smaller opportunistic deposit feeders (usually polychaetes), a pattern that characterizes nutrient enrichment from a variety of anthropogenic sources (Pearson and

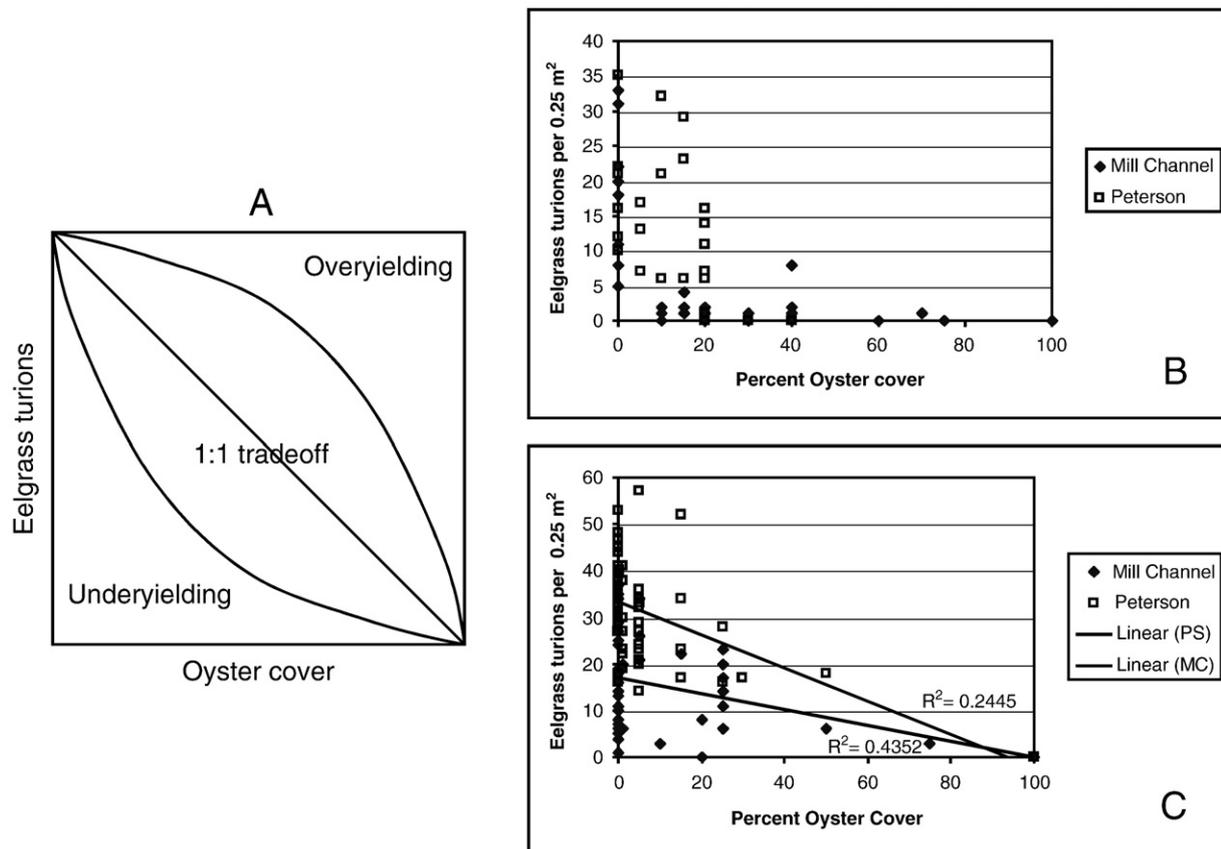


Fig. 3. A) Competition between eelgrass and oysters can be viewed on a continuum from overyielding, in which total production is larger than expected from averaging the 2 species because individuals perform better in combination, to underyielding, in which total production is lower than expected. B) Results of a field experiment in Willapa Bay, Washington where oysters were added to 2 m × 2 m plots at two locations (Mill Channel and Peterson Station). Measurements taken after 2 years indicated that eelgrass had entirely disappeared when oyster cover was greater than 20% (E.L. Wagner, unpubl. data). C) Measurements taken after 3 years showed some recovery and almost a 1:1 tradeoff between oysters and eelgrass.

Rosenberg, 1978). However, because biodeposition from shellfish farms is generally low relative to that of finfish farming or other anthropogenic sources (Pohle et al., 2001; Crawford et al., 2003), responses by infauna are variable and depend on species cultured, biomass or stocking density, and the environment in which culture takes place (Hartstein and Rowden, 2004; Miron et al., 2005; Callier et al., 2006). In some cases enrichment either does not occur or does not alter infauna (Grant et al., 1995; Chamberlain et al., 2001; Crawford et al., 2003), while in others, significant effects have been documented (Dahlback and Gunnarsson, 1981; Mattsson and Linden, 1983; Kaiser et al., 1998; Mirto et al., 2000; Christensen et al., 2003). Similarly, intertidal oyster culture on racks and trestles has variable consequences for infauna, likely based on the balance of biodeposit production versus water flow. Trestle culture of Pacific oysters in New Zealand, England, and France resulted in increased biodeposition, lower sediment redox potential, and altered macrofaunal communities (reduced diversity and abundance; Castel et al., 1989; Nuges et al., 1996; Forrest and Creese, 2006). However, oysters cultured in floating bags over intertidal areas in eastern Canada were shown to increase both organic content and initial colonization of de-faunated sediment by benthic infauna (Lu and Grant, 2008) whereas high currents at other sites in Canada and Ireland swept away biodeposits and few changes in infaunal community were seen (De Grave et al., 1998; Mallet et al., 2006). Finally, for on-bottom culture, it is difficult to separate effects of biodeposition from structural complexity and space competition and relatively few studies outside the West Coast of the U.S. have been conducted. Mussels cultured on the bottom were shown to negatively influence richness and abundance of some infauna in Wales (e.g. cirratulid polychaetes and two species of amphipods declined with increasing mussel density; Beadman et al., 2004) while Murray et al. (2007) found species dependent results when comparing communities in subtidal mussel culture (both on-bottom and rope) to naturally occurring intertidal mussel beds in Maine, U.S.

How do infaunal species respond to bivalve aquaculture on the West Coast? Several studies in West Coast estuaries have documented abundant, highly-diverse infaunal communities associated with on-bottom oyster culture. Abundance, biomass and diversity of infauna in Humboldt Bay on-bottom oyster culture were higher than that found in open mudflat, but lower than that in eelgrass (10.2 cm dia cores, 1 mm mesh; Trianni, 1995). At the time of this study oysters were harvested with a suction dredge in this estuary, a disturbance which likely also influenced the infaunal community in the oyster beds, and comparisons made suffered from statistical interaction between season and habitat factors. Similarly, Hosack et al. (2006) found infaunal macrofauna were more abundant in eelgrass in Willapa Bay, Washington than on open mudflat, and moderate levels found in oyster ground culture were not significantly different from either of these habitat types (10.5 cm diameter cores 0.5 mm mesh). Ferraro and Cole (2007) sampled multiple habitat types in Willapa Bay (2 × 8 cm diameter core, 0.5 mm mesh), using a strict sampling protocol throughout the estuary over two years. Oysters and eelgrass supported equally diverse assemblages, with unstructured habitats having less diversity. The equivalence of oyster and eelgrass habitats, in contrast to the other two studies, may have emerged from sampling aquaculture beds that had 2–3 year old oysters present and had not been disturbed for several years. The lowest-diversity samples came from areas influenced by burrowing shrimp (*N. californiensis*). This result is consistent with direct studies of bioturbation by these shrimp in U.S. West Coast estuaries (Bird, 1982; Posey, 1986; Dumbauld et al., 2001) and elsewhere around the world (Wynberg and Branch, 1994; Dittmann, 1996; Berkenbusch et al., 2000; Berkenbusch and Rowden, 2007; Pillay et al., 2007). Thus, the primary result of removing burrowing shrimp with the pesticide carbaryl is to reduce bioturbation and then add a three-dimensional architecture by planting oysters, which further influences the community (Dumbauld et al., 2001).

