

Accepted Manuscript

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PII: S0044-8486(09)00192-6
DOI: doi: [10.1016/j.aquaculture.2009.02.033](https://doi.org/10.1016/j.aquaculture.2009.02.033)
Reference: AQUA 628657

To appear in: *Aquaculture*

Received date: 30 October 2008
Revised date: 22 February 2009
Accepted date: 23 February 2009



Please cite this article as: Dumbauld, Brett R., Ruesink, Jennifer L., Rumrill, Steven S., 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, *Aquaculture* (2009), doi: [10.1016/j.aquaculture.2009.02.033](https://doi.org/10.1016/j.aquaculture.2009.02.033)

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**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.

Keywords: Aquaculture, Disturbance, Eelgrass, Estuary, Bivalve, Ecology

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),

48 which asserts jurisdiction under the Clean Water Act (Section 404) and the Rivers and Harbors
49 Act (Section 10). In March 2007, the ACOE issued a new nationwide permit for shellfish
50 aquaculture which in turn requires consultation with the US Fish and Wildlife Service (USFWS)
51 and the National Oceanic and Atmospheric Administration (NOAA) for their regulatory
52 authority under the Endangered Species Act (ESA) and Essential Fish Habitat (EFH) provisions
53 of the Magnuson Stevens Fishery Conservation and Management Act.
54

55 Because the “best available science” with which these agencies have chosen to address
56 regulatory issues is limited, especially for aquaculture on the West Coast, the agencies have
57 tended to be very cautious about perceived impacts to habitats and/or communities of estuarine
58 organisms that have been studied in greater detail elsewhere. Perhaps the best example is simply
59 not permitting or requiring mitigation for aquaculture activities in areas where submerged
60 aquatic vegetation is present, due to its recognized importance to fish and invertebrates
61 elsewhere and a federal goal of “no net loss of wetlands” that is generally applied to any activity
62 in these environments. This “precautionary” approach has directly affected existing aquaculture
63 operations in California and Oregon, where growers have been forced to abandon historic culture
64 areas or switch to off-bottom culture, particularly in areas where seagrasses are present (Chew,
65 2001; Rumrill and Poulton, 2004). A federal review is currently underway by ACOE and
66 NOAA to determine how the laws discussed above will be administered on a nationwide basis.
67 Commercial shellfish growers have taken a pro-active role in this issue by developing their own
68 environmental management system, codes of practice and a regional research plan (PCSGA,
69 2001; PSI, 2005). This scientific review is a response to the need for establishing a baseline of
70 relevant scientific information to inform impending management decisions.
71

72 In this review of the role of bivalve mariculture in estuarine ecosystems, we use an ecological
73 framework that describes aquaculture practices as a disturbance (c.f. Simenstad and Fresh, 1995).
74 We adopt the definition of disturbance used by Pickett and White (1985): “a disturbance is any
75 relatively discrete event in time that disrupts ecosystem, community, or population structure and
76 changes resources, substrate availability, or the physical environment”. In this context
77 disturbances vary in their spatial scale, frequency, and intensity, which are relevant, respectively,
78 to bed size, crop cycle, and type of aquaculture activity. We qualitatively distinguish “pulse”
79 (short discrete events) from “press” disturbances (longer-lasting chronic events), despite their
80 subjective definitions that imply a difference in the pace of the response (Glasby and
81 Underwood, 1996). Nevertheless, the distinction is useful in considering, for instance, the
82 effects of the farmed organisms, which are regularly present (press disturbance), and the effects
83 of harvest operations, which occur periodically in the crop cycle (pulse disturbance). Disturbance
84 has been viewed as a key process influencing marine benthic community dynamics for several
85 decades (Sousa, 2001). Indeed, natural disturbances are essential components in the maintenance
86 of community structure in some ecosystems (e.g. fire in many terrestrial ecosystems), even
87 though they can have immediate negative effects on the abundance of some species.
88 Anthropogenic disturbances may mimic such natural disturbances, although multiple, novel
89 perturbations can exceed a system’s capacity to maintain its characteristic state (Sousa, 1984;
90 Paine et al., 1998). This capacity to recover, or resilience (Holling, 1973), depends on such
91 factors as the extent of the disturbance relative to the mobility of key species, and the frequency
92 of disturbance relative to generation time (Paine et al., 1998; Peterson et al., 1998). Recent
93 ecological literature suggests that the likelihood of regime shifts to alternate states can increase

94 when anthropogenic disturbance causes reduced “ecological” resilience (Gunderson, 2000; Folke
95 et al., 2004; Scheffer et al., 2005; Groffman et al., 2006; Walker et al., 2006; Levin and
96 Lubchenco, 2008). Using “disturbance” as a descriptor in a management context may involve a
97 perception that disturbances are “negative”. This is true only if the species of interest has
98 “positive” value to the manager and the disturbance causes loss. Here, we describe aquaculture
99 disturbance effects on species and ecosystems, but leave positive or negative value judgments to
100 readers and managers.

101
102 Bivalve shellfish aquaculture influences the system in three primary ways 1) material processes -
103 bivalves process food and produce wastes; 2) physical structure – aquaculture introduces the
104 cultured organisms themselves and in many cases a physical anchoring structure; and 3) pulse
105 disturbances – harvest activities, in addition to some bed maintenance practices, can remove
106 species in addition to the cultured organisms themselves, and change resource or habitat
107 availability (Figure 1). These influences occur on the time scale of the crop cycle (1-6 years,
108 depending on area, method, and species) and do not include such longer-term changes as the
109 introduction of non-native organisms during imports for aquaculture. Introduction of non-native
110 species is an important management issue, particularly when they become invasive, but
111 aquaculture and other vectors for marine invasions have been reviewed elsewhere (Gruet et al.,
112 1976; Carlton and Mann, 1996; McKindsey et al., 2007; Minchin, 2007), and regulations and
113 practices have changed to reduce the role of aquaculture imports in homogenizing biota (e.g.
114 ICES Code of Practice on the Introductions and Transfers of Marine Organisms, ICES 2005).

115
116 Our focus is on the intertidal culture of bivalve mollusks in estuaries along the West Coast of
117 North America, particularly oysters because of the great spatial extent of estuarine area devoted
118 to their culture and relatively large amount of research conducted to date. Although a similar
119 review was conducted by Simenstad and Fresh (1995), substantial progress has been made
120 toward quantifying the role of bivalve aquaculture in the estuarine environment since that time.
121 Our intent is not to repeat their earlier effort, nor provide an exhaustive bibliography, but instead
122 to update with new results and place in context with recent ecological literature from outside the
123 U.S. West Coast. We begin with sections highlighting why these West Coast estuaries are
124 distinct and how bivalves have been and are currently cultured there. Material processing,
125 physical structure, and pulse disturbance associated with some aquaculture practices represent
126 three interrelated aspects of the ecological role of shellfish aquaculture. Each topic is considered
127 in its own section, first with generalizations from research worldwide, and then a summary of
128 results from studies on the West Coast of North America in particular. In many cases, the
129 evidence from West Coast estuaries aligns well with international perspectives; in some cases,
130 the characteristics of West Coast estuaries lead to different ecological roles of shellfish
131 aquaculture than have been demonstrated elsewhere; and finally, in most cases, the relatively
132 nascent area of research on environmental impacts means that the picture for West Coast
133 estuaries remains incomplete. In the final section, we address important research gaps,
134 particularly at the landscape level that remain to be filled in order to make sound management
135 decisions, though we recognize that such decisions clearly involve social and economic criteria
136 as well.

137
138 **2. Characteristics of West Coast Estuaries**

139

140 The major shellfish-growing areas on the West Coast of the U.S. include small coastal estuaries
141 in California, Oregon, and Washington, as well as Puget Sound, which is a deep fjord extending
142 several hundred km inland. Similarly, in British Columbia, Canada, bivalve aquaculture occurs
143 both in small sounds on the west side of Vancouver Island and within the Strait of Georgia.
144 Alaska's shellfish aquaculture industry is in its infancy but has grown markedly and oyster
145 culture occurs primarily in remote geographic locations within areas like Kachemak Bay and
146 Prince William Sound (Harrington, 2005; Oliveira et al., 2006). Four bivalve species contribute
147 99% of production from aquaculture in this region with Pacific oysters (*Crassostrea gigas*)
148 representing 89%, and Washington leads production on a per-state basis, with production split
149 about evenly between outer coast estuaries and Puget Sound (Table 1). West Coast estuaries
150 have three general characteristics that set the context for aquaculture: they are geologically
151 young and small; they have substantial oceanic influence; and they harbor distinct and relatively
152 species-poor ecological communities. We treat each of these issues in turn.

153
154 Estuaries on the West Coast of North America are geologically young and relatively small
155 compared to other well studied estuarine systems like Chesapeake Bay, but comparable in size to
156 other shellfish growing areas (Table 2). Only small remnants of the larger estuaries once present
157 along the U.S. Pacific Coast in the Miocene and Pliocene epochs remain, due to subsequent
158 uplift of the nearby landmass and estuarine infill (Jacobs et al., 2004). Further disturbances and
159 oscillations due to glaciation and sea level change have subjected these estuaries to frequent
160 flooding and emptying due to their small size (e.g. subsidences of 0.5 to 2m have occurred
161 multiple times with tectonic events in the last 7,000 years (Atwater, 1987; Hagstrum et al.,
162 2004). Combined with a relatively steep elevation gradient nearby, this causes these estuaries to
163 provide much more spatially restricted and less stable environments than their larger counterparts
164 on the Atlantic and Gulf Coasts. On the other hand, it would be incorrect to consider all of the
165 region's estuaries as identical in abiotic features: substantial variation occurs in climate,
166 mesoscale oceanographic features, and bathymetry, especially along the wide latitudinal range
167 stretching from Alaska to California. Mesoscale oceanographic features establish faunal
168 discontinuities (e.g. Cape Mendocino, Point Conception, Columbia River plume). Bathymetry
169 varies because estuaries have formed at drowned river valleys (small coastal estuaries) and in
170 deep fjords (especially Puget Sound and the Strait of Georgia; Emmett et al., 2000). Human
171 impacts also vary regionally, for instance San Francisco estuary in California experienced
172 substantial shoreline development, urbanization, and tideflat "reclamation", which caused severe
173 water quality impairment and abandonment by the oyster industry in 1939 (Barrett, 1963) as
174 have other smaller estuaries in Southern California (Pitman, 1995). Smaller coastal estuaries of
175 Northern California, Washington and Oregon generally have lower human population densities
176 than does the Puget Sound trough, where water quality problems have also been more pervasive
177 (Glasoe and Christy, 2004).

178
179 West Coast estuaries experience pronounced effects of the nearshore coastal ocean (Hickey and
180 Banas, 2003). Coastal estuaries lie along an upwelling coast, and mesotidal conditions, combined
181 with small size and extensive intertidal flats, contribute to substantial tidal exchange with the
182 ocean (Table 2). For instance, Willapa Bay, Washington can exchange nearly half its volume
183 during a single spring tide and the tidal exchange is about 40% in Coos Bay, Oregon. Even Puget
184 Sound, due to the influx of ocean water at depth, shows signs (salinity, carbon) of ocean
185 influence throughout its length (Babson et al., 2006; Ruesink et al., in prep). In addition,

186 freshwater input is restricted during summer due to a Mediterranean climate pattern of winter
187 rain and summer drought to the extent that smaller estuaries in California are hypersaline lagoons
188 (Largier et al., 1997). Thus terrestrial inputs are generally less important for food webs than in
189 other estuaries, because winter inputs coincide with low temperatures that limit productivity.
190 Nevertheless local effects of rivers and small streams have been demonstrated in the riverine
191 region of both Willapa Bay and smaller coastal estuaries in summer (Ruesink et al., 2003;
192 Rumrill and Sowers, 2008). Winter inputs have been studied in San Francisco Bay where the
193 North Bay shows evidence of terrestrially driven production despite anthropogenic water
194 diversion (Thompson, 2005). Overall, oceanic conditions greatly influence both primary and
195 secondary production within these systems (Roegner et al., 2002; Ruesink et al., 2003). Although
196 the Mediterranean climate pattern ameliorates two types of natural disturbances with strong
197 effects elsewhere in the U.S (winter ice in Northeast estuaries and hurricanes on the Southeast
198 and Gulf Coasts), shallow intertidal flats in West Coast estuaries and extreme tidal exchange
199 may nevertheless result in severe pulse disturbances from winter storms.