Other West Coast studies of infauna have occurred in aquaculture types that include structures (e.g. suspended bags, stakes, racks), so

any differences reflect the presence of both bivalves and structures. Nevertheless, differences have been small. Although biodeposition was observed under deep-water suspended oyster and mussel culture using sediment traps in British Columbia, Canada, and Totten Inlet, Puget Sound, Washington respectively, there appeared to be little buildup of organic matter when measured outside the traps. The major change in the benthic community observed was enhanced abundance of epifaunal predators which capitalized on the drop-off of fouling organisms from the culture operations (Brooks, 2004; Switzer et al., 2008). Harbin-Ireland (2004) found no difference in percent organic matter in areas directly below and those adjacent to a single set of subtidal oyster racks in Drakes Estero, California, nor was there any difference in overall infaunal community indices. The relative abundance of amphipods was higher under racks while other taxa like bivalves and ostracods were less abundant. In contrast, experimental deployment of oyster stakes and racks in Coos Bay, Oregon, resulted in biodeposition within the stake plots and erosion and reduction of carbon content of the sediments below rack plots (Everett et al., 1995). Stake culture resulted in lower recruitment and survival of tellinid clams, while increased abundance of cumaceans and amphipods was observed in the oyster rack plots (Carlton et al., 1991). In a relatively short term follow-up study, Pregnall (1993) observed no significant difference in sediment grain size and only a slight difference in benthic infaunal diversity between oyster stake culture plots and eelgrass controls. Diversity and abundance of infaunal invertebrates around long line oyster culture in Humboldt Bay, California were also similar to those observed at eelgrass reference areas (Rumrill and Poulton, 2004). In both cases, similarity may have arisen not simply due to flow dispersing biodeposits, but because both aquaculture and control areas included eelgrass, which has characteristic effects on sediment (reducing flow, allowing particles to settle out; Madsen et al., 2001).

From the above discussion, it is clear that engineered habitats differ from unstructured tideflat in terms of static community-level metrics. Differences have also emerged from the few but important studies addressing species interactions. Small mobile crustaceans including juvenile Dungeness crab (*Cancer magister*) had higher density and biomass in oyster shell habitat placed in intertidal areas of Grays Harbor, Washington than in nearby control areas without shell. When small clams recruited to the structured shell habitat in higher numbers, they also experienced higher predation by crabs (Iribarne et al., 1995; Dumbauld et al., 2000).

5.2. Epibenthic meiofauna

Epibenthic invertebrates are important food items for juvenile estuarine fish (Alheit and Scheibel, 1982; Gee, 1989) including juvenile Pacific salmon and small (<50 mm) English sole on the U.S. West Coast (Toole, 1980; Simenstad et al., 1982). Structurally complex habitats like seagrass have been shown to enhance meiofaunal abundance (Bell et al., 1984; Attrill et al., 2000; Jenkins et al., 2002). We found only two studies on the effects of either oysters or aquaculture on epibenthic meiofauna. Castel et al. (1989) found enhanced epibenthic meiofaunal abundance in both on-bottom and bag culture of oysters in France over that found in adjacent un-structured habitat, but highest abundance was found in nearby seagrass beds. Similarly meiofauna densities were higher in both eelgrass and oyster habitats than over open mudflat in Willapa Bay on the West Coast (Hosack et al., 2006). Simenstad and Fresh (1995) noted that taxa diversity of epibenthic harpacticoid copepods was higher on an active on-bottom oyster culture plot with 3 year old oysters present than an in-active plot where oysters and eelgrass were present in the same estuary, but prey taxa for epibenthic feeding fish such as juvenile salmonids were more abundant on the in-active plot. This trend was reversed for English sole prey taxa suggesting species specific differences in affinity, but no comparisons were made with eelgrass or other habitats. Recent

experimental work with experimental additions of the much smaller native oyster (*O. lurida*) attached to Pacific oyster cultch shells in Puget Sound, Washington also showed increased abundance of epibenthic organisms, but not necessarily enhanced taxa richness with the pool of available species being determined by background conditions at the enhancement site (Cordell, pers. comm.).

5.3. Nekton

For larger mobile species, complex structure formed by foundation species or ecosystem engineers is likely to provide a place both to search for prey and to avoid becoming prey to larger organisms. Indeed, higher densities of estuarine fish and invertebrates have been widely found in association with structured habitats like seagrass (Orth et al., 1984; Jackson et al., 2001; Heck et al., 2003) and oyster reefs (Breitberg, 1999; Coen et al., 1999; Lenihan et al., 2001; Lehnert and Allen, 2002; Glancy et al., 2003; Peterson et al., 2003; Coen and Grizzle, 2007; Horinouchi, 2007; Taylor and Bushek, 2008) when compared to open un-structured mudflat or subtidal channel bottom. However, abundance measures are not a definitive indicator of how structured habitat contributes to nekton production, and in some cases even densities do not differ across habitat types (Heck and Thoman, 1984; Ferrell and Bell, 1991; Jenkins et al., 1997). We discuss possible explanations for these discrepancies in Section 7 below. Nekton response to aquaculture as habitat has not been extensively studied, except in the context of off-bottom culture operations. Order of magnitude higher densities of some fish and invertebrates (American eel, oyster toadfish, rock gunnel, Atlantic tomcod, and American lobster) were found in areas with rack and bag culture of *C. virginica* in Rhode Island, USA, compared to those in eelgrass or unstructured habitats, but eelgrass also harbored a few unique species (northern pipefish and winter flounder; Dealteris et al., 2004). Tautog and scup were more abundant at oyster grow-out sites than natural rocky reefs in Narragansett Bay, Rhode Island and a tagging study found that though scup grew at slightly higher rates on the rocky reefs, they had greater site fidelity to oyster grow-out cages (Tallman and Forrester, 2007). Erbland and Ozbay (2008) found higher abundance of several reef oriented fish species (gag grouper, grey snapper, sheepshead, and tautog) and greater overall species richness in experimental oyster bags compared to a nearby oyster reef in Delaware. Juvenile sole were found to utilize areas with oyster trestle culture for protection during the day while foraging on surrounding tideflats at night (Laffargue et al., 2006). Researchers in New Zealand established a framework for the expected effect of suspended culture on fish which includes three mechanisms: attraction to structure, direct influence on recruitment, and indirect food web effects (Gibbs, 2004). A case study which examined suspended culture of green mussels suggested few realized effects on abundance of one species (blue cod) and that the primary effect might be on pelagic fish that consume zooplankton should the footprint of farms be expanded (Jiang and Gibbs, 2005). These mussel farms have also been shown to enhance abundance and aggregation of starfish on the bottom, presumably due to drop-off of both culture species and fouling organisms (Inglis and Gust, 2003; D'Amours et al., 2008). Clynick et al. (2008) found species specific differences in abundance when comparing areas under mussel culture lines to adjacent eelgrass and open unstructured habitat, but found no differences in integrated growth of winter flounder, sand shrimp and rock crab measured using RNA/DNA ratios.

Substantial research on nekton associated with both on-bottom and long-line oyster culture has been carried out recently along the West Coast of the U.S. In one case, diversity and abundance of fish were highest in aquaculture. Specifically, oyster longlines in Humboldt Bay, California, harbored more fish than did eelgrass or open mud habitats (Pinnix et al. 2005). However a more common result has been that community-level indices (abundance and diversity) are equiva-

lent across habitats with a few species specific affiliations. Few statistically significant differences in density were found among the >20 species of fish and crabs collected at intertidal locations in Willapa Bay, Washington where eelgrass, oyster bottom culture and open mudflat habitats were surveyed (Dumbauld et al., 2005; Hosack et al., 2006, Fig. 4). In general, nekton density reflected physical location in the estuary rather than habitat type, although some species like rock crab (*Cancer productus*) were more abundant in oyster aquaculture and tube snouts (*Aulorhynchus flavidus*) in eelgrass. Higher abundance of rock crab and smaller shore crabs (*Hemigrapsus* spp.), sculpins and blennies, occurred in small oyster stake culture plots compared with nearby eelgrass control areas in Coos Bay, Oregon (Pregunn, 1993). Staghorn sculpin (*Leptocottus armatus*) and caridean shrimp (*Crangon franciscorum*) were more abundant within high-density oyster long-line plots compared to lower-density oyster plots in Humboldt Bay, California (Rumrill and Poulton, 2004). In a study of fish associated with oyster racks, no significant differences in species richness or abundance were observed in fish samples collected adjacent to the racks compared to an area without culture in separate arms of Drakes Estero, California. At the same time, structure-oriented feeders like kelp surfperch (*Brachyistius frenatus*) and crevice-dwelling fish like gunnels and kelpfish (*Pholis ornata* and *Gibbonsia metzi*) were disproportionately associated with racks particularly during the day when refuge from predators could be most important (Weschler, 2004). Although oysters *C. gigas* were not included in the comparison, adjacent cobble habitats, supported lower fish diversity than eelgrass in British Columbia (Kelly et al., 2008).