200
201 Although the continental shelf fauna along the West Coast is diverse, estuaries are relatively
202 species-poor in a number of functional groups, possibly as a result of their comparatively short
203 geologic history. We suspect that this short list of native species contributes to: 1) the availability
204 of few native bivalves suitable for aquaculture, and therefore the adoption of primarily non-
205 native species, 2) small numbers of estuarine-dependent fishes, and 3) “empty niches” for high-
206 impact invasions. Cultured species in West Coast estuaries are predominantly non-native and
207 have developed self-sustaining feral populations in some areas. This dependence on non-native
208 bivalve species makes the U.S. West Coast similar to Europe (where Pacific oysters and Manila
209 clams are also introduced and cultured), and different from the rest of the U.S. and Asia (Ruesink
210 et al., 2005). West Coast estuaries contain fewer species of estuarine dependent fish and
211 invertebrates, particularly those that use estuaries as nurseries, than their U.S. East and Gulf
212 Coast counterparts and display latitudinal trends in both abundance and diversity (Percy and
213 Myers, 1974; Horn and Allen, 1976; Haedrich, 1983; Monaco et al., 1992; Nelson and Monaco,
214 2000). This could simply be due to small estuary size, but also the relatively large proportion of
215 intertidal area, lack of significant freshwater input and their short geologic history. Similar
216 latitudinal differences between estuaries and less diverse fish communities in small shallow
217 estuaries have also been found in European, Tasmanian, South American, Australian and South
218 African estuaries (Potter and Hyndes, 1999; Edgar et al., 2000; Araujo and de Azevedo, 2001;
219 Pihl et al., 2002; Harrison and Whitfield, 2006). The mid to high intertidal flats of West Coast
220 estuaries are typically unstructured. High marsh occurs only above mean higher high water in
221 West Coast estuaries, and seagrass (native eelgrass, *Zostera marina*) occurs around mean lower
222 low water (Borde et al., 2003; Thom et al., 2003). With the exception of some relatively steep
223 gravel and cobble beaches in fjords from Puget Sound, Washington north to Alaska, nearly all
224 intertidal aquaculture activities take place on low gradient mud and sandflats, habitats that
225 naturally have little structure in the region, except where aquaculture overlaps with native
226 eelgrass. However some unwanted species have also entered this zone, forming structure in what
227 is essentially an “empty niche”. These include several species of cordgrass (*Spartina* spp.)
228 which have prompted multi-million dollar control efforts and, from British Columbia to northern
229 California, an introduced seagrass, *Zostera japonica* (Daehler and Strong, 1996; Feist and
230 Simenstad, 2000; Bando, 2006; Ruesink et al., 2006; Rumrill, 2006). Although species-poor in
231 general, West Coast estuaries harbor several species of Pacific salmon (*Oncorhynchus* spp.),

232 anadromous fish that spend variable amounts of their early life-history in estuaries. Due to their
233 cultural importance and longstanding fisheries, salmon drive substantial management activity
234 and many subpopulations of salmon are extinct or listed as threatened or endangered under the
235 US Endangered Species Act. Although the declines are likely from a variety of causes extending
236 from freshwater to the ocean (Kareiva et al., 2000; Ruckelshaus et al., 2002; Good et al., 2007),
237 loss and/or substantial modification of estuarine habitat may not be compatible with salmon
238 recovery.

239
240

241 3. Historical Fisheries and Current Farming Practices

242

243 The most widely cultured bivalves in the United States are oysters, clams and mussels. Because
244 of the presence of shells in middens, it is clear that bivalves have been harvested from North
245 American estuaries for thousands of years (Trigger, 1986; Cannon, 2000). Coincident with
246 European colonialism, extensive harvest of native oysters (*Ostrea lurida*) on the West Coast
247 began in the mid-1800s (Baker, 1995), slightly after similar activity (for eastern oysters,
248 *Crassostrea virginica*) along the Atlantic and Gulf Coasts in the 17th and 18th centuries (Kirby,
249 2004). Initial harvest implements included sailing vessels, poled bateaux, and a variety of hand
250 tools (e.g. tongs), followed by dredges. Natural beds were gradually depleted on both U.S.
251 coasts, in part due to the lack of return of shell material for natural recruitment (Kirby, 2004;
252 Ruesink et al., 2005). When the native Pacific Coast oyster declined due to overharvest in the
253 late 1800's, eastern oysters (*C. virginica*) and later Pacific or Japanese oysters (*Crassostrea*
254 *gigas*) were transplanted to estuaries along the U.S. West Coast (Collins, 1892; Townsend, 1896;
255 Steele, 1964; Sayce, 1976; Lindsay and Simons, 1997; Robinson, 1997; Shaw, 1997). From at
256 least 1928 until 1977 (except during WWII), "seed" oysters were shipped from Japan to the U.S.
257 West Coast annually for transplant. Additionally, after Pacific oysters established naturally-
258 reproducing populations, some local production was possible. Waters were warm enough for
259 "natural" spawning and setting to take place in Pendrell Sound and Ladysmith Harbor in British
260 Columbia, and Dabob Bay and Willapa Bay, Washington (Scholz et al., 1984; Quayle, 1988).

261

262 With the advent of hatchery technology in the early 1980's (Nosho and Chew, 1991), oyster
263 aquaculture along the West Coast of the U.S. became a completely integrated farming operation
264 (see Conte et al., 1994 for a detailed description). Hatcheries are now essential to oyster
265 aquaculture in Alaska, Oregon, and California, and contribute substantially in Washington and
266 British Columbia, although naturally-set oysters continue to be incorporated when they are
267 available. Most production involves *C. gigas*, but several other oyster species are also cultivated:
268 *C. virginica*, *C. sikamea*, *C. ariakensis*, *Ostrea edulis*, and the native oyster *O. lurida*. In
269 hatcheries, adult broodstock are conditioned and induced to spawn. Larval oysters are fed
270 cultured phytoplankton until they are competent to settle and attach to a substrate (Muller-Feuga,
271 2000). This substrate is either pieces of shell (cultch) or ground shell or sand (cultchless). When
272 the oysters are moved into estuaries, they are grown utilizing a variety of methods including
273 bottom culture, floating bags, rack and bag systems, long lines and trays. In bottom culture,
274 cultch with attached oysters is placed directly on intertidal (generally <0.6 m MLLW) and
275 shallow subtidal bottom where it is left until the oysters reach market size, usually in one to three
276 years depending on location and temperature. In Willapa Bay, where oyster growth varies
277 substantially by area, oysters may be seeded to one area, allowed to grow for a period of one to

278 two years and then transplanted to a second area called a fattening bed for final growth. Beds
279 may also be harrowed with implements fashioned after the English pasture harrow (Sayce and
280 Larson, 1966) to bring oysters back to the surface and break up clusters. Oysters are harvested
281 (or collected for re-laying) from bottom culture by hand or with mechanical or suction dredges.
282 In long line culture, seeded cultch is strung on lines or ropes that are suspended from stakes or
283 rails and harvest is usually by hand. Cultchless oysters are often grown in high-density
284 polyethylene (HDPE) or polypropylene mesh bags placed on the bottom, suspended off the
285 bottom on racks, or placed in floating bags attached to longlines (Conte *et al.* 1994). Although
286 not a focus of this review, suspended culture is typically used in areas that are relatively deep
287 such as Puget Sound and especially British Columbia, Canada: seeded cultch is strung on lines or
288 cultchless oysters are placed in trays or lantern nets, and these are suspended from floats. After
289 harvest, single oysters are generally destined for the half shell market, and oyster clusters are
290 either separated into singles, or processed at a shucking plant where the meats are packaged in
291 containers for sale.

292
293 Oyster aquaculture contends with several pest species, most of which are predators or
294 competitors and controlled by hand removal (Buhle *et al.*, 2005). However, one species deserves
295 special attention because its control involves the application of a chemical pesticide. Burrowing
296 shrimp (*Neotrypaea californiensis*) are native deposit-feeders that bioturbate sediments up to 1 m
297 in depth. At high densities, they preclude on-bottom oyster culture because the oysters are
298 smothered or sink due to disturbance of the sediment by the shrimp. Since the 1960s, shrimp
299 have been removed from oyster beds through the application of carbaryl (Sevin™), a general
300 arthropocide (Feldman *et al.*, 2000). Its use is now only legal in Willapa Bay and Grays Harbor,
301 Washington where about 170 ha and 60 ha respectively (4% of the cultivated area and less than
302 1% of the tidelflat in Willapa Bay) are treated by aerial application from a helicopter each year.
303 Many species in addition to shrimp are killed by the pesticide, but the longer-term changes,
304 including appearance of eelgrass, derive from the removal of shrimp and addition of oysters
305 (Dumbauld *et al.*, 2001; Dumbauld and Wyllie-Echeverria, 2003; Dumbauld *et al.*, 2004). This
306 pesticide is scheduled to be phased out of use in these estuaries by 2012, but the most effective
307 alternative method of shrimp control discovered to date may also be chemical.

308
309 The West Coast harbors several native clams of historical importance to subsistence and
310 commercial fisheries. These include: butter clams (*Saxidomus giganteus*), littlenecks (*Protothaca*
311 *staminea*), horse clams or gapers (*Tresus capax* and *T. nutalli*), and geoducks (*Panopea*
312 *abrupta*). On outer coast sandy beaches, razor clams (*Siliqua patula*) are fished commercially
313 and recreationally (Lindsay and Simons, 1997). Eastern softshell clams (*Mya arenaria*) provided
314 a small commercial fishery after their introduction from the East Coast in the late 1800's, but
315 only during an initial post-invasion "boom" (Palacios *et al.*, 2000) and more recently in Puget
316 Sound. Clam aquaculture currently focuses on two species, one introduced (*Ruditapes*
317 *philippinarum*, Manila clam) and one native (*P. abrupta*). Manila clams apparently arrived from
318 Asia in the 1930s as a hitchhiker with oyster seed (Quayle, 1941; Chew, 1990). Growth in
319 production occurred when growers were able to "seed" areas with small clams produced in
320 hatcheries, at about the same time (1970s-80s) that such techniques were developed for oysters.
321 Farmed Manila clams produced in hatcheries are held in trays or upwellers during a nursery
322 period before being planted in a growout area or placed in mesh bags for growout (Toba *et al.*,
323 1992). Several techniques are employed to enhance ground for clam production. Growers

324 sometimes add gravel or oyster shell (Toba et al., 1992; Thompson, 1995), which provides
325 substrate for the attachment of naturally-settled clams and likely makes feeding more difficult by
326 some predators. Plastic or nylon netting of varying mesh is also often placed over clam beds to
327 reduce predation. Manila clam aquaculture tends to occur higher (0.6-1.2 m MLLW) in the
328 intertidal than does oyster culture. Harvest of planted tideflats is generally with a hand operated
329 rake to collect clams, which grow close to the surface, but some mechanized harvest methods
330 have also been developed (B. Dewey, pers. comm.). Worldwide, Manila clams are grown in
331 China and Korea where they are native (Zhang and Yan, 2006), and in Europe from Italy to
332 Great Britain, where they are introduced (Chew, 1990; Spencer et al., 1997).

333
334 A second clam species, the geoduck (*Panopea abrupta*) has recently become important for
335 aquaculture in Washington and British Columbia. Geoducks are very large clams (up to 3.25 kg
336 whole weight, Goodwin and Pease, 1991; Hoffmann et al., 2000) that have provided a valuable
337 subtidal fishery for several decades. As a fishery, clams are not planted, and “recovery” of
338 harvest tracts depends on recruitment which has only recently been assessed over appropriate
339 temporal and spatial scales (Orensanz et al., 2004). Aquaculture techniques have been applied
340 primarily to intertidal flats and have achieved crop cycles of ca. 5-6 years since growth is fast
341 during initial years and then slows (clams can grow to be well over 100 years old; Goodwin,
342 1976; Shaul and Goodwin, 1982; Hoffmann et al., 2000). Geoduck culture techniques continue
343 to evolve with survival in the hatchery and growout phases being highly variable. Protecting the
344 hatchery produced geoduck “seed” from predation and drying out at low tide is essential. To date
345 growers have largely used nursery tubes made by cutting 4-6” diameter PVC pipe into foot long
346 sections and partially embedding them in the sediment. Several small (1 cm) geoducks are
347 added, and mesh is placed over the top to exclude crabs and predatory snails (Beattie, 1992).
348 This mesh may cover tubes individually or extend over an array of many tubes, anchored only at
349 the edges (more like anti-predator nets used for Manila clams). The tubes are removed after 1-2
350 years, at which point the geoducks have reached a size and depth that avoids most predators and
351 precludes desiccation at low tide. The geoducks continue to grow for several more years before
352 reaching market size (15 cm shell length, approx. 1 kg whole weight). Harvest methods have
353 been borrowed from the capture fishery and involve loosening the sediment around each
354 geoduck with low pressure but high volume seawater forced through narrow tubes (stingers);
355 geoducks are then removed by hand.

356 357 **4. Shellfish as Filter Feeders and Material Processors**

358
359 When abundant, suspension feeding bivalve mollusks can serve as important links between
360 benthic and pelagic processes (benthic pelagic coupling) because they filter large volumes of
361 suspended particles from the water column and eject them as both uningested pseudofeces and
362 unassimilated feces which sink to the bottom (Newell, 2004). Bivalve aquaculture differs
363 importantly from the culture of most finfish and crustaceans (Pohle et al., 2001; Crawford et al.,
364 2003) in that cultured bivalves exploit naturally occurring phytoplankton at the base of the
365 estuarine food chain, thus obviating the need for external feed inputs. For this reason, shellfish
366 aquaculture does not result in additional nutrient loading, but rather, a transfer of nutrients from
367 water column particles to benthic sediments in biodeposits, rapid nutrient cycling when dissolved
368 inorganic nutrients are released into the overlying water, and a net removal of a portion of those
369 nutrients when shellfish are harvested.

370
371 Particles filtered by bivalves range in size from bacterioplankton to less mobile zooplankton and
372 include both living and non-living material, but most species are generally efficient at retaining
373 material down to 3 – 5 μm (LeGall et al., 1997; Ward and Shumway, 2004; Prins and
374 Escaravage, 2005; Lehane and Davenport, 2006; Lonsdale et al., 2007; Trotter et al., 2007).
375 Bivalves can influence the community of plankton present via selective feeding favoring removal
376 of picoplankton and phototrophic nanoflagellates over heterotrophic flagellates and diatoms in
377 summer months at some locations (Bougrier et al., 1997; Wetz et al., 2002) but also feed on re-
378 suspended microphytobenthos (Malet et al., 2007). Bivalves actively pump water through the
379 gills and the particles are sorted on the ctenidia and labial palps. Capture efficiency increases
380 non-linearly with particle diameter (Ward et al., 1998a). Captured particles are actively sorted by
381 both size and quality (though the mechanism for the latter is not well studied; Shumway et al.,
382 1985), and rejected particles become pseudofeces (Beninger et al., 1999). Oysters transport
383 smaller phytoplankton to the dorsal ctenidial tract and detritus and larger particles to the ventral
384 groove for sorting by the labial palps (Cognie et al., 2003). In contrast, particle sorting by
385 mussels occurs primarily at the labial palps (Ward et al., 1997; 1998b). Oysters also tend to be
386 able to cope with high seston loads by augmenting pseudofeces production, whereas clams and
387 scallops lower their clearance rates as particle concentrations increase (Newell and Langdon,
388 1996; Defosse and Hawkins, 1997; Hawkins et al., 1998; Chauvaud et al., 2000). Finally some
389 post-ingestive particle selection occurs in the stomach as the particle slurry moves across ridged
390 sorting areas and pouches to the digestive diverticula (Cognie et al., 2001; Brillant and
391 MacDonald, 2002; 2003). Assimilation efficiency varies with food source and how susceptible
392 the particles are to enzymatic breakdown (Langdon and Newell, 1996). Some of the absorbed
393 nitrogen is excreted as urine (primarily as NH_4). Both feces and pseudofeces are excreted by
394 bivalves as mucous-bound aggregates with higher sinking velocity (up to 40x) than the ingested
395 particles (Widdows et al., 1998). The particles gradually undergo a de-watering process and are
396 incorporated into the sediment adding to the nitrogen and phosphorous pools (Deslous-Paoli et
397 al., 1992; Hatcher et al., 1994). The feeding activities described here potentially allow bivalve
398 shellfish aquaculture to alter larger material processes in the estuary in the following ways: water
399 quality, sediment properties, and resources for primary producers indirectly through the release
400 of inorganic nutrients. We treat each of these in turn.

401 402 *4.1. Alteration of water quality*

403
404 Measurable effects on water properties hinge on the filtration capacity of bivalves relative to the
405 residence time of water in the estuary (Prins et al., 1998; Prins and Escaravage, 2005) –
406 simplistically, longer residence times give suspension-feeders more opportunity to remove
407 particles. This relationship is complicated however, not only by estuarine hydrography, but also
408 because phytoplankton population growth, not just grazing, influences density, particularly if
409 phytoplankton are supplied with readily available nutrients released by the grazers themselves or
410 by anthropogenic sources (Dame, 1996; Prins et al., 1998; Chapelle et al., 2000; Souchu et al.,
411 2001; Mazouni, 2004; Asmus and Asmus, 2005) Also, clearance rates are difficult to estimate in
412 the field (Riisgard, 2001), sensitive to seasonal variation, and only relevant to the volume of
413 water accessible to the benthos which can be modulated by structure created by the bivalves
414 themselves (Lenihan et al., 1996). The contribution of cultured bivalves to clearance is further
415 obscured when they represent an unknown fraction of all suspension-feeders (Heip et al., 1995;

416 Leguerrier et al., 2004; Pomeroy et al., 2006; Dubois et al., 2007; Putland and Iverson, 2007),
417 though this has also been measured and models developed to quantify it in some places (Sauriau
418 et al., 1989; Leguerrier et al., 2004; Grizzle et al., 2008; Sequeira et al., 2008). Although it
419 represents a relatively small contribution (1% of the meat weight), nitrogen is also removed from
420 the system when actively growing shellfish are harvested (Lindahl et al. 2005). Finally, even if
421 one is able to assess and detect alterations in water quality due to the presence of farmed
422 bivalves, questions regarding scale and relevance such as whether they “improve water quality”
423 or “exceed the system’s carrying capacity” remain. We suggest that water clarity improvement
424 will be more important in areas experiencing cultural eutrophication, and carrying capacity
425 concerns will be informed by considering current relative to historic bivalve and other filter
426 feeder densities.

427
428 Substantial work has been carried out worldwide on bivalve carrying capacity, especially via
429 coupled biological-physical models (Dame and Prins, 1998; Gangnery et al., 2001; Sara and
430 Mazzola, 2004; Duarte et al., 2005; McKindsey et al., 2006; Ferreira et al., 2007; Grant et al.
431 2008; Wang et al., 2008) because experimental work at the scale of whole estuaries is daunting.
432 Several reports exist of bivalve growth rates declining as aquaculture densities increase over
433 time, consistent with reduced phytoplankton densities available as food, particularly in areas
434 such as lagoons with long water residence periods and/or shallow water column and high bivalve
435 density often in three dimensional culture systems (Rodhouse and Roden, 1987; Heral, 1993;
436 Comeau et al., 2008). One recent monitoring effort documented the effects of removal of
437 extensive oyster aquaculture from a eutrophic bay in Taiwan with mean chlorophyll levels and
438 phytoplankton production being enhanced 4-fold in a less flushed portion of the bay (Huang et
439 al., 2008). Invasive bivalves such as *Potamocorbula amurensis* in San Francisco Bay
440 (Thompson, 2005), *Corbicula fluminea* in the Potomac River (Cohen et al., 1984), and
441 dreissenids in the Hudson River and Great Lakes (Strayer et al., 1999) also provide evidence of
442 top-down control of phytoplankton. Finally, depletion has been documented at spatial scales of
443 individual aquaculture operations, and sophisticated models have been developed to explore the
444 effects of hydrography and bivalve configuration on seston depletion at this scale (Newell et al.,
445 1998; Drapeau et al., 2006; Grant et al., 2007). The results of these models align well with actual
446 measurements of particle concentrations, but they generally indicate little impact on water
447 properties beyond the immediate “footprint” of the aquaculture operation (but see Grant et al.
448 2008).

449
450 Many aquaculture areas on the West Coast of North America remain relatively pristine, that is,
451 they have experienced low levels of cultural eutrophication. Consequently, carrying capacity
452 concerns may be more relevant than the ability of cultured organisms to ameliorate water quality
453 in these areas, although aquaculturists themselves can clearly be beneficial as an effective lobby
454 for continued low-impact shoreline development (Steele, 1964; Glasoe and Christy, 2004). The
455 calculation of present relative to historic bivalve densities has not been carried out for many
456 locations, but in Willapa Bay, Washington, *C. gigas* occurs at >2.5 times historic biomass of *O.*
457 *lurida* (Ruesink et al., 2005); the difference in filtration rate is probably less because the smaller
458 native oyster should have higher mass-specific filtration. Willapa Bay shows a gradient in
459 phytoplankton concentration from the mouth to upper estuary, and three competing hypotheses
460 involve physical mixing of rich ocean and poor river water along the estuarine gradient, longer
461 residence time of water in the upper estuary, and grazing by oysters that are farmed, especially

462 near the mouth of the bay. Overlaying oyster filtration on a circulation model indicates that
463 phytoplankton concentration declines into the bay more than would be expected from simple
464 mixing, and the extra loss is consistent with the capacity of cultured oysters to filter it out (Banas
465 et al., 2007). Interestingly, this result is achieved even though a large fraction of the bay's water
466 (>80%) never moves over a shallow tideflat and is not susceptible to filtration (Banas et al.,
467 2007). Empirically, however, the water that moves across Willapa Bay's tideflats is measurably
468 affected by cultured oysters growing there. Wheat et al. (in prep.) documented declines of about
469 10% per 100 m in phytoplankton when tracking parcels of water across oyster beds on flood
470 tides (Figure 2), whereas water flowing across newly-planted beds or other habitat types showed
471 no such change. One West Coast area where public concern has been raised about aquaculture
472 exceeding carrying capacity is in the southern end of Puget Sound, Washington. Interestingly,
473 this is also one area where excessive nutrients from upland sources and some eutrophication have
474 also been documented. However, the area of most extensive aquaculture (Totten Inlet) maintains
475 higher bivalve growth than elsewhere in Puget Sound (Ruesink et al. in prep.), and only local
476 phytoplankton depletion around raft structures has been documented (Cheney, pers. comm).
477 Overall, existing evidence from the West Coast confirms that cultured bivalves affect water
478 properties, but the effect is largely evident at small spatial scales (except see Banas et al., 2007).
479 While water quality is certainly impaired in some West Coast shellfish growing areas, this is
480 most often due to the presence of fecal coliforms which do not affect water clarity and
481 eutrophication has not yet been described as a significant problem in most areas.