On-bottom structure appears to have different implications for Dungeness crab (*C. magister*), depending on phase of the life cycle. These crabs represent a multi-million dollar annual fishery on the U.S. West Coast and the role of estuaries as nurseries supporting these populations has been extensively studied (Armstrong et al., 2003). Ground cultured oysters and intertidal shell provide equal or better habitat than eelgrass for juvenile 0+ Dungeness crab (0–30 mm carapace width), which in turn provides better habitat than open

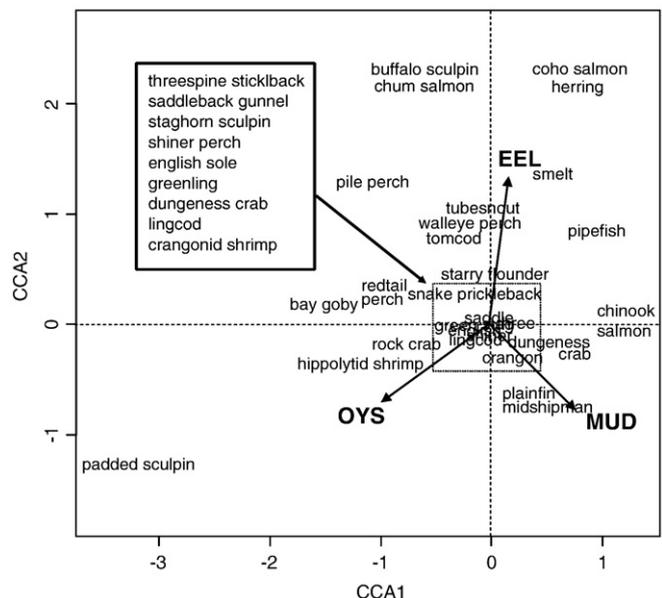


Fig. 4. Canonical correlation biplot of catch per unit effort data from fyke nets deployed over three intertidal habitats: oyster aquaculture (OYS), eelgrass, *Zostera marina* (EEL), and open mud (MUD) in Willapa Bay, Washington in 2001. Species close to vectors and far from the midpoint are closely associated with that habitat. Many commonly collected species (box and circle) show no association with habitat, but some others like tubenout and smelt in eelgrass, and rock crab and hippolytid shrimp in oyster show loose association with habitat.

unstructured mud or sand based on higher recruitment and survival rates due to protection from predators (Armstrong et al., 1994; Eggleston and Armstrong, 1995; Dumbauld et al., 2000; Feldman et al., 2000; Williamson, 2006). Shore crabs (*Hemigrapsus oregonensis*) can also recruit to shell and outcompete *C. magister* depending on location and tidal elevation (Visser et al., 2004). Older age classes of Dungeness crab (1+ and 2+), however, favor open unstructured littoral habitats for foraging at high tide and are less likely to move across structured habitat including both eelgrass and oyster aquaculture (Holsman et al., 2003; Holsman et al., 2006).

For some Pacific salmon, on-bottom oysters appear to be lower quality habitat than eelgrass, especially for predator avoidance, based on individual behavior. However, salmon are distributed broadly across habitat types, and the amount of aquaculture in an estuary does not appear to influence salmon returns. Pacific salmon occupy estuaries during a critical life-history stage as juveniles smoltify and transition from fresh to marine waters (Quinn, 2004). The diversity of life-history patterns among and within species of salmon influences their use of estuaries: Chinook salmon (*Oncorhynchus tshawytscha*) have the longest estuarine residence, whereas pink and chum salmon (*O. gorbuscha* and *O. keta*) move through estuaries relatively rapidly on their way to sea (Groot and Margolis, 1991; Bottom et al., 2005). Juvenile coho salmon (*O. mykiss*) generally move directly to neritic waters as older 1+ fish that have reared in freshwater for longer periods, but recent evidence suggests that both age-0 and yearling fish utilize estuarine areas (mostly salt marsh and sloughs) relatively extensively (Healey, 1982; Miller and Simenstad, 1997; Miller and Sadro, 2003). Across West Coast estuaries, successful returns of salmon do not appear to be related to the presence or absence of aquaculture; in fact, the best estuarine predictor of pit-tag returns of Chinook salmon was the percent of land cover in natural condition (Magnusson and Hilborn, 2003). In a field study to assess habitat preferences, salmon smolts were sampled across habitat types in Willapa Bay, Washington with a towed net, and gut lavage performed on captured individuals. No differences in abundance or diet occurred across habitat types, although seasonal and larger-scale spatial differences were evident (Dumbauld et al. 2005, Fig. 5). Laboratory studies of Chinook salmon smolt behavior indicated that eelgrass may provide a better refuge than other habitat types. Larger juveniles preferred the structure of eelgrass as a refuge over oysters or open sand substrate when exposed to a mock heron predator (Dumbauld et al., 2005). In a separate field experiment, hatchery-raised Chinook salmon smolts were released into a large intertidal enclosure (3000 m²) containing eelgrass (*Z. marina* and *Z. japonica*), oyster clusters, unstructured sediment, and introduced cordgrass (*Spartina alterniflora*). They were implanted with acoustic tags that allowed their movements to be tracked in 2-dimensions at sub-meter accuracy (Radio Acoustic Positioning and Telemetry). After effects of tidal elevation and enclosure were accounted for, smolts never entered areas with *Spartina* and otherwise responded only to the presence of *Z. marina*, where they moved more slowly than in other habitat types (Semmens, 2008). Thus it seems that juvenile salmon move over the entire matrix of estuarine habitats, but eelgrass may represent a preferred habitat for refuge from predation which cannot be compensated by transformation to on-bottom oyster aquaculture. Assessing the functional value of habitats including aquaculture however, will ultimately require a larger landscape approach as suggested by Simenstad and Cordell (2000) for restoration (see further discussion in Section 7 below).

5.4. Birds

Estuarine tidelands provide foraging habitat for numerous species of shorebirds, waders and waterfowl during migration and for a few species that overwinter. Some farmed bivalves are directly consumed by birds (e.g. mussels by seaducks and oystercatchers; Caldow et al., 2004). However, other bird species appear to avoid

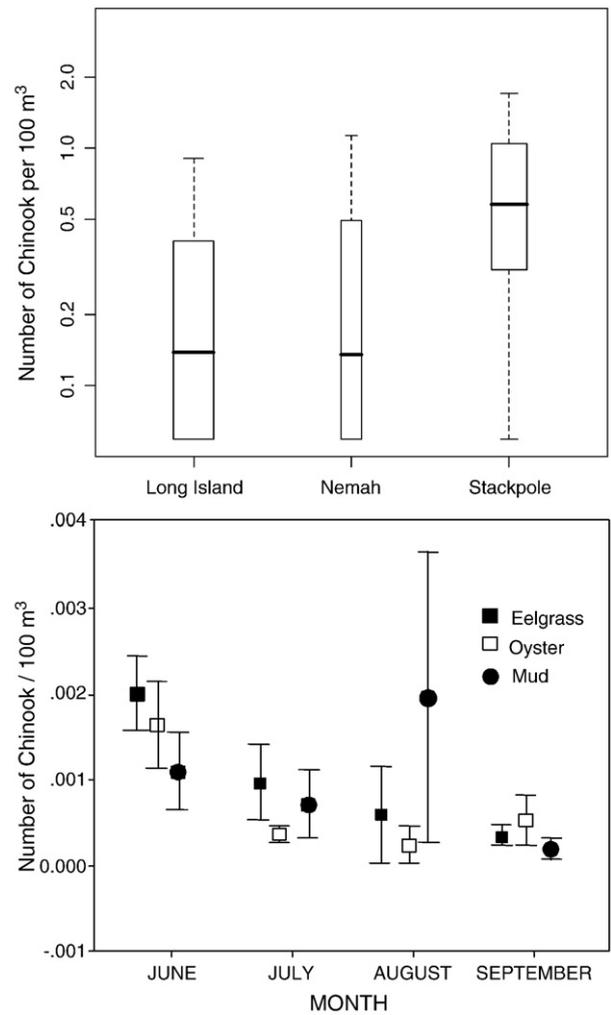


Fig. 5. Mean catch per unit water flow of juvenile Chinook salmon smolts by area fished with a modified two boat trawl net in Willapa Bay, Washington during 2003–2005. Catch varied by location (top), and over time (bottom), but no difference was evident between habitats.

densely-structured habitats, preferring instead to feed in open mudflat areas (Luckenbach, 1984). Like nekton, the response of birds to aquaculture is likely to be species and perhaps environment specific due to bird feeding and roosting behavior relative to the tides and the presence of other birds and predators. In Ireland, dunlin (*Calidris* spp.) were more frequent beneath trellis cultured oysters, whereas gulls, curlew and oystercatchers occurred in significantly lower numbers in culture areas (Hilgerloh et al., 2001). Experimental additions of mussels to intertidal areas in Wales resulted in increased use by curlew and redshank over time (Caldow et al., 2003), due apparently to increased diversity in benthic fauna as food provided by increased habitat complexity.