482

483 *4.2. Alteration of sediment properties*

484

485 As with water quality, measurable effects of bivalves on sediment properties hinge on the density
486 of shellfish relative to water flow. In the case of sediment alteration, however, the effects of
487 bivalves are expected to be quite local, and flow enters into consideration because of its role in
488 dispersing biodeposits (Callier et al., 2006). Much of the work on sediment effects has been
489 carried out in the context of suspended culture. The buildup of biodeposits under or within
490 culture operations reduces grain size and increases organic content, which can reduce oxygen
491 content (Rodhouse and Roden, 1987; Christensen et al., 2003; Nizzoli et al., 2006; Mesnage et
492 al., 2007; Richard et al., 2007; Hargrave et al., 2008). Nitrogen content in sediments (porewater)
493 is often also elevated (Kautsky and Evans, 1987; Deslous-Paoli et al., 1992; Hatcher et al., 1994;
494 Giles and Pilditch, 2006), but the more important consequence is for nitrogen cycling. Rates of
495 NH_4^+ flux from bivalve communities can be fairly high ($1 - 5 \text{ mmol N m}^{-2} \text{ h}^{-1}$, Dame et al., 1992;
496 Giles and Pilditch, 2006), however burial of N and P and removal of N from the system via
497 denitrification (Figure 1) are also enhanced by deposition from bivalves (Kaspar et al., 1985;
498 Kautsky and Evans, 1987; Hatcher et al., 1994). Denitrification requires adjacent layers of
499 oxygenated sediments supporting nitrifying bacteria and anaerobic conditions that support
500 denitrifying anaerobes (Newell et al., 2002; Newell et al., 2005). Further feedback comes from
501 microphytobenthos, which can intercept dissolved organic nitrogen being regenerated from the
502 sediments and produce oxygen which further alters sediment chemistry and/or can be used by
503 bacteria at the sediment-water interface to maintain nitrification (Rysgaard et al., 1995). These
504 biochemical pathways are challenging to measure and quantify at larger scales in the field, for
505 instance due to the presence of other nutrient regenerators like nekton in salt marsh creeks
506 (Haertel-Borer et al., 2004). Laboratory studies are hampered by inappropriate boundary layer
507 flows which were shown to greatly influence microphytobenthos and thus nutrient regeneration

508 in mesocosm studies (Porter et al., 2004). A difference in nutrient cycling has also been
509 observed across species. For instance on-bottom farming of clams stimulates transfer of both
510 organic matter and oxygen to the sediment due to bioturbation by these animals whereas
511 suspended mussel culture results in only the former and thus reduced oxygen (Nizzoli et al.,
512 2006). Thus clam farming results in more balanced benthic metabolism with net losses of
513 nitrogen from the sediment. The multitude of factors and number of ecosystem processes
514 influenced by shellfish and complexity of the interactions make modeling efforts attractive tools
515 for examining ecosystem effects on nutrient cycling (Cranford et al., 2007).

516
517 In general, there do not seem to be any characteristics of West Coast estuaries that would cause
518 expectations of sediment effects to differ from those reported elsewhere, however sediment
519 chemistry and chemical fluxes are largely unexplored there. When oyster aquaculture and natural
520 habitat types were surveyed in Willapa Bay, the metabolic activity of aerobic microbes was
521 lower in on-bottom oyster aquaculture, consistent with a larger contribution from anaerobes
522 (Richardson et al., 2008), however no differences were found in sediment grain size, organic
523 content, or oxidation-reduction potential. While these results may initially suggest weaker
524 effects of cultured bivalves on sediment properties than have been observed in other systems, it
525 is more likely that their effects were obscured in this comparative study by underlying sediment
526 heterogeneity or the influence of local hydrodynamics. Indeed Rumrill and Poulton (2004)
527 measured small-scale topographical alteration of sediment profiles directly beneath suspended
528 long-line cultures of *Crassostrea gigas* in Humboldt Bay, California, and changes in sediment
529 dynamics were most evident in experimental plots with high densities of oysters. Similarly
530 experimental manipulation of oysters in Willapa Bay has produced sediment changes more
531 consistent with those measured elsewhere: the addition of high density oysters to small (2m x
532 2m) plots in eelgrass reduced grain size and increased organic content relative to nearby controls
533 (E. L. Wagner unpubl. data). There was also evidence that oysters actually lowered ammonium
534 concentrations in sediment porewater with one possible mechanism being rapid denitrification
535 that occurs at the interface of organic and inorganic sediment layers created by biodeposition. In
536 contrast, a similar experiment adding geoduck clams to small plots with eelgrass in Puget Sound
537 resulted in slightly raised porewater ammonium concentrations, but grain size and organic
538 content were apparently affected primarily by eelgrass and not the clams (Ruesink and Rowell in
539 prep).

540 541 4.3. *Feedbacks to primary producers*

542
543 The previous sections have addressed how bivalve feeding removes particles from the water and
544 releases nutrients in two forms: packaged in biodeposits or dissolved into the water column and
545 sediment porewater. These dissolved nutrients may stimulate the population growth of
546 phytoplankton and benthic microphytobenthos (Kaspar et al., 1985; Swanberg, 1991; Mazouni,
547 2004; Asmus and Asmus, 2005; Sara, 2007). Microphytobenthos may be directly fertilized via
548 biodeposition whereas phytoplankton may be either directly fertilized via ammonia release into
549 the water or indirectly fertilized via re-suspension of biodeposits and/or stimulated nutrient
550 recycling in the sediments (Figure 1). Submerged aquatic vegetation and microphytobenthos may
551 also benefit from improved light penetration if bivalves exert top-down control on phytoplankton
552 (Phelps, 1994; Newell and Koch, 2004; Wall et al., 2008). Nutrients released by bivalves into
553 sediment porewater can stimulate production of seagrasses, as documented for mussels growing

554 with seagrass in Europe, Florida, and southern California (Reusch et al., 1994; Reusch and
555 Williams, 1998; Peterson and Heck Jr., 1999; 2001). In general an increase in sediment
556 porewater ammonium toward optimal levels ($\sim 100 \mu\text{M}$) should enhance plant biomass and
557 growth (Dennison et al., 1987; Hughes et al., 2004), although high levels of biodeposits could
558 lead to toxic sulfide concentrations especially in already eutrophic areas (Sorokin et al., 1999;
559 Stenton-Dozey et al., 2001; Holmer et al., 2005; Vinther and Holmer, 2008; Vinther et al., 2008).
560 Aquaculture also has the potential to stimulate competitors with seagrass, for instance providing
561 attachment sites for epiphytic macroalgae and enriching nutrients used by algae (De Casabianca
562 et al., 1997; Thomsen and McGlathery, 2006; Vinther and Holmer, 2008; Vinther et al., 2008).
563 Seagrasses tend to be negatively affected by both epiphytic algal growth and macroalgal blooms
564 (Hauxwell et al., 2001; McGlathery, 2001; Hauxwell et al., 2003).

565
566 What evidence exists for West Coast bivalve aquaculture to affect primary producers through
567 nutrient or light pathways? In studies unrelated to aquaculture, eelgrass shoot growth and depth
568 distribution have been shown to be light limited in Pacific Northwest estuaries (Thom et al.,
569 2008). The addition of fertilizer to sediments around eelgrass growing in Padilla Bay resulted in
570 NH_4 in excess of $1000 \mu\text{mol l}^{-1}$ and higher eelgrass shoot growth (approximately 0.5 cm/shoot/d
571 Williams and Ruckelshaus, 1993). Thus, to the extent that bivalves improve light availability or
572 augment nutrient concentrations in sediment porewater, aquaculture could improve conditions
573 for eelgrass growth. However total production of eelgrass was lower in aquaculture than in
574 nearby eelgrass beds in Willapa Bay, due to a combination of reduced shoot density and smaller
575 shoot size (Tallis et al., in press). The interaction has been explored experimentally in two
576 additions of bivalves to eelgrass. On a per-shoot basis, eelgrass with geoducks grew faster than
577 without (due to larger shoot size). The mechanism could be from a 20% enhancement of
578 porewater ammonium, or from reduced intraspecific competition because eelgrass occurred at
579 lower density in the presence of clams (Ruesink and Rowell in prep.). In contrast, eelgrass with
580 oysters grew slower than without (due to smaller shoot size). The plants may have been
581 responding to an unexpected reduction in porewater ammonium associated with high-density
582 oysters, but more likely were “clipped” by sharp shells (E.L. Wagner, unpubl. data). So far, the
583 interaction between bivalves and eelgrass on the West Coast appears weak in terms of light or
584 nutrient pathways (as opposed to strong effects via competition; see section 5 below). Eelgrass
585 growth responses to direct manipulations of light and nutrients have involved large changes in
586 these drivers, whereas bivalves may not change the ambient levels so substantially. In any case,
587 documented ambient porewater ammonium is close to the optimum for eelgrass growth in many
588 of the region’s estuaries, especially during summer months: Willapa Bay, Washington ($80 \mu\text{M}$,
589 J.L. Ruesink unpubl. data), Yaquina Bay, Oregon ($60\text{-}170 \mu\text{M}$ and $750\text{-}2500 \mu\text{M}$; Larned, 2003;
590 Kaldy, 2006, respectively), San Diego Bay, California ($20\text{-}120 \mu\text{M}$; Reusch and Williams,
591 1998), south Puget Sound, Washington ($50\text{-}90 \mu\text{M}$; Ruesink and Rowell in prep.), and Padilla
592 Bay, Washington ($30 - 137 \mu\text{M}$; Williams and Ruckelshaus, 1993). Eelgrass growth appears
593 consistently depressed below maximum when ammonium concentrations are below $40 \mu\text{M}$
594 (Dennison et al., 1987).

595
596
597
598

5. Press Disturbance - Shellfish Aquaculture as Structured Habitat

599 Bivalve shellfish act as ecosystem engineers or foundation species by influencing habitat and
600 resources available for other species (Jones et al., 1997; Bruno and Bertness, 2001). While
601 engineering roles, such as the provision of complex hard substrate, are most obvious for oysters
602 and mussels living above the substrate, all shell-producers including infaunal clams alter solute
603 concentrations and their shells may contribute to surface structure after they perish (Palacios et
604 al., 2000; Lehnert and Allen, 2002; Gutierrez et al., 2003). Ecosystem engineers have both
605 positive and negative effects on ecological communities – they provide habitat and resources for
606 some species, whereas other species may be displaced. Thus the effect of aquaculture involves
607 both its “footprint” locally (for instance, percent physical cover within a small area) and
608 regionally (for instance, density of farms), and its value for other species. Habitat “value” is not
609 easily measured, as is evident in recent debates about “essential fish habitat” and “nursery
610 habitat” (Able, 1999; Beck et al., 2001). Ideally, one is interested in how such habitats influence
611 production of other species, but in practice lower-level indicators are generally measured:
612 reproduction and survival, distribution and abundance, or simply presence and absence (Able,
613 1999). In this section, we first address the press disturbance resulting from ecosystem
614 engineering by cultured organisms themselves, followed by structures added as part of
615 aquaculture methods (e.g. stakes, tubes, racks, and nets).

616
617 The paradigm for soft-sediment tideflat communities is that they are structured by predation,
618 which keeps prey densities at such low levels that larval recruitment and competition are
619 relatively unimportant (Posey, 1990; Olafsson et al., 1994; Lenihan and Micheli, 2001).
620 However, larger bioengineering species are an exception to this rule including large bioturbators
621 (burrowing shrimp in West Coast estuaries; Posey, 1986; Posey et al., 1991; Dumbauld et al.,
622 2001) and structure forming species like bivalve shellfish and eelgrass. Competition between
623 cultured bivalves and eelgrass has been studied more thoroughly on this coast than in other
624 locations, perhaps because aquaculture is so important and the two habitat types often co-occur
625 or are adjacent. The relevance of eelgrass is two-fold: first, seagrasses in general are declining
626 worldwide (Orth et al., 2006), and second, they form structured habitats and have consequently
627 served as a benchmark for habitat provided by shellfish (Jackson et al., 2001; Heck et al., 2003;
628 Bostrom et al., 2006). Because both shellfish and eelgrass shoots occupy space, it is no surprise
629 that competition occurs. The focus of research has been to document the mechanism and strength
630 of this competition. In terms of mechanism, oysters may influence eelgrass through both their
631 “footprint” and abrasion or drying of leaves when exposed at low tide (Simenstad and Fresh,
632 1995; Schreffler and Griffen, 2000; Boese et al., 2003). Repeated damage is a possible
633 explanation for smaller shoot sizes on aquaculture beds relative to nearby eelgrass (Tallis et al. in
634 press). Living within the sediment, clams are not expected to cause leaf damage but may
635 nevertheless compete for space. Geoduck clams at aquaculture densities (10 m^{-2}) reduced
636 eelgrass density by ~30% in south Puget Sound during summer months; this difference
637 disappeared during winter when shoot densities naturally thinned in control plots (Ruesink and
638 Rowell in prep.).

639
640 The strength of competition between shellfish and eelgrass can usefully be explored by
641 examining how each species performs by itself and in combination (Figure 3A, see example
642 below). Some combinations generate overyielding, in which total production is larger than
643 expected from averaging the 2 species. Overyielding can occur because individuals perform
644 better in combination with another species than on their own. Other combinations result in

645 underyielding, in which total production is lower than expected from the average of 2 species,
646 often a result of strong interspecific competition. Thus, a key issue has been to elucidate the
647 relationship between cultured bivalve density and eelgrass – does eelgrass do better or worse
648 than expected from the percentage of area transformed to hard substrate? As a thought
649 experiment, imagine that light limitation in the eelgrass canopy sets up low shoot density, and
650 oysters at low densities simply insert themselves into unoccupied space. This may be the case,
651 for instance, in an experimental addition of oysters at 10 - 20% cover in Willapa Bay, where
652 eelgrass densities were not distinguishable from controls (shoot density = 25 – 50 m⁻²; B.R.
653 Dumbauld unpubl. data). This would constitute a case of overyielding, because shoot density was
654 apparently not reduced by the amount of oyster cover. On the other hand, to the extent that
655 oysters damage nearby eelgrass shoots, it is possible to imagine eelgrass declining by more than
656 the percent cover of oysters. At a site in the South Slough estuary (Coos Bay, Oregon)
657 experimental addition of low densities of oysters (ca. 13 shells m⁻² or 10% cover) resulted in a
658 decline in eelgrass cover relative to an adjacent control plot (Rumrill and Christy, 1996),
659 particularly at a higher tidal elevation (from 10% cover at deployment to 3% cover after 75 days
660 versus an increase from 8% cover at deployment to 10% cover measured on the control plot). In
661 Tillamook Bay, Oregon eelgrass shoot survival was only 1% in 3 x 3 m plots where oyster
662 clusters (4 – 50 individuals) and eelgrass were transplanted compared to 59% survival in
663 adjacent plots where only eelgrass was transplanted (Schreffler and Griffen, 2000). Both
664 eelgrass and oyster cover may vary over time as demonstrated two years after clumps of oysters
665 were added to 2 x 2 m plots in Willapa Bay, when eelgrass entirely disappeared from plots that
666 had >20% oyster cover (Figure 3B; E.L. Wagner unpubl. data). Interestingly, however, a year
667 later these plots showed a simple 1:1 tradeoff between oysters and eelgrass (Figure 3C). At a
668 still larger scale, on cobble shores in British Columbia, density of eelgrass transplanted down-
669 slope from oysters declined more than density of similar transplants to areas not below oysters
670 (Kelly and Volpe, 2007). If this spatial relationship was indeed causal, the competitive effects of
671 oysters extended for several meters beyond their immediate location. Based on available
672 evidence, eelgrass can coexist with bivalves at low densities used in on-bottom aquaculture on
673 soft sediments, but more research needs to be directed at best management practices that could
674 raise the likelihood of overyielding.

675
676 Introduced Pacific oysters are cultivated in many of the same West Coast estuaries once
677 occupied by extensive beds of native oysters, *O. lurida*, raising the possibility of negative
678 competitive effects between these oyster species. Despite relaxed fishing pressure, *O. lurida* has
679 mostly failed to recover since it was overexploited in the late 1800's. Native oysters persist at
680 very low abundance at many West coast locations and many factors likely contribute to their
681 scarcity; however, one unexpected consequence of presence of cultured *C. gigas* in the intertidal
682 is the development of a “recruitment sink” (Trimble et al. in press). Given a standardized
683 recruitment surface (a stack of 11 Pacific oyster shells), native oysters disproportionately
684 recruited to reefs of *C. gigas*, rather than eelgrass or unstructured tideflat in Willapa Bay,
685 Washington. This gregarious settlement was an advantageous strategy when beds of native
686 oysters were primarily found subtidally, but the modern shell distribution has shifted to be more
687 intertidal due to *C. gigas* culture. Since *O. lurida* is sensitive to desiccation and temperature
688 extremes, showing <5% annual survival at tidal elevations emerging from the water just 2-10%
689 of the time, compared to >20% survival when continually submerged (Trimble et al. in press),
690 native oyster recruits to intertidal shell habitat provided by *C. gigas* cannot persist.

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

706

707 *5.1. Benthic Infauna*

708

709 When suspended culture occurs over soft sediments, organic enrichment via biodeposition can
710 transform a diverse benthic community dominated by suspension feeders (bivalves, crustaceans,
711 and some polychaetes) into one dominated by smaller opportunistic deposit feeders (usually
712 polychaetes), a pattern that characterizes nutrient enrichment from a variety of anthropogenic
713 sources (Pearson and Rosenberg, 1978). However, because biodeposition from shellfish farms is
714 generally low relative to that of finfish farming or other anthropogenic sources (Pohle et al.,
715 2001; Crawford et al., 2003), responses by infauna are variable and depend on species cultured,
716 biomass or stocking density, and the environment in which culture takes place (Hartstein and
717 Rowden, 2004; Miron et al., 2005; Callier et al., 2006). In some cases enrichment either does
718 not occur or does not alter infauna (Grant et al., 1995; Chamberlain et al., 2001; Crawford et al.,
719 2003), while in others, significant effects have been documented (Dahlback and Gunnarsson,
720 1981; Mattsson and Linden, 1983; Kaiser et al., 1998; Mirto et al., 2000; Christensen et al.,
721 2003). Similarly, intertidal oyster culture on racks and trestles has variable consequences for
722 infauna, likely based on the balance of biodeposit production vs. water flow. Trestle culture of
723 Pacific oysters in New Zealand, England, and France resulted in increased biodeposition, lower
724 sediment redox potential, and altered macrofaunal communities (reduced diversity and
725 abundance; Castel et al., 1989; Nugues et al., 1996; Forrest and Creese, 2006). However, oysters
726 cultured in floating bags over intertidal areas in eastern Canada were shown to increase both
727 organic content and initial colonization of de-faunated sediment by benthic infauna (Lu and
728 Grant, 2008) whereas high currents at other sites in Canada and Ireland swept away biodeposits
729 and few changes in infaunal community were seen (De Grave et al., 1998; Mallet et al., 2006).
730 Finally, for on-bottom culture, it is difficult to separate effects of biodeposition from structural
731 complexity and space competition and relatively few studies outside the West Coast of the U.S.
732 have been conducted. Mussels cultured on the bottom were shown to negatively influence
733 richness and abundance of some infauna in Wales (e.g. cirratulid polychaetes and two species of
734 amphipods declined with increasing mussel density; Beadman et al., 2004) while Murray et al.
735 (2007) found species dependent results when comparing communities in subtidal mussel culture
736 (both on-bottom and rope) to naturally occurring intertidal mussel beds in Maine, U.S.

737
738 How do infaunal species respond to bivalve aquaculture on the West Coast? Several studies in
739 West Coast estuaries have documented abundant, highly-diverse infaunal communities
740 associated with on-bottom oyster culture. Abundance, biomass and diversity of infauna in
741 Humboldt Bay on-bottom oyster culture was higher than that found in open mudflat, but lower
742 than that in eelgrass (10.2 cm dia cores, 1 mm mesh; Trianni, 1995). At the time of this study
743 oysters were harvested with a suction dredge in this estuary, a disturbance which likely also
744 influenced the infaunal community in the oyster beds, and comparisons made suffered from
745 statistical interaction between season and habitat factors. Similarly, Hosack et al. (2006) found
746 infaunal macrofauna were more abundant in eelgrass in Willapa Bay, Washington than on open
747 mudflat, and moderate levels found in oyster ground culture were not significantly different from
748 either of these habitat types (10.5 cm diameter cores 0.5 mm mesh). Ferraro and Cole (2007)
749 sampled multiple habitat types in Willapa Bay (2 x 8 cm diameter core, 0.5 mm mesh), using a
750 strict sampling protocol throughout the estuary over two years. Oysters and eelgrass supported
751 equally diverse assemblages, with unstructured habitats having less diversity. The equivalence of
752 oyster and eelgrass habitats, in contrast to the other two studies, may have emerged from
753 sampling aquaculture beds that had 2-3 year old oysters present and had not been disturbed for
754 several years. The lowest-diversity samples came from areas influenced by burrowing shrimp
755 (*Neotrypaea californiensis*). This result is consistent with direct studies of bioturbation by these
756 shrimp in U.S. West Coast estuaries (Bird, 1982; Posey, 1986; Dumbauld et al., 2001) and
757 elsewhere around the world (Wynberg and Branch, 1994; Dittmann, 1996; Berkenbusch et al.,
758 2000; Berkenbusch and Rowden, 2007; Pillay et al., 2007). Thus, the primary result of removing
759 burrowing shrimp with the pesticide carbaryl is to reduce bioturbation and then add a three-
760 dimensional architecture by planting oysters, which further influences the community
761 (Dumbauld et al., 2001).

762
763 Other West Coast studies of infauna have occurred in aquaculture types that include structures
764 (e.g. suspended bags, stakes, racks), so any differences reflect the presence of both bivalves and
765 structures. Nevertheless, differences have been small. Although biodeposition was observed
766 under deep-water suspended oyster and mussel culture using sediment traps in British Columbia,
767 Canada, and Totten Inlet, Puget Sound, Washington respectively, there appeared to be little
768 buildup of organic matter when measured outside the traps. The major change in the benthic
769 community observed was enhanced abundance of epifaunal predators which capitalized on the
770 drop-off of fouling organisms from the culture operations (Brooks, 2004; Barnes et al. 2007).
771 Harbin-Ireland (2004) found no difference in percent organic matter in areas directly below and
772 those adjacent to a single set of subtidal oyster racks in Drakes Estero estuary, California, nor
773 was there any difference in overall infaunal community indices. The relative abundance of
774 amphipods was higher under racks while other taxa like bivalves and ostracods were less
775 abundant. In contrast, experimental deployment of oyster stakes and racks in the Coos Bay,
776 Oregon, resulted in biodeposition within the stake plots and erosion and reduction of carbon
777 content of the sediments below rack plots (Everett et al., 1995). Stake culture resulted in lower
778 recruitment and survival of tellinid clams, while increased abundance of cumaceans and
779 amphipods was observed in the oyster rack plots (Carlton et al., 1991). In a relatively short term
780 follow-up study, Pregnall (1993) observed no significant difference in sediment grain size and
781 only a slight difference in benthic infaunal diversity between oyster stake culture plots and
782 eelgrass controls. Diversity and abundance of infaunal invertebrates around long line oyster

783 culture in Humboldt Bay, California were also similar to those observed at eelgrass reference
784 areas (Rumrill and Poulton, 2004). In both cases similarity may have arisen not simply due to
785 flow dispersing biodeposits, but because both aquaculture and control areas included eelgrass,
786 which has characteristic effects on sediment (reducing flow, allowing particles to settle out;
787 Madsen et al., 2001).

788
789 From the above discussion, it is clear that engineered habitats differ from unstructured tideflat in
790 terms of static community-level metrics. Differences have also emerged from the few but
791 important studies addressing species interactions. Small mobile crustaceans including juvenile
792 Dungeness crab (*Cancer magister*) had higher density and biomass in oyster shell habitat placed
793 in intertidal areas of Grays Harbor, Washington than in nearby control areas without shell.
794 When small clams recruited to the structured shell habitat in higher numbers, they also
795 experienced higher predation by crabs (Iribarne et al., 1995; Dumbauld et al., 2000).