Evidence for the effects of aquaculture on birds on the West Coast suggests species specific differences due to behavior. In Humboldt Bay, California five of 13 species of shorebirds (whimbrel, willet, dowitchers, peeps and black turnstones) and three of four species of waders (snowy egret, great egret, and black-crowned night heron) were more abundant in long-line oyster culture areas than in nearby “control” areas (Connolly and Colwell, 2005), possibly responding to higher densities of invertebrate prey associated with long-lines. Black bellied plovers and great blue herons were more abundant in control areas and the other shorebirds displayed location specific behavior. Kelly et al. (1996) found that peeps and dunlin avoided rack and bag oyster culture in Tomales Bay while willet were attracted. Mussels

settling on aquaculture structures were shown to enhance food resources for surf scoters and Barrow's goldeneye in British Columbia (Kirk et al., 2007). One species of waterfowl of particular concern are Brant geese (*Branta bernicla*), which graze heavily on eelgrass in estuaries at stopovers during their long migration to Arctic breeding grounds and in temperate over-wintering areas (Ganter, 2000). Humboldt Bay, California ranks fourth among West Coast spring staging areas for brant with peak numbers reaching 38,000 while Willapa Bay historically averaged 23,393 (1936–1960; and now 6900) and ranks sixth (Wilson and Atkinson, 1995; Moore et al., 2004). Effects of geese themselves on eelgrass tend to be low due to the seasonally brief presence of these birds during migration, but Canada geese (*Branta canadensis*) as well as several species of dabbling ducks have been shown to have more substantial long term effects on eelgrass in areas elsewhere in the U.S., particularly where they overwinter in some years (Nacken and Reise, 2000; Rivers and Short, 2007). Dabbling ducks have switched their foraging habits to feed primarily on the introduced species of eelgrass *Z. japonica* in West Coast estuaries where this species is now present (Lovvorn and Baldwin, 1996). While goose density is positively correlated with spatial eelgrass coverage in West Coast estuaries, the relationship is more complex and also influenced by proximity to the next estuary along the coast and other factors like frequency of winter storms and within season foraging dynamics due to tides (Baldwin and Lovvorn, 1994; Wilson and Atkinson, 1995; Moore et al., 2004; Moore and Black, 2006). Thus both eelgrass and associated brant numbers could be negatively associated with aquaculture in a given area, but the long-term temporal decline in brant numbers along the West coast is not likely associated with shellfish aquaculture given the relatively stable presence of this industry in these systems for the last 100 years.

5.5. Aquaculture structures

Some bivalve aquaculture methods introduce physical structures to the intertidal flat in addition to the organisms themselves (e.g. stakes, longlines, and bags for off-bottom oyster culture, and gravel, tubes and anti-predator nets for clam culture). These physical structures can modify water flow, in some cases accelerating flow and causing erosion, in other cases leading to deposition. They can also provide attachment sites and attract settlement of other invertebrates and algae. For eelgrass in particular, reduced density is a common response to the shade from overwater structures, studied most intensively for docks (Burdick and Short, 1999; Thom et al., 2005). We have already considered effects of suspended and rack culture in sections above, although the species versus method effects were not distinguishable. Distinguishing these effects requires two treatments (species + method, and either species alone, or method alone [preferably both]), in addition to a control without either. This design was employed by Spencer et al. (1997), who showed that predator netting deployed to protect clam aquaculture substantially increased sedimentation to tideflats in Great Britain, whereas biodeposits from clams alone did not (but see Jie et al., 2001 who document increased biodeposits from clams can occur in areas with current velocities below critical re-suspension rates). Further, this sedimentation resulted in slightly enhanced organic content and enhanced abundance of deposit feeding polychaetes. Clam mariculture conducted in bags on the East Coast of the U.S. has been shown to affect sediment but not water column characteristics (Mojica and Nelson, 1993). Macro-algae attached to clam culture bags in North Carolina enhanced use by mobile invertebrates and juvenile fishes over that in nearby shallow subtidal sand bottom and resulted in comparable abundances with seagrass habitat (Powers et al., 2007). Both substrate modification (gravel addition) and predator netting effectively increase survival by protecting juvenile seed clams (*Mercenaria mercenaria* and *M. arenaria*) from various predators on the East Coast of the U.S. (Kraeuter and Castagna, 1985; Beal and Kraus, 2002) and *R.*

philippinarum in Spain (Cigarria and Fernandez, 2000), but these studies were primarily confined to effects on the clams themselves.

What evidence exists for ecological effects of aquaculture structures on the West Coast? For oyster culture most regional attention has focused on response by eelgrass (*Z. marina*) and results have been quite variable. At one extreme, oyster stake culture conducted in the middle of an intertidal eelgrass meadow in Coos Bay, Oregon reduced eelgrass cover by 75% relative to nearby controls, possibly due to increased sedimentation (5–10 cm buildup) and physical disturbance (Everett et al., 1995). Oyster racks caused 100% loss of eelgrass under the structure from both erosion of sediment (10–15 cm around structure) and shading. Macro-algal biomass was enhanced around stakes and significantly lower in rack plots than in eelgrass reference plots (Everett et al., 1995). At the other extreme, a broad survey of Willapa Bay showed that eelgrass density in longlines could not be distinguished from uncultured areas at the same tidal elevation, although in a subset of these beds, longlines harbored smaller plants (32%) and reduced production per unit area (70%) (Tallis et al., in press). Also, in a separate study in Willapa Bay, lower eelgrass densities were found in longlines than in nearby eelgrass reference areas (Wisehart et al. 2007). Seedlings were less abundant in longlines and reference areas compared with dredge harvest beds, possibly from seed supply or because shading and sedimentation impact these small plants (Wisehart et al. 2007). In an experimental study in which the effect of space between oyster longlines on eelgrass was examined in Humboldt Bay, California, eelgrass metrics tended to scale directly with the density of oysters (Rumrill and Poulton, 2004). Eelgrass declined in cover and density as spacing between lines decreased; spatial cover and density of eelgrass under lines spaced at 1.5 ft and 2.5 ft were significantly lower than those spaced at 5 and 10 feet apart. Eelgrass metrics observed within these wider spaced lower-density treatments were comparable to those observed at a nearby untreated site, a former oyster ground culture site, and a series of eelgrass reference sites located throughout the bay at the end of the 22 month study period (Fig. 6). They were also comparable to those measured within full-scale commercial long-line culture areas. Increased sedimentation and more variable light conditions (incident light levels diminished by as much as 35%) were found under narrowly spaced long-lines (<5 foot spacing), but the “shade zone” migrated with movement of the sun and irradiance was not reduced enough to limit *Z. marina* growth. Structures clearly have the potential to limit eelgrass, but the effects are context specific, may not even be apparent when observed over larger spatial and longer temporal scales (e.g. see Ward et al. 1993 for lack of observed effects of rack culture), and can be ameliorated with management practices. West coast growers have also reported that eelgrass often appears in areas formerly devoid of this plant after structures are put in place. Given the lack of evidence for nutrient enhancement (Section 4.3 above), this could be due to either localized effects on water clarity or sediment stabilization, but no studies have addressed the mechanism.

For clam culture on the West Coast, two modifications have been studied: addition of shell or gravel to the substrate and addition of anti-predator nets. Gravel and crushed oyster shell have been widely used to develop or maintain hard clam (primarily *R. philippinarum*) habitat in West Coast estuaries and these additions have been shown to enhance juvenile clam survival (Toba et al., 1992; Thompson, 1995). Thom et al. (1994) found that gravel addition to soft sediment significantly increased benthic respiration rates but had little effect on water quality parameters in south Puget Sound. They found site specific changes in surface macroalgae, chlorophyll, and benthic assemblage, likely due to local conditions and time since the areas had been graveled. Secondary effects on the infaunal and epibenthic community were also shown to be site specific in later studies conducted in two sub-estuaries of south Puget Sound. Thompson (1995) found a general trend of enhanced abundance of gammaridean amphipods and nemerteans in modified substrate plots and reduced abundance of glycerid, sabellid and nereid polychaetes. Simenstad and Fresh (1995) documented site specific responses of the epibenthic

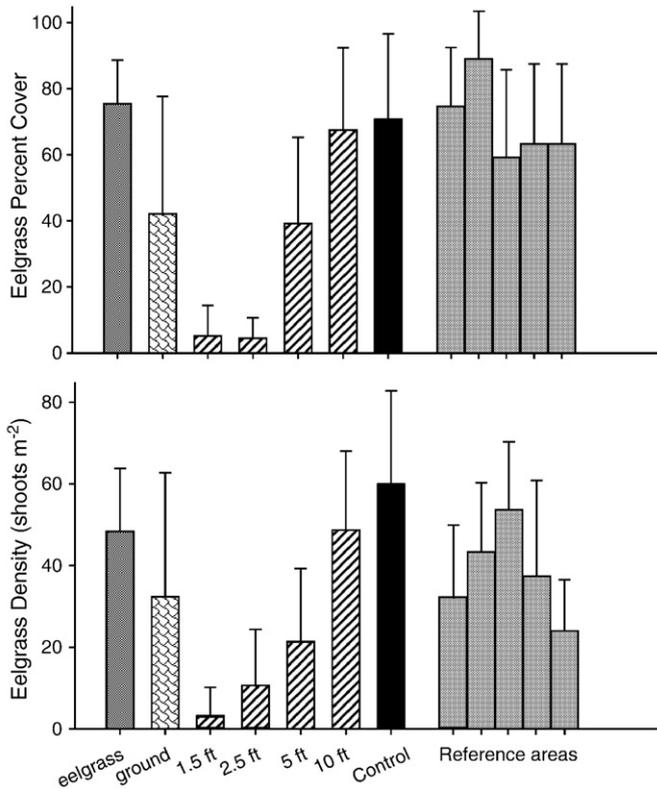


Fig. 6. Eelgrass spatial cover (top) and density of shoots (bottom) measured in experimental oyster long-line plots (1.5 to 10 ft spacing) in Humboldt Bay, California just before harvest at the end of the experiment compared to an eelgrass reference area nearby, ground culture plot (ground), a control plot with stakes but no lines (control) and 5 distant reference eelgrass beds (Mad River, Sand Island, East Bay, and Arcata Channel).

harpacticoid copepod community to the combination of gravel additions and predator exclusion netting.

Predator exclusion netting and/or bags are widely used for clam culture without substrate modification in West Coast estuaries and have been shown to increase the amount of organic carbon present in the sediment, likely due to biodeposition from larger age classes of *R. philippinarum* which were more abundant in netted plots at farmed sites in British Columbia, Canada (Munroe and McKinley, 2007a,b). Little consistent effect however was shown for sediment grain size or the abundance of other bivalves. Settlement of the cultured species *R. philippinarum* displayed highly significant interannual differences and the effect of netting was marginally significant (decreased settlement), but could be negative or positive depending on presence and size class of older clams (Munroe and McKinley, 2007b; Whiteley and Bendell-Young, 2007). Finally, in Baynes Sound, British Columbia where some growers also installed beach fences around their plots, Zydels et al. (2006) found densities and distribution of important wintering populations of surf and white-winged scoters to be primarily related to environmental factors and not shellfish aquaculture though 76 ha or 5% of the intertidal area was recorded to be covered by predator exclusion nets.

6. Harvest practices as pulse disturbances

Fisheries harvests in general can remove non-target species and re-set systems to early-succession conditions. However, the initial impact and pace of recovery clearly vary with harvest method, type of habitat present, and organism being studied (Kaiser et al., 2006). In their recent review, Kaiser et al. (2006) found just 6 examples of intertidal raking, which is perhaps most relevant to shellfish

aquaculture (since intertidal dredging involved sediment removal and longer recovery times linked to infill rates; see also Dernie et al., 2003). Their meta-analysis showed that initial impacts to biota were relatively small and harvested areas matched controls within 50 days. Recovery was slower however in muddy sand and in biogenic habitats (especially when the latter included larger, older organisms such as corals and bivalves which contributed directly to biomass removed; see also Lenihan and Peterson, 2004). This is likely to be the case after disturbance to seagrasses which are sensitive to a variety of activities with some parallels to aquaculture harvest practices: dredge and fill (Fonseca et al., 1984; Onuf, 1994; Erfteimeijer and Lewis, 2006), boat propellers (Zieman, 1976; Dawes et al., 1997), and boat anchor and mooring chain scars (Walker et al., 1989; Thom et al., 1998). Repeated trampling (mimicking recreational visitors) reduced the biomass of *Thalassia testudinum* in Puerto Rico, especially in softer substrates (Eckrich and Holmquist, 2000), but harvest activities for shellfish are unlikely to occur this frequently. Trawling and dredging for wild shellfish also negatively affect seagrass (Fonseca et al., 1984; Peterson et al., 1987; Orth et al., 2002; Neckles et al., 2005), although an extension to aquaculture must consider gear, technique, species ecology of seagrass (e.g. Erfteimeijer and Lewis, 2006), and the physical environment (e.g. Kaiser et al. 2006). Several hard clam harvest methods have been shown to reduce eelgrass, including mechanical “clam kicking” with propeller wash (Peterson et al., 1987) and hand digging when rhizomes were extensively fragmented (Cabaco et al., 2005). The scale of harvest activity has also been shown to be important for both the direct effect on seagrass and associated organisms and the secondary impact of harvest on food for shorebirds and waterfowl. Small scale harvest of clams by hand in a national park in Spain (Navedo and Maseró, 2008) appeared to have low impact and be sustainable, while larger scale effects of dredge harvesting on wild stocks of mussels and cockles in intertidal areas of the Dutch Wadden Sea are highly debated (Piersma et al., 2001; Verhulst et al., 2004; Kraan et al., 2007).

Recovery time after disturbance to seagrass should vary with seagrass species, disturbance size, disturbance intensity, and sediment characteristics. Seasonal time of disturbance is also likely a factor. Seagrass can recover via lateral rhizome spread or via sexual reproduction and seed dispersal depending on location and species. In fact, both natural and human disturbances have been shown to enhance sexual reproduction in seagrass (Marba and Duarte, 1995; Peterken and Conacher, 1997; Plus et al., 2003; Olesen et al., 2004). With respect to aquaculture, intertidal clam harvest in Portugal resulted in 2 fold higher seed production and an extended reproductive season for *Z. noltii* which enabled it to recover from harvest within a year (Alexandre et al., 2005).

Most of the research outlined above on press disturbances due to aquaculture in West Coast estuaries has not addressed the direct response of the benthic community to the pulse effect of harvest practices because it is not generally possible to distinguish these from effects of just adding the cultured organisms themselves. Consequently, the most valuable insight into harvest practices comes from before–after comparisons, which can then be tracked over time to determine pace of recovery. Both the initial impact and time to recovery have been variable in studies of the effect of oyster harvest to eelgrass on the U.S. West Coast. Results of experimental dredging using a toothed metal dredge at relatively large scale (0.33 ha plots) in Willapa Bay, Washington provide one explanation for this variation. At a muddy site, eelgrass initially declined 42%, where shoot and rhizome removal by the dredge implement was substantial, requiring 4 years for recovery, whereas at a sandy site, initial decline was only 15% and recovery occurred in 1 year (Tallis et al., in press). The effects of multiple passes with a suction dredge were evaluated by Wadell (1964) who found up to 96% initial loss of eelgrass biomass in Humboldt Bay with recovery taking up to 2 years. Treatment frequency also varies substantially and growers suggest that suction

dredges are no longer common, each company designs their own mechanical implements, operator experience can be a factor, and mechanical harvest is rarely used in soft muddy sediments. In a comparison of eelgrass across three types of aquaculture (longlines, hand-picked, dredged), it proved possible to separate the effects of different culture practices from the effects of oysters, because oyster cover was included as a continuous variable ranging from <5% to >50% across beds. Relative shoot growth rates were 15% higher in both ground and long-line culture beds, but eelgrass production per unit area was driven by density and plant size differences and therefore lower in all aquaculture beds than in nearby eelgrass reference areas. Hand-picked beds had higher eelgrass production per unit area than did dredged beds (Tallis et al., in press), indicating higher impacts of mechanical harvest than picking up oysters by hand in eelgrass. For large areas such as aquaculture beds to regain eelgrass requires seed germination or asexual reproduction of remnant adults. In Willapa Bay, Washington seed germination can be high ($>4\text{ m}^{-2}$), particularly on dredged beds (Wisehart et al. 2007), although seedling survival appears universally low (1–2%; Wisehart 2006). Rhizome branching appears to be important for recovery of gaps in eelgrass (up to 16 m^2), but only occurs seasonally and thus gaps created experimentally in mid-summer did not begin to recover from the edges until the following spring (E.L. Wagner, unpubl. data). Clearly how much sexual versus asexual reproduction contributes to eelgrass resilience is important and may vary both temporally and spatially, but these dynamics have not been investigated on the U.S. West Coast.