796

797 5.2. Epibenthic meiofauna

798

799 Epibenthic invertebrates are important food items for juvenile estuarine fish (Alheit and
800 Scheibel, 1982; Gee, 1989) including juvenile Pacific salmon and small (<50mm) English sole
801 on the U.S. West Coast (Toole, 1980; Simenstad et al., 1982). Structurally complex habitats like
802 seagrass have been shown to enhance meiofaunal abundance (Bell et al., 1984; Attrill et al.,
803 2000; Jenkins et al., 2002). We found only two studies on the effects of either oysters or
804 aquaculture on epibenthic meiofauna. Castel et al. (1989) found enhanced epibenthic meiofaunal
805 abundance in both on-bottom and bag culture of oysters in France over that found in adjacent un-
806 structured habitat, but highest abundance was found in nearby seagrass beds. Similarly
807 meiofauna densities were higher in both eelgrass and oyster habitats than over open mudflat in
808 Willapa Bay on the West Coast (Hosack et al., 2006). Simenstad and Fresh (1995) noted that
809 taxa diversity of epibenthic harpacticoid copepods was higher on an active on-bottom oyster
810 culture plot with 3 year old oysters present than an in-active plot where oysters and eelgrass were
811 present in the same estuary, but prey taxa for epibenthic feeding fish such as juvenile salmonids
812 were more abundant on the in-active plot. This trend was reversed for English sole prey taxa
813 suggesting species specific differences in affinity, but no comparisons were made with eelgrass
814 or other habitats. Recent experimental work with experimental additions of the much smaller
815 native oyster (*Ostrea lurida*) attached to Pacific oyster cultch shells in Puget Sound, Washington
816 also showed increased abundance of epibenthic organisms, but not necessarily enhanced taxa
817 richness with the pool of available species being determined by background conditions at the
818 enhancement site (Cordell, pers. comm.).

819

820 5.3. Nekton

821

822 For larger mobile species, complex structure formed by foundation species or ecosystem
823 engineers is likely to provide a place both to search for prey and to avoid becoming prey to larger
824 organisms. Indeed, higher densities of estuarine fish and invertebrates have been widely found in
825 association with structured habitats like seagrass (Orth et al., 1984; Jackson et al., 2001; Heck et
826 al., 2003) and oyster reefs (Breitberg, 1999; Coen et al., 1999; Lenihan et al., 2001; Lehnert and
827 Allen, 2002; Glancy et al., 2003; Peterson et al., 2003; Coen and Grizzle, 2007; Horinouchi,
828 2007; Taylor and Bushek, 2008) when compared to open un-structured mudflat or subtidal

829 channel bottom. However, abundance measures are not a definitive indicator of how structured
830 habitat contributes to nekton production, and in some cases even densities do not differ across
831 habitat types (Heck and Thoman, 1984; Ferrell and Bell, 1991; Jenkins et al., 1997). We discuss
832 possible explanations for these discrepancies in Section 7 below. Nekton response to
833 aquaculture as habitat has not been extensively studied, except in the context of off-bottom
834 culture operations. Order of magnitude higher densities of some fish and invertebrates
835 (American eel, oyster toadfish, rock gunnel, Atlantic tomcod, and American lobster) were found
836 in areas with rack and bag culture of *C. virginica* in Rhode Island, USA, compared to those in
837 eelgrass or unstructured habitats, but eelgrass also harbored a few unique species (northern
838 pipefish and winter flounder; Dealeris et al., 2004). Tautog and scup were more abundant at
839 oyster grow-out sites than natural rocky reefs in Narragansett Bay, Rhode Island and a tagging
840 study found that though scup grew at slightly higher rates on the rocky reefs, they had greater
841 site fidelity to oyster grow-out cages (Tallman and Forrester, 2007). Erbland and Ozbay (2008)
842 found higher abundance of several reef oriented fish species (gag grouper, grey snapper,
843 sheepshead, and tautog) and greater overall species richness in experimental oyster bags
844 compared to a nearby oyster reef in Delaware. Juvenile sole were found to utilize areas with
845 oyster trestle culture for protection during the day while foraging on surrounding tideflats at
846 night (Laffargue et al., 2006). Researchers in New Zealand established a framework for the
847 expected effect of suspended culture on fish which includes three mechanisms: attraction to
848 structure, direct influence on recruitment, and indirect food web effects (Gibbs, 2004). A case
849 study which examined suspended culture of green mussels suggested few realized effects on
850 abundance of one species (blue cod) and that the primary effect might be on pelagic fish that
851 consume zooplankton should the footprint of farms be expanded (Jiang and Gibbs, 2005). These
852 mussel farms have also been shown to enhance abundance and aggregation of starfish on the
853 bottom, presumably due to drop-off of both culture species and fouling organisms (Inglis and
854 Gust, 2003 D'Amours et al., 2008). Clynick et al. (2008) found species specific differences in
855 abundance when comparing areas under mussel culture lines to adjacent eelgrass and open
856 unstructured habitat, but found no differences in integrated growth of winter flounder, sand
857 shrimp and rock crab measured using RNA/DNA ratios.

858
859 Substantial research on nekton associated with both on-bottom and long-line oyster culture has
860 been carried out recently along the West Coast of the U.S. In one case, diversity and abundance
861 of fish was highest in aquaculture. Specifically, oyster longlines in Humboldt Bay, California,
862 harbored more fish than did eelgrass or open mud habitats (Pinnix et al. 2005). However a more
863 common result has been that community-level indices (abundance and diversity) are equivalent
864 across habitats with a few species specific affiliations. Few statistically significant differences in
865 density were found among the >20 species of fish and crabs collected at intertidal locations in
866 Willapa Bay, Washington where eelgrass, oyster bottom culture and open mudflat habitats were
867 surveyed (Dumbauld et al., 2005; Hosack et al., 2006, Figure 4). In general, nekton density
868 reflected physical location in the estuary rather than habitat type, although some species like rock
869 crab (*Cancer productus*) were more abundant in oyster aquaculture and tube snouts (*Aulorhynchus*
870 *flavidus*) in eelgrass. Higher abundance of rock crab and smaller shore crabs (*Hemigrapsus*
871 spp.), sculpins and blennies, occurred in small oyster stake culture plots compared with nearby
872 eelgrass control areas in Coos Bay, Oregon (Pregnall, 1993). Staghorn sculpin (*Leptocottus*
873 *armatus*) and caridean shrimp (*Crangon franciscorum*) were more abundant within high-density
874 oyster long-line plots compared to lower-density oyster plots in Humboldt Bay, California

875 (Rumrill and Poulton, 2004). In a study of fish associated with oyster racks, no significant
876 differences in species richness or abundance were observed in fish samples collected adjacent to
877 the racks compared to an area without culture in separate arms of Drakes Estero Bay, California.
878 At the same time, structure-oriented feeders like kelp surfperch (*Brachyistius frenatus*) and
879 crevice-dwelling fish like gunnels and kelpfish (*Pholis ornata* and *Gibbonsia metzi*) were
880 disproportionately associated with racks particularly during the day when refuge from predators
881 could be most important (Weschler, 2004). Although oysters *C. gigas* were not included in the
882 comparison, they can also occur in cobble habitats, which have lower fish diversity than eelgrass
883 in British Columbia (Kelly et al., 2008).

884
885 On-bottom structure appears to have different implications for Dungeness crab (*Cancer*
886 *magister*), depending on phase of the life cycle. These crab represent a multi-million dollar
887 annual fishery on the U.S. West Coast and the role of estuaries as nurseries supporting these
888 populations has been extensively studied (Armstrong et al., 2003). Ground cultured oysters and
889 intertidal shell provide equal or better habitat than eelgrass for juvenile 0+ Dungeness crab (0 –
890 30mm carapace width), which in turn provides better habitat than open unstructured mud or sand
891 based on higher recruitment and survival rates due to protection from predators (Armstrong et
892 al., 1994; Eggleston and Armstrong, 1995; Dumbauld et al., 2000; Feldman et al., 2000;
893 Williamson, 2006). Shore crabs (*Hemigrapsus oregonensis*) can also recruit to shell and
894 outcompete *C. magister* depending on location and tidal elevation (Visser et al., 2004). Older
895 age classes of Dungeness crab (1+ and 2+), however, favor open unstructured littoral habitats for
896 foraging at high tide and are less likely to move across structured habitat including both eelgrass
897 and oyster aquaculture (Holsman et al., 2003; Holsman et al., 2006).

898
899 For some Pacific salmon, on-bottom oysters appear to be lower quality habitat than eelgrass,
900 especially for predator avoidance, based on individual behavior. However, salmon are
901 distributed broadly across habitat types, and the amount of aquaculture in an estuary does not
902 appear to influence salmon returns. Pacific salmon occupy estuaries during a critical life-history
903 stage as juveniles smoltify and transition from fresh to marine waters (Quinn, 2004). The
904 diversity of life history patterns among and within species of salmon influences their use of
905 estuaries: Chinook salmon (*Oncorhynchus tshawytscha*) have the longest estuarine residence,
906 whereas pink and chum salmon (*O. gorbuscha* and *O. keta*) move through estuaries relatively
907 rapidly on their way to sea (Groot and Margolis, 1991; Bottom et al., 2005). Juvenile coho
908 salmon (*O. mykiss*) generally move directly to neritic waters as older 1+ fish that have reared in
909 freshwater for longer periods, but recent evidence suggests that both age-0 and yearling fish
910 utilize estuarine areas (mostly salt marsh and sloughs) relatively extensively (Healey, 1982;
911 Miller and Simenstad, 1997; Miller and Sadro, 2003). Across West Coast estuaries, successful
912 returns of salmon do not appear to be related to the presence or absence of aquaculture; in fact,
913 the best estuarine predictor of pit-tag returns of Chinook salmon was the percent of land cover in
914 natural condition (Magnusson and Hilborn, 2003). In a field study to assess habitat preferences,
915 salmon smolts were sampled across habitat types in Willapa Bay, Washington with a towed net,
916 and gut lavage performed on captured individuals. No differences in abundance or diet occurred
917 across habitat types, although seasonal and larger-scale spatial differences were evident
918 (Dumbauld et al. 2005, Figure 5). Laboratory studies of Chinook salmon smolt behavior
919 indicated that eelgrass may provide a better refuge than other habitat types. Larger juveniles
920 preferred the structure of eelgrass as a refuge over oysters or open sand substrate when exposed to

921 a mock heron predator (Dumbauld et al., 2005). In a separate field experiment, hatchery-raised
922 Chinook salmon smolts were released into a large intertidal enclosure (3000 m²) containing
923 eelgrass (*Z. marina* and *Z. japonica*), oyster clusters, unstructured sediment, and cordgrass
924 (*Spartina alterniflora*). They were implanted with acoustic tags that allowed their movements to
925 be tracked in 2-dimensions at sub-meter accuracy (Radio Acoustic Positioning and Telemetry).
926 After effects of tidal elevation and enclosure were accounted for, smolts never entered areas with
927 *Spartina* and otherwise responded only to the presence of *Z. marina*, where they moved more
928 slowly than in other habitat types (Semmens, 2008). Thus it seems that juvenile salmon move
929 over the entire matrix of estuarine habitats, but eelgrass may represent a preferred habitat for
930 refuge from predation which cannot be compensated by transformation to on-bottom oyster
931 aquaculture. Assessing the functional value of habitats including aquaculture however, will
932 ultimately require a larger landscape approach as suggested by Simenstad and Cordell (2000) for
933 restoration (see further discussion in Section 7 below).