For clams, effects of harvest appear related to the extent and depth to which sediment is dislodged. Effects of recreational clam harvest using rakes on *Z. marina* were undetectable, but digging clams with shovels reduced eelgrass cover and biomass over the short term, although recovery occurred fairly rapidly (months) in Yaquina Bay (Boese, 2002). Though the introduced seagrass, *Z. japonica* has expanded into areas and often now interferes with clam aquaculture on the West Coast of the U.S., clam aquaculture does not co-occur with *Z. marina*. Recreational clam harvest in the San Juan Islands, Washington caused short term impacts to non-target clam species abundance and polychaete species richness due to sediment displacement with shovels (Griffiths et al., 2006), but this does not typically occur for aquaculture where harvesting is typically done by hand or small rake and sediment replaced. In an experimental study of the effects of geoduck aquaculture on eelgrass density in south Puget Sound, Washington small (1 m^2) gaps in eelgrass beds required >1 year for recovery via regrowth from the edges, because flowering and seed germination were very rare (Ruesink and Rowell, in prep.). When the geoducks were harvested, eelgrass shoot density dropped $>70\%$ and recovery was subsequently difficult to gauge because control plots also declined in density over the 3-year study (Ruesink and Rowell, in prep.).

7. Landscape considerations

The available evidence discussed above for the U.S. West Coast indicates that some types of bivalve shellfish aquaculture can have effects on other species, and these effects may be place- and time-specific in part due to the scale at which observations are made. The vagueness of this conclusion is to be expected from ecological studies: unfortunately, it leads to the potential for selective use of evidence to support a conclusion of strong positive, strong negative, or weak effects of aquaculture. An important avenue of future research lies in documenting and understanding the role of aquaculture at an appropriate landscape scale, where aquaculture is intermixed (literally overlapping, as with eelgrass in oysters; or distributed as meadows and patches) with other habitat types.

There is no particular scale inherent in the concept of a landscape, only that it has a spatial dimension. For the purposes of this discussion however, we use a common definition of a spatially defined mosaic of

heterogeneous elements that differ in their qualitative or quantitative properties (Wiens, 2005). We consider the estuarine landscape on which aquaculture acts as a disturbance and therefore define it to be larger than the scale of an individual lease, bed, reef, or set of structures used to culture shellfish. Conceptually this differs from estuary to estuary and is influenced by aquaculture practice and the cultural/political framework that exists in a given place. A series of questions that might then be asked regarding this landscape include (after Ahern, 2005):

- What is the proper spatial and temporal scale for understanding ecological patterns and processes in the estuarine landscape?
- How large a habitat patch (shellfish bed, eelgrass meadow) is required to support a given species or ecological process?
- Do these habitats form a “corridor” that connects larger habitat areas and if so what configuration of corridors is necessary to sustain species or ecological processes across the estuarine landscape?
- Which species or species group should be planned for? Can a particular “indicator” species represent the habitat needs of a group of species?
- Are there ecological interactions between shellfish aquaculture and other common anthropogenic disturbances at landscape scales?
- How does a particular estuary constrain or support an ecological process?
- Estuaries are open systems and connected and influenced by the nearshore coastal ocean and the watershed – how does this affect the ecological processes?
- How should aquaculture as a disturbance be understood in the estuarine landscape?
- Within cultural and economic constraints, can aquaculture be incorporated into estuary planning to lessen or enhance the potential effects to these other habitats and therefore species that utilize them?

These questions about the influence of habitat configuration on organism abundance and behavior at broad spatial scales (relative to the organism being studied) have been widely examined in terrestrial systems (Kareiva, 1987; Forman, 1995; Mazerolle and Villard, 1999; Debinski and Holt, 2000; Lindenmayer and Fischer, 2006), but only recently considered for marine habitats like eelgrass beds and oyster reefs (Brooks and Bell, 2001; Fonseca et al., 2002; Salita et al., 2003; Harwell, 2004; Darcy and Eggleston, 2005; Grabowski et al., 2005; Hovel and Fonseca, 2005; Bostrom et al., 2006; Connolly and Hindell, 2006; Johnson and Heck, 2006; Tanner, 2006; Hinchey et al., 2008). Increased connectivity between marine populations due to passive dispersal of larval stages and juveniles over large areas suggests that landscape scale processes differ in marine systems though there are clearly parallel processes to be explored. Corridors and habitat fragmentation have been shown to be less important, particularly for many invertebrates with pelagic larvae, but also for more sedentary adults (e.g. bivalves and small polychaetes, Bowden et al., 2001; Tanner, 2005; Cole et al., 2007). Fragmentation, patchy seagrass beds, and increased habitat edges may actually enhance diversity and increase the density of some bottom feeding invertebrates like decapod crustaceans and fish, whereas larger seagrass meadows may harbor higher numbers of smaller cryptic species (Salita et al., 2003; Tanner, 2005; Selgrath et al., 2007). Clearly other factors are also important like water depth, water movement, predation and organism behavior and motility (Irlandi et al., 1995; Darcy and Eggleston, 2005; Jackson et al., 2006; Horinouchi, 2007). Effects at the estuarine landscape scale are potentially more important for motile organisms with increased perception of structure at this scale and a greater home range which also provides important linkages between habitats like seagrass and

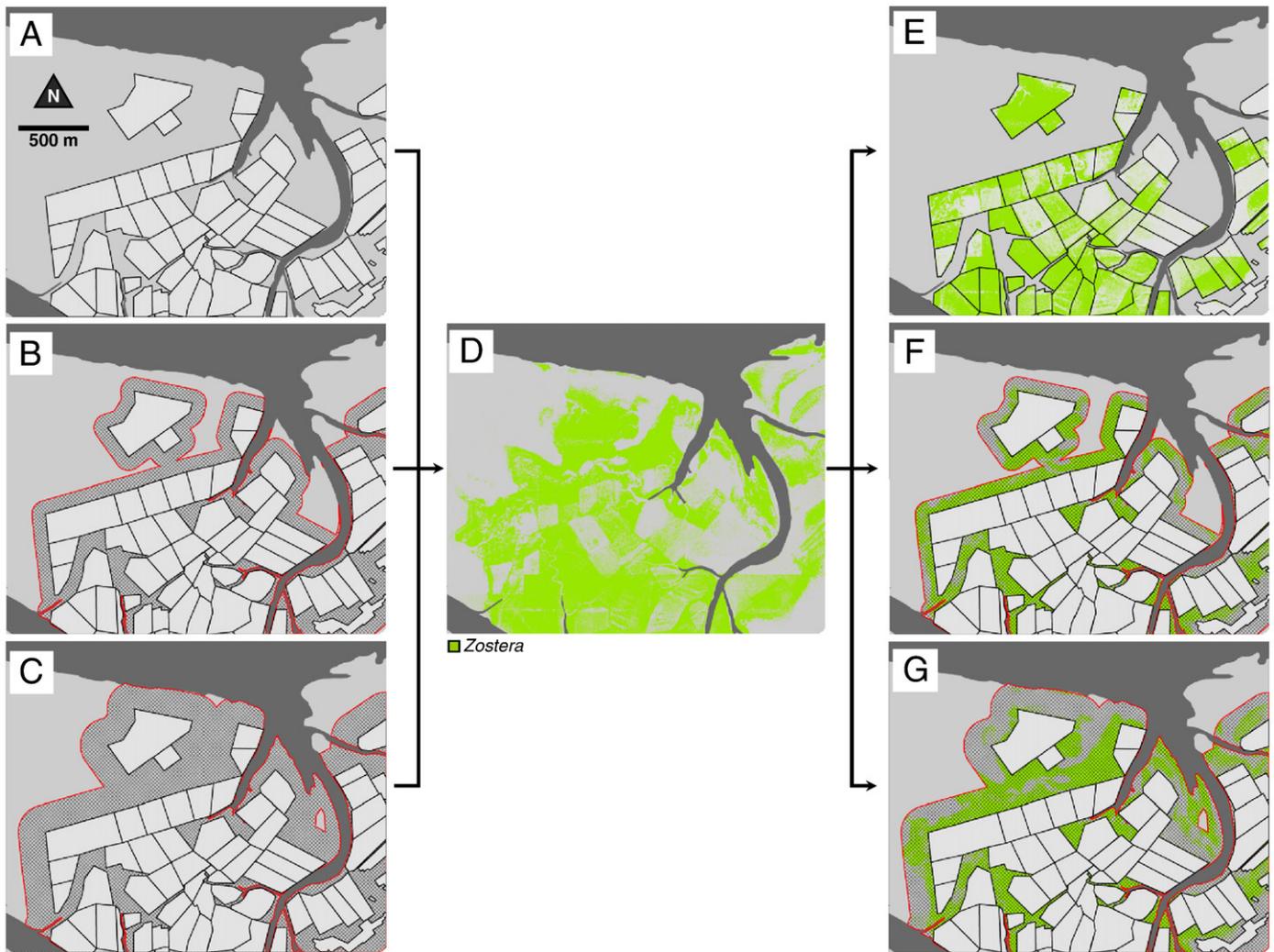


Fig. 7. Infrared aerial photography of an area near Stony Point in Willapa Bay, Washington was used to determine presence of intertidal vegetation (*Zostera* green shading, D). A separate layer was created which shows the distribution of active oyster aquaculture (A, top left) based on interviews with growers and both a 100 m and 200 m buffer zone around the edge of the culture areas (B and C). Estimates were then made of the proportion of the total area represented by *Zostera* in each of these zones (E, F, G). Although it represents a temporal snapshot (May 2005), the proportion of area covered by vegetation is comparable inside and outside aquaculture in these zones (46% inside aquaculture, 50% in 100 m buffer, and 44% in 200 m buffer).

marsh (Irlandi and Crawford, 1997; Simenstad and Cordell, 2000; Bostrom et al., 2006).

There have been few landscape-level approaches to bivalve shellfish aquaculture, although some progress has been made in Willapa Bay, Washington. Here, there are estimates of the total amount of different habitat types and how these have changed over time. In addition, the behavioral response of selected species (salmon, crab) has been studied across habitat types including bivalve shellfish aquaculture areas by these larger mobile organisms as discussed in Section 5.3 above (Pinnix et al., 2005; Holsman et al., 2006; Hosack et al., 2006; Semmens, 2008). Nonetheless, the influence of aquaculture has not yet been examined at a landscape scale on the West Coast of the U.S. and new work will need to be done to address such landscape-level features as patch size, connectivity, and the population response of organisms. Managers and regulators rightly suggested a general “no net loss” policy for estuarine wetlands which include eelgrass. This constraint has focused their efforts to date on protecting existing eelgrass as valued structured benthic habitat without much consideration of other forms of habitat or the location and scale of eelgrass habitat. Studies to date have also mostly examined organism presence and density in a given habitat and not broad scale spatial pattern or functional roles of these habitats. It could be that some habitats are more important than others at a

broader landscape scale (e.g., as protective cover near channel edges for juvenile salmon) and that the configuration of both shellfish and submerged aquatic vegetation as habitat is also important because it provides food for larger more mobile organisms at that scale (e.g., for juvenile salmon, English sole, or shorebirds and waterfowl as discussed above) and protective cover and food for others (e.g. for juvenile crab). Applications might be gleaned from work in the terrestrial environment where agricultural field margins and forest edges have been considered and managed as valuable habitat (New, 2005).

Despite the generally negative results of disturbance to eelgrass from aquaculture on small spatial and short temporal scales discussed above, eelgrass is generally present and intermingles with shellfish on all aquaculture beds at the tidal elevation where it is found naturally in Willapa Bay, Washington. Studies conducted to date have not evaluated historical records to indicate either loss or gains in eelgrass habitat over time, nor whether eelgrass would have been present regardless of subsequent aquaculture activity. Across Willapa Bay as a whole, shellfish aquaculture currently occupies about 13% of the estuary (4625 ha) and 20% of the tidelflat (B.R. Dumbauld, unpubl. data; Feldman et al., 2000). It has likely historically replaced at least two other habitat types: monospecific eelgrass (*Z. marina*) and burrowing shrimp (*N. californiensis* and/or *Upogebia pugettensis*).

Interestingly, the application of carbaryl to remove burrowing shrimp may actually enhance eelgrass (both the native species and a non-native congener *Z. japonica*, Dumbauld and Wyllie-Echeverria, 2003). With the exception of changes in practices like switching from on-bottom culture to off-bottom culture in some locations, the press (oyster addition) and pulse (planting and harvest operations) disturbances of oyster culture have not changed materially for decades (Ruesink et al., 2006), so there is no reason eelgrass would necessarily be worse off now than in the recent past. Indeed, there is scientific evidence that eelgrass fluctuates with environmental conditions (Thom et al., 2003) and compelling evidence that it has been expanding its distribution in Willapa Bay (Ruesink et al., in review) and other estuaries along the open coast of the western U.S. even though it is declining elsewhere in the world (Orth et al., 2006) and in isolated locations on the U.S. West Coast (e.g. Hood Canal and San Juan Archipelago in Puget Sound, Gaeckle et al., 2007; Mumford, 2007). Based simply on tidal elevation, Willapa Bay was estimated to contain 3139 ha suitable for *Z. marina* (0 to –1.2 m MLLW) in the 1850 s, increasing to 4845 ha in the 1950s as the bathymetry became shallower (Borde et al. 2003). A recent estimate based on aerial photography (3424 ha) may be slightly lower than the potential area because other habitat types (e.g. aquaculture, burrowing shrimp) also occur at the same elevations (Ruesink et al. 2006). The two *Zostera* species together may cover 4935 ha (B.R. Dumbauld, unpubl. data) or 6162 ha (Ruesink et al. 2006). Despite their chemical control for aquaculture, burrowing shrimp currently also occupy a very large intertidal area in Willapa Bay (3060 ha = 13.5% of the intertidal; B.R. Dumbauld, unpubl. data). They have probably fluctuated in abundance and would have the potential to occupy a much larger area if shrimp control had not occurred, with attendant effects on both native and non-native species of *Zostera* and associated benthic community. Simenstad and Fresh (1995) estimated that 12.6% of an area near Stony Point in Willapa Bay was highly disturbed due to aquaculture with little to no eelgrass present. Despite the obvious signature from oyster culture disturbance however, when we re-examined the proportion of area with eelgrass present in oyster culture beds and

compared it to that area at a similar tidal elevation just outside oyster culture (where eelgrass would be expected to occur) in the same Stony Point vicinity (2005 data, Fig. 7), we found little difference in eelgrass cover (46 versus 50%). Such comparisons are merely one-time snapshots of the presence of vegetative cover and more thorough analyses of a larger area over a slightly longer temporal scale with more descriptive categorizations of bed use will reflect the importance of vegetative recovery processes and perhaps other details discussed in above sections. In contrast, historical estimates do not account for occupation by other species, for instance, based on crude maps from the late 1800's, native oyster *O. lurida* beds occupied 2700 ha (12% of the low intertidal and shallow subtidal) that now consists of relatively undisturbed and dense native eelgrass meadows (Collins, 1892; Townsend, 1896; Sayce, 1976). Thus shell habitat has always been present in Willapa Bay, although its current distribution is at a higher tidal elevation than would be assumed from a contemporary projection, or than is present at other important West Coast locations (Tables 2 and 3). These spatial analyses have rarely been conducted in West Coast estuaries (but see Carswell et al., 2006 for Baynes Sound, British Columbia, Canada and Ward et al., 2003 for Bahia San Quentin, Mexico).

8. Resilience – management implications and research needs

Shellfish aquaculture has been an important activity and has supported local economies along the West Coast of the U.S. for at least 100 years. At present temporal and spatial scales in West Coast estuaries, our review suggests that the practice of shellfish aquaculture viewed as an ecological disturbance seems much more sustainable than other human activities such as freshwater diversion, coastal development and pollution, which continue to degrade estuarine function. On a global scale however, aquaculture is expanding and so may pressure to increase regional use of estuaries for bivalve culture. We end this review with some conclusions, caveats, and research needs which we hope will be useful to managers and decision-makers.

Table 3
Status of aquaculture in some U.S. West Coast estuaries and a possible classification system (after Weinstein and Reed, 2005) which could be used as a starting point for discussing sustainability and future planning.

Estuary	Area (km ²)	Existing aquaculture (h)	Proportion	Types	Other anthropogenic disturbances in order of importance	Possible classification zones
Baynes Sound, British Columbia, Canada	87	458	0.053	Oyster – bottom–deepwater clams	Nutrients	Zones: Production, Conservation
Totten Inlet, Puget Sound WA	24.7	85	0.034	Clams, geoducks, oysters on bottom, racks, off-bottom	Nutrients,	Production/conservation
Grays Harbor, WA	255	364	0.014	Oyster – longline, bottom	Nutrients, dredging	Zones: Production, urban-industrial
Willapa Bay, WA	358	4626	0.129	Oyster – longline, bottom clams	Marsh fill	Production
Tillamook Bay, OR	37.3	1014.8	0.272	Oyster – bottom, long-line	Nutrients, marsh fill	Production
Netarts Bay, OR	11.1	154.2	0.139	Oyster – bottom	Nutrients	Production/conservation
Salmon River, OR	1.8	0	0	Na	Marsh fill	Conservation
Siletz Bay, OR	5.9	0	0	Na	Nutrients	Conservation
Yaquina Bay, OR	17.6	210	0.119	Oyster – raft, on bottom	Marsh fill, nutrients, dredging	Zones: Urban industrial, production/conservation
Alsea Bay, OR	10.2	0	0	Na	Nutrients	Conservation
Coos Bay, OR	53.8	97.3	0.018	Oyster – bottom, long-line	Nutrients, Marsh Fill, Dredging	Zones: Production, conservation, urban-industrial
Humboldt Bay, CA	67	121.4	0.018	Oyster – longline	Marsh Fill, Nutrients	Zones: NB = production SB = conservation
Drakes Estero, CA	9.2	12.1	0.013	Oyster – racks and bag on bottom	Nutrients	Conservation/production
Tomaes Bay, CA	28.5	240	0.08	Clams	Nutrients	Production
San Francisco Bay, CA	1060	0	0	Historical oyster harvest	Diking and fill, Modified FW flow, nutrients	Zones: Urban industrial, conservation

Aquaculture numbers represent estimates of actual ground used for culture as determined from grower interviews for Willapa Bay and Grays Harbor, WA and actual fingerprint used for California estuaries (Tom Moore, Calif. Dept. Fish and Game).