934

935

5.4. Birds

936

937 Estuarine tidelands provide foraging habitat for numerous species of shorebirds, waders and
938 waterfowl during migration and for those species that overwinter. Some farmed bivalves are
939 directly consumed by birds (e.g. mussels by seaducks and oystercatchers; Caldow et al., 2004).
940 However, other bird species appear to avoid densely-structured habitats, preferring instead to
941 feed in open mudflat areas (Luckenbach, 1984). Like nekton, the response of birds to
942 aquaculture is likely to be species and perhaps environment specific due to bird feeding and
943 roosting behavior relative to the tides and the presence of other birds and predators. In Ireland,
944 dunlin (*Calidris* spp.) were more frequent beneath trestle cultured oysters, whereas gulls, curlew
945 and oystercatchers occurred in significantly lower numbers in culture areas (Hilgerloh et al.,
946 2001). Experimental additions of mussels to intertidal areas in Wales resulted in increased use
947 by curlew and redshank over time (Caldow et al., 2003), due apparently to increased diversity in
948 benthic fauna as food provided by increased habitat complexity.

949

950

951 Evidence for the effects of aquaculture on birds on the West Coast suggests species specific
952 differences due to behavior. In Humboldt Bay, California five of 13 species of shorebirds
953 (whimbrel, willet, dowitchers, peeps and black turnstones) and three of four species of waders
954 (snowy egret, great egret, and black-crowned night heron) were more abundant in long-line
955 oyster culture areas than in nearby “control” areas (Connolly and Colwell, 2005), possibly
956 responding to higher densities of invertebrate prey associated with long-lines. Black bellied
957 plovers and great blue herons were more abundant in control areas and the other shorebirds
958 displayed location specific behavior. Kelly et al. (1996) found that peeps and dunlin avoided
959 rack and bag oyster culture in Tomales Bay while willet were attracted. Mussels settling on
960 aquaculture structures were shown to enhance food resources for surf scoters and Barrow’s
961 goldeneye in British Columbia (Kirk et al., 2007). One species of waterfowl of particular
962 concern are Brant geese (*Branta bernicla*), which graze heavily on eelgrass in estuaries at
963 stopovers during their long migration to Arctic breeding grounds and in temperate over-
964 wintering areas (Ganter, 2000). Humboldt Bay, California ranks fourth among West Coast spring
965 staging areas for brant with peak numbers reaching 38,000 while Willapa Bay historically
966 averaged 23,393 (1936- 1960 and now 6,900) and ranks sixth (Wilson and Atkinson, 1995;
967 Moore et al., 2004). Effects of geese themselves on eelgrass tend to be low due to the seasonally

968 brief presence of these birds during migration, but Canada geese (*Branta canadensis*) as well as
969 several species of dabbling ducks have been shown to have more substantial long term effects on
970 eelgrass in areas elsewhere in the U.S., particularly where they overwinter in some years
971 (Nacken and Reise, 2000; Rivers and Short, 2007). Dabbling ducks have switched their
972 foraging habits to feed primarily on the introduced species of eelgrass *Z. japonica* in West Coast
973 estuaries where this species is now present (Lovvorn and Baldwin, 1996). While goose density
974 is positively correlated with spatial eelgrass coverage in West Coast estuaries, the relationship is
975 more complex and also influenced by proximity to the next estuary along the coast and other
976 factors like frequency of winter storms and within season foraging dynamics due to tides
977 (Baldwin and Lovvorn, 1994; Wilson and Atkinson, 1995; Moore et al., 2004; Moore and Black,
978 2006). Thus both eelgrass and associated brant numbers could be negatively associated with
979 aquaculture in a given area, but the long-term temporal decline in brant numbers along the coast
980 is not likely associated with shellfish aquaculture given the relatively stable presence of this
981 industry in these systems for the last 100 years.

982

983 5.5. Aquaculture structures

984

985 Some bivalve aquaculture methods introduce physical structures to the intertidal flat in addition
986 to the organisms themselves (e.g. stakes, longlines, and bags for off-bottom oyster culture, and
987 gravel, tubes and anti-predator nets for clam culture). These physical structures can modify water
988 flow, in some cases accelerating flow and causing erosion, in other cases leading to deposition.
989 They can also provide attachment sites and attract settlement of other invertebrates and algae.
990 For eelgrass in particular, reduced density is a common response to the shade from overwater
991 structures, studied most intensively for docks (Burdick and Short, 1999; Thom et al., 2005). We
992 have already considered effects of suspended and rack culture in sections above, although the
993 species vs. method effects were not distinguishable. Distinguishing these effects requires two
994 treatments (species + method, and either species alone, or method alone [preferably both]), in
995 addition to a control without either. This design was employed by Spencer et al. (1997), who
996 showed that predator netting deployed to protect clam aquaculture substantially increased
997 sedimentation to tideflats in Great Britain, whereas biodeposits from clams alone did not (but see
998 Jie et al., 2001 who document increased biodeposits from clams can occur in areas with current
999 velocities below critical re-suspension rates). Further, this sedimentation resulted in slightly
1000 enhanced organic content and enhanced abundance of deposit feeding polychaetes. Clam
1001 mariculture conducted in bags on the East Coast of the U.S. has been shown to affect sediment
1002 but not water column characteristics (Mojica and Nelson, 1993) Macro-algae attached to clam
1003 culture bags in North Carolina enhanced use by mobile invertebrates and juvenile fishes over that
1004 in nearby shallow subtidal sand bottom and resulted in comparable abundances with seagrass
1005 habitat (Powers et al., 2007). Both substrate modification (gravel addition) and predator netting
1006 effectively increase survival by protecting juvenile seed clams (*Mercenaria mercenaria* and *Mya*
1007 *arenaria*) from various predators on the East Coast of the U.S. (Kraeuter and Castagna, 1985;
1008 Beal and Kraus, 2002) and *Ruditapes philippinarum* in Spain (Cigarria and Fernandez, 2000),
1009 but these studies were primarily confined to effects on the clams themselves.

1010

1011 What evidence exists for ecological effects of aquaculture structures on the West Coast? For
1012 oyster culture most regional attention has focused on response by eelgrass (*Z. marina*) and
1013 results have been quite variable. At one extreme, oyster stake culture conducted in the middle of

1014 an intertidal eelgrass meadow in Coos Bay, Oregon reduced eelgrass cover by 75% relative to
1015 nearby controls, possibly due to increased sedimentation (5-10 cm buildup) and physical
1016 disturbance (Everett et al., 1995). Oyster racks caused 100% loss of eelgrass under the structure
1017 from both erosion of sediment (10 – 15 cm around structure) and shading. Macro-algal biomass
1018 was enhanced around stakes and significantly lower in rack plots than in eelgrass reference plots
1019 (Everett et al., 1995). At the other extreme, a broad survey of Willapa Bay showed that eelgrass
1020 density in longlines could not be distinguished from uncultured areas at the same tidal elevation,
1021 although in a subset of these beds, longlines harbored smaller plants (32%) and reduced
1022 production per unit area (70%) (Tallis et al. in press). Also, in a separate study in Willapa Bay,
1023 lower eelgrass densities were found in longlines than in nearby eelgrass reference areas
1024 (Wisehart et al. 2007). Seedlings were less abundant in longlines and reference areas compared
1025 with dredge harvest beds, possibly from seed supply or because shading and sedimentation
1026 impact these small plants (Wisehart et al. 2007). In an experimental study in which the effect of
1027 space between oyster longlines on eelgrass was examined in Humboldt Bay, California, eelgrass
1028 metrics tended to scale directly with the density of oysters (Rumrill and Poulton, 2004). Eelgrass
1029 declined in cover and density as spacing between lines decreased; spatial cover and density of
1030 eelgrass under lines spaced at 1.5 feet and 2.5 feet were significantly lower than those spaced at
1031 5 and 10 feet apart. Eelgrass metrics observed within these wider spaced lower density
1032 treatments were comparable to those observed at a nearby untreated site, a former oyster ground
1033 culture site, and a series of eelgrass reference sites located throughout the bay at the end of the
1034 22 month study period (Figure 6). They were also comparable to those measured within full-
1035 scale commercial long-line culture areas. Increased sedimentation and more variable light
1036 conditions (incident light levels diminished by as much as 35%) were found under narrowly
1037 spaced long-lines (< 5 foot spacing), but the “shade zone” migrated with movement of the sun
1038 and irradiance was not reduced enough to limit *Z. marina* growth. Structures clearly have the
1039 potential to limit eelgrass, but the effects are context specific and can be ameliorated with
1040 management practices. West coast growers have also reported that eelgrass often appears in
1041 areas formerly devoid of this plant after structures are put in place. Given the lack of evidence
1042 for nutrient enhancement (section 4.3 above), this could be due to either localized effects on
1043 water clarity or sediment stabilization, but no studies have addressed the mechanism.

1044
1045 For clam culture on the West Coast, two modifications have been studied: addition of shell or
1046 gravel to the substrate and addition of anti-predator nets. Gravel and crushed oyster shell have
1047 been widely used to develop or maintain hard clam (primarily *R. philippinarum*) habitat in West
1048 Coast estuaries and these additions have been shown to enhance juvenile clam survival (Toba et
1049 al., 1992; Thompson, 1995). Thom et al (1994) found that gravel addition to soft sediment
1050 significantly increased benthic respiration rates but had little effect on water quality parameters
1051 in south Puget Sound. They found site specific changes in surface macroalage, chlorophyll, and
1052 benthic assemblage, likely due to local conditions and time since the areas had been graveled.
1053 Secondary effects on the infaunal and epibenthic community were also shown to be site specific
1054 in later studies conducted in two sub-estuaries of south Puget Sound. Thompson (1995) found a
1055 general trend of enhanced abundance of gammaridean amphipods and nemertean in modified
1056 substrate plots and reduced abundance of glycerid, sabellid and nereid polychaetes. Simenstad
1057 and Fresh (1995) documented site specific responses of the epibenthic harpacticoid copepod
1058 community to the combination of gravel additions and predator exclusion netting.

1059

1060 Predator exclusion netting and/or bags are widely used for clam culture without substrate
1061 modification in West Coast estuaries and have been shown to increase the amount of organic
1062 carbon present in the sediment, likely due to biodeposition from larger age classes of *R.*
1063 *philippinarum* which were more abundant in netted plots at farmed sites in British Columbia,
1064 Canada (Munroe and McKinley, 2007a; b). Little consistent effect however was shown for
1065 sediment grain size or the abundance of other bivalves. Settlement of the cultured species *R.*
1066 *philippinarum* displayed highly significant interannual differences and the effect of netting was
1067 marginally significant (decreased settlement), but could be negative or positive depending on
1068 presence and size class of older clams (Munroe and Mckinley, 2007b; Whiteley and Bendell-
1069 Young, 2007). Finally, in Baynes Sound, British Columbia where some growers also installed
1070 beach fences around their plots, Zydalis et al. (2006) found densities and distribution of
1071 important wintering populations of surf and white-winged scoters to be primarily related to
1072 environmental factors and not shellfish aquaculture though 76 ha or 5% of the intertidal area was
1073 recorded to be covered by predator exclusion nets.