In contrast, figures include total area leased from the state for Oregon estuaries (John Byer, Oregon Dept. of Agriculture) and total owned and/or leased ground for Totten Inlet (Dan Cheney, Pacific Shellfish Institute), and total tenures from Carswell et al. (2006) for Baynes Sound. Thus proportion of estuary occupied by culture for some estuaries is likely over-estimated. Estuarine areas for Oregon are from (Cortright et al., 1987).

From a manager or land-use planner's perspective, the first consideration in evaluating shellfish aquaculture in a given estuary should be an answer to the question: What are we and/or should we be managing for? Estuaries have a wide range of potential functions, have been and will continue to be influenced by many human activities, and similarly are influenced by many natural disturbances in addition to shellfish aquaculture. While the current paradigm for most managers is whole “ecosystem based” management (Grumbine, 1997), in reality managers have only progressed to varying degrees down this path, especially for marine systems. Thus the answer to “what are we managing for?” is driven by a wide variety of stakeholders and societal values (social historical, political, moral and aesthetic as well as economic; Leslie and McLeod, 2007; Weinstein, 2007; Ruckelshaus et al., 2008). Although these values are outside the purview of our intended review, we found it instructive to at least classify West Coast estuaries by the current level of aquaculture and other anthropogenic disturbance as Weinstein (2007) propose. Willapa Bay and Humboldt Bay might therefore be considered “production” estuaries with greater than 10% of the area occupied by shellfish aquaculture, while numerous other smaller estuaries with little aquaculture could be classified as other types (though the proportion of total estuarine area leased for aquaculture in some of these systems is also greater than 10%, leased does not necessarily mean actively used, Table 3). Portions of estuaries might also be classified or zoned separately this way (e.g. the South Slough portion of Coos Bay, Oregon or South Bay portion of Humboldt Bay, California). These classifications would then further help set goals and priorities for management and restoration, an activity which also involves social decisions about what should be “restored” (Simenstad et al., 2006). Classifications of production and production/conservation would be compatible with sustainable aquaculture, whereas areas classed as conservation or conservation marine within estuaries might not include aquaculture depending on the level of anthropogenic influence and goals for sustaining traditional commercial and recreational products desired. These decisions would obviously vary by jurisdiction. In Washington state for example, a critical societal decision was made in 1895 with passage of the Bush and Callow Acts which deeded 18,932 h of tidelands to private ownership specifically for the purpose of commercial shellfish culture. This set the stage for continued industry involvement and emphasis as a priority activity. Within such a framework which simply recognizes the current status and constraints on these systems, we offer the following conclusions specific to bivalve aquaculture as disturbance, its relevance to resilience in West Coast estuaries, and suggestions for future research:

1. Bivalves process phytoplankton and alter the forms and distribution of nitrogen in a system. In typical U.S. West Coast systems evaluated to date, water column and sediment nutrient concentrations are generally relatively high and greatly influenced by the proximity to deeper nearshore ocean waters where upwelling controls production during summer months. The situation may be different for small systems such as coastal lagoons or portions of large fjords like Hood Canal in Puget Sound, Washington where circulation is restricted. Very little modeling of whole-system energy and nutrient budgets, including aquaculture, has been done regionally, although the methods are well worked out in Europe. We suspect, however, that terrestrial and anthropogenic nutrients will figure less prominently than in many other places where bivalves are grown. Studies that expand on work like that completed for Willapa Bay, Washington showing the potential for bivalves in one part of the estuary to limit production in another part (Banas et al., 2007), and comparisons with other systems including portions of fjords like Puget Sound, Washington would be extremely useful research avenues. Intermediate bed scale studies such as those conducted using flow models and benthic nutrient flux estimations within given estuaries (Newell et al., 1998; Porter

et al., 2004) will still be necessary to calibrate the larger landscape scale estimations, particularly with new species or culture techniques (e.g. geoducks in tubes, oysters on longlines).

2. Some bivalves and culture practices modify estuarine habitat at local community and at landscape scales. The effect of aquaculture is most often evaluated against existing structured habitat in the form of submerged aquatic vegetation. While bivalve aquaculture might be viewed as a press disturbance over the long term in a given area, the individual activities act as pulse disturbances and *Z. marina* in U.S. West Coast estuaries can recover to pre-disturbance levels relatively rapidly (within a period of 2 years in some systems). This is usually before the next planting or harvest disturbance occurs, but depends on conditions and the aquaculture practice (e.g. oyster fattening beds might be rotated on a yearly basis and thus disturbance is frequent, while seed-harvest beds are left undisturbed for 2 to 4 years). Furthermore, the extent of the effect depends on the practice (hand harvest versus dredge harvest, longlines versus on-bottom culture). The current distribution of eelgrass reflects a balance of space competition, pulse disturbance and recovery, and is therefore at dynamic equilibrium on aquaculture beds (albeit generally lower than in undisturbed eelgrass meadows). Research is still needed on factors that cause plants to alter their reproductive strategy and enhance seedling production (Wisehart et al. 2007), whether plants respond differently to disturbance across seasons, particularly since densities vary naturally over the year (Ruesink et al., in review) and finally on the effect this has at larger spatial scales (growing areas to estuary) and over relevant temporal scales (at least the lifetime of a shellfish crop = 3 or 4 years).
3. The role of aquaculture (organisms themselves and support structures) as estuarine habitat should also be considered. For small benthic infauna and mobile epibenthic fauna, structure provided by aquaculture appears functionally similar to eelgrass, based on invertebrate abundances and composition measured to date in West Coast estuaries. For larger benthic invertebrates and fish, use of habitat depends on mobility and varies with life-history stage and taxon being evaluated, so temporal and spatial scales are important considerations. Though less is known about habitat function for these larger more mobile organisms, they can use structure for protection from even larger predators (juvenile salmon in eelgrass and 0+ Dungeness crab in oyster), but still rely on other habitats for foraging (1+ Dungeness crab in unstructured open habitat). Given the presence of mixed habitats (i.e. eelgrass within aquaculture beds), it would be valuable to determine relationships between eelgrass density and its ecosystem function, effective habitat patch sizes, and corridor use at a larger landscape scale. This may be an area where best management plans can be designed and implemented since the shellfish industry would likely be supportive of maintaining habitat corridors (e.g. eelgrass along channel edges) and timing windows (e.g. limited harvest operations in some areas during fish spawning or bird migration periods) should they prove necessary.
4. Finally, it is important to consider estuarine changes not simply in terms of departure from baseline, but as they influence resilience, that is, capacity of the system to withstand or recover from other shocks. Aquaculture as disturbance is generally within the scope of existing “natural” disturbances to the system (e.g. winter storms) and other ecosystem engineers (e.g. eelgrass and burrowing shrimp) are also inherently adapted to this scale of disturbance. Certain anthropogenic disturbances have reduced estuarine resilience, for instance habitat removal via wetland diking and filling, hardening of surfaces in the watershed, nutrient additions, invasive species such as *Spartina*, and possibly food web modifications like removal (sharks, skates and sturgeon) or protection (harbor seals and sea lions) of large predators. In contrast, bivalve aquaculture does not remove area from the estuary or degrade water quality,

and thus is less likely to undermine resilience. Though local and short term effects are clearly evident in U.S. West Coast estuaries, bivalve aquaculture has not been implicated in shifts to alternate states or reduced adaptive capacity of the larger ecological system. Typical thresholds that might be involved in such catastrophic change would likely be reached first with other human disturbances (e.g. nutrients and predator removal), although location and scale remain important management considerations (e.g. small inlets with stratified water columns and less routine physical disturbance might exhibit lower thresholds to large scale aquaculture operations).

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