1074

1075 **6. Harvest Practices as Pulse Disturbances**

1076

1077 Fisheries harvests in general can remove non-target species and re-set systems to early-
1078 succession conditions. However, the initial impact and pace of recovery clearly vary with harvest
1079 method, type of habitat present, and organism being studied (Kaiser et al., 2006). In their recent
1080 review, Kaiser et al. (2006) found just 6 examples of intertidal raking, which is perhaps most
1081 relevant to shellfish aquaculture (since intertidal dredging involved sediment removal and longer
1082 recovery times linked to infill rates; see also Dernie et al., 2003). Their meta-analysis showed
1083 that initial impacts to biota were relatively small and harvested areas matched controls within 50
1084 days. Recovery was slower however in muddy sand and in biogenic habitats (especially when
1085 the latter included larger, older organisms such as corals and bivalves which contributed directly
1086 to biomass removed; see also Lenihan and Peterson, 2004). This is likely to be the case after
1087 disturbance to seagrasses which are sensitive to a variety of activities with some parallels to
1088 aquaculture harvest practices: dredge and fill (Fonseca et al., 1984; Onuf, 1994; Erftemeijer and
1089 Lewis, 2006), boat propellers (Zieman, 1976; Dawes et al., 1997), and boat anchor and mooring
1090 chain scars (Walker et al., 1989; Thom et al., 1998). Repeated trampling (mimicking
1091 recreational visitors) reduced the biomass of *Thalassia testudinum* in Puerto Rico, especially in
1092 softer substrates (Eckrich and Holmquist, 2000), but harvest activities for shellfish are unlikely
1093 to occur this frequently. Trawling and dredging for wild shellfish also negatively affect seagrass
1094 (Fonseca et al., 1984; Peterson et al., 1987; Orth et al., 2002; Neckles et al., 2005), although an
1095 extension to aquaculture must consider gear, technique, species ecology of seagrass (e.g.
1096 Erftemeijer and Lewis, 2006), and the physical environment (e.g. Kaiser et al. 2006). Several
1097 hard clam harvest methods have been shown to reduce eelgrass, including mechanical “clam
1098 kicking” with propeller wash (Peterson et al., 1987) and hand digging when rhizomes were
1099 extensively fragmented (Cabaco et al., 2005). The scale of harvest activity has also been shown
1100 to be important for both the direct effect on seagrass and associated organisms and the secondary
1101 impact of harvest on food for shorebirds and waterfowl. Small scale harvest of clams by hand in
1102 a national park in Spain (Navedo and Masero, 2008) appeared to have low impact and be
1103 sustainable, while larger scale effects of dredge harvesting on wild stocks of mussels and cockles
1104 in intertidal areas of the Dutch Wadden Sea are highly debated (Piersma et al., 2001; Verhulst et
1105 al., 2004; Kraan et al., 2007).

1106
1107 Recovery time after disturbance to seagrass should vary with seagrass species, disturbance size,
1108 disturbance intensity, and sediment characteristics. Seasonal time of disturbance is also likely a
1109 factor. Seagrass can recover via lateral rhizome spread or via sexual reproduction and seed
1110 dispersal depending on location and species. In fact, both natural and human disturbances have
1111 been shown to enhance sexual reproduction in seagrass (Marba and Duarte, 1995; Peterken and
1112 Conacher, 1997; Plus et al., 2003; Olesen et al., 2004). With respect to aquaculture, intertidal
1113 clam harvest in Portugal resulted in 2 fold higher seed production and an extended reproductive
1114 season for *Z. noltii* which enabled it to recover from harvest within a year (Alexandre et al.,
1115 2005).
1116
1117 Most of the research outlined above on press disturbances due to aquaculture in West Coast
1118 estuaries has not addressed the direct response of the benthic community to the pulse effect of
1119 harvest practices because it is not generally possible to distinguish these from effects of just
1120 adding the cultured organisms themselves. Consequently, the most valuable insight into harvest
1121 practices comes from before-after comparisons, which can then be tracked over time to
1122 determine pace of recovery. Both the initial impact and time to recovery have been variable in
1123 studies of the effect of oyster harvest to eelgrass on the U.S. West Coast. Results of
1124 experimental dredging using a toothed metal dredge at relatively large scale (0.33 ha plots) in
1125 Willapa Bay, Washington provide one explanation for this variation. At a muddy site, eelgrass
1126 initially declined 42%, where shoot and rhizome removal by the dredge implement was
1127 substantial, requiring 4 yr for recovery, whereas at a sandy site, initial decline was only 15% and
1128 recovery occurred in 1 yr (Tallis et al. in press). The effects of multiple passes with a suction
1129 dredge were evaluated by Wadell (1964) who found up to 96% initial loss of eelgrass biomass in
1130 Humboldt Bay with recovery taking up to 2 years. Treatment frequency also varies substantially
1131 and growers suggest that suction dredges are no longer common, each company designs their
1132 own mechanical implements, operator experience can be a factor, and mechanical harvest is
1133 rarely used in soft muddy sediments. In a comparison of eelgrass across three types of
1134 aquaculture (longlines, hand-picked, dredged), it proved possible to separate the effects of
1135 different culture practices from the effects of oysters, because oyster cover was included as a
1136 continuous variable ranging from <5% to >50% across beds. Relative shoot growth rates were
1137 15% higher in both ground and long-line culture beds, but eelgrass production per unit area was
1138 driven by density and plant size differences and therefore lower in all aquaculture beds than in
1139 nearby eelgrass reference areas. Hand-picked beds had higher eelgrass production per unit area
1140 than did dredged beds (Tallis et al. in press), indicating higher impacts of mechanical harvest
1141 than picking up oysters by hand in eelgrass. For large areas such as aquaculture beds to regain
1142 eelgrass requires seed germination or asexual reproduction of remnant adults. In Willapa Bay,
1143 Washington seed germination can be high (>4 m⁻²), particularly on dredged beds (Wishart et al.
1144 2007), although seedling survival appears universally low (1-2%; Wishart 2006). Rhizome
1145 branching appears to be important for recovery of gaps in eelgrass (up to 16 m²), but only occurs
1146 seasonally and thus gaps created experimentally in mid-summer did not begin to recover from
1147 the edges until the following spring (E.L. Wagner, unpubl. data). Clearly how much sexual vs
1148 asexual reproduction contributes to eelgrass resilience is important and may vary both temporally
1149 and spatially, but these dynamics have not been investigated on the U.S. West Coast.
1150

1151 For clams, effects of harvest appear related to the extent and depth to which sediment is
1152 dislodged. Effects of recreational clam harvest using rakes on *Z. marina* were undetectable, but
1153 digging clams with shovels reduced eelgrass cover and biomass over the short term, although
1154 recovery occurred fairly rapidly (months) in Yaquina Bay (Boese, 2002). Though the introduced
1155 seagrass, *Z. japonica* has expanded into areas and often now interferes with clam aquaculture on
1156 the West Coast of the U.S., clam aquaculture does not co-occur with *Z. marina*. Recreational
1157 clam harvest in the San Juan Islands, Washington caused short term impacts to non-target clam
1158 species abundance and polychaete species richness due to sediment displacement with shovels
1159 (Griffiths et al., 2006), but this does not typically occur for aquaculture where harvesting is
1160 typically done by hand or small rake and sediment replaced. In an experimental study of the
1161 effects of geoduck aquaculture on eelgrass density in south Puget Sound, Washington small (1
1162 m²) gaps in eelgrass beds required >1 year for recovery via regrowth from the edges, because
1163 flowering and seed germination were very rare (Ruesink and Rowell in prep.). When the
1164 geoducks were harvested, eelgrass shoot density dropped >70% and recovery was subsequently
1165 difficult to gauge because control plots also declined in density over the 3-year study (Ruesink
1166 and Rowell in prep.).

1167

1168 7. Landscape Considerations

1169

1170 The available evidence discussed above for the U.S. West Coast indicates that some types of
1171 bivalve shellfish aquaculture can have effects on other species, and these effects may be place-
1172 and time-specific in part due to the scale at which observations are made. The vagueness of this
1173 conclusion is to be expected from ecological studies: unfortunately, it leads to the potential for
1174 selective use of evidence to support a conclusion of strong positive, strong negative, or weak
1175 effects of aquaculture. An important avenue of future research lies in documenting and
1176 understanding the role of aquaculture at an appropriate landscape scale, where aquaculture is
1177 intermixed (literally overlapping, as with eelgrass in oysters; or distributed as meadows and
1178 patches) with other habitat types.

1179

1180 There is no particular scale inherent in the concept of a landscape, only that it has a spatial
1181 dimension. For the purposes of this discussion however, we use a common definition of a
1182 spatially defined mosaic of heterogenous elements that differ in their qualitative or quantitative
1183 properties (Wiens, 2005). We consider the estuarine landscape on which aquaculture acts as a
1184 disturbance and therefore define it to be larger than the scale of an individual lease, bed, reef, or
1185 set of structures used to culture shellfish. Conceptually this differs from estuary to estuary and is
1186 influenced by aquaculture practice and the cultural/political framework that exists in a given
1187 place. A series of questions that might then be asked regarding this landscape include (after
1188 Ahern, 2005):

1189

1190 What is the proper spatial and temporal scale for understanding ecological patterns and processes
1191 in the estuarine landscape?

1192

1193 How large a habitat patch (shellfish bed, eelgrass meadow) is required to support a given species
1194 or ecological process?

1195

Ecological role of bivalve shellfish aquaculture

1196 Do these habitats form a “corridor” that connects larger habitat areas and if so what
1197 configuration of corridors is necessary to sustain species or ecological processes across the
1198 estuarine landscape?
1199

1200 Which species or species group should be planned for? Can a particular “indicator” species
1201 represent the habitat needs of a group of species?
1202

1203 Are there ecological interactions between shellfish aquaculture and other common anthropogenic
1204 disturbances at landscape scales?
1205

1206 How does a particular estuary constrain or support an ecological process?
1207

1208 Estuaries are open systems and connected and influenced by the nearshore coastal ocean and the
1209 watershed – how does this affect the ecological processes?
1210

1211 How should aquaculture as a disturbance be understood in the estuarine landscape?
1212

1213 Within cultural and economic constraints, can aquaculture be incorporated into estuary planning
1214 to lessen or enhance the potential effects to these other habitats and therefore species that utilize
1215 them?
1216

1217 These questions about the influence of habitat configuration on organism abundance and
1218 behavior at broad spatial scales (relative to the organism being studied) have been widely
1219 examined in terrestrial systems (Kareiva, 1987; Forman, 1995; Mazerolle and Villard, 1999;
1220 Debinski and Holt, 2000; Lindenmayer and Fischer, 2006), but only recently considered for
1221 marine habitats like eelgrass beds and oyster reefs (Brooks and Bell, 2001; Fonseca et al., 2002;
1222 Salita et al., 2003; Harwell, 2004; Darcy and Eggleston, 2005; Grabowski et al., 2005; Hovel and
1223 Fonseca, 2005; Bostrom et al., 2006; Connolly and Hindell, 2006; Johnson and Heck, 2006;
1224 Tanner, 2006; Hinchey et al., 2008). Increased connectivity between marine populations due to
1225 passive dispersal of larval stages and juveniles over large areas suggests that landscape scale
1226 processes differ in marine systems though there are clearly parallel processes to be explored.
1227 Corridors and habitat fragmentation have been shown to be less important, particularly for many
1228 invertebrates with pelagic larvae, but also for more sedentary adults (e.g. bivalves and small
1229 polychaetes, Bowden et al., 2001; Tanner, 2005; Cole et al., 2007). Fragmentation, patchy
1230 seagrass beds, and increased habitat edges may actually enhance diversity and increase the
1231 density of some bottom feeding invertebrates like decapod crustaceans and fish, whereas larger
1232 seagrass meadows may harbor higher numbers of smaller cryptic species (Salita et al., 2003;
1233 Tanner, 2005; Selgrath et al., 2007). Clearly other factors are also important like water depth,
1234 water movement, predation and organism behavior and motility (Irlandi et al., 1995; Darcy and
1235 Eggleston, 2005; Jackson et al., 2006; Horinouchi, 2007). Effects at the estuarine landscape
1236 scale are potentially more important for motile organisms with increased perception of structure
1237 at this scale and a greater home range which also provides important linkages between habitats
1238 like seagrass and marsh (Irlandi and Crawford, 1997; Simenstad and Cordell, 2000; Bostrom et
1239 al., 2006).
1240

1241 There have been few landscape-level approaches to bivalve shellfish aquaculture, although some
1242 progress has been made in Willapa Bay, Washington. Here, there are estimates of the total

1243 amount of different habitat types and how these have changed over time. In addition, the
1244 behavioral response of selected species (salmon, crab) have been studied across habitat types
1245 including bivalve shellfish aquaculture areas by these larger mobile organisms as discussed in
1246 Section 5.3 above (Pinnix et al., 2005; Holsman et al., 2006; Hosack et al., 2006; Semmens,
1247 2008). Nonetheless, the influence of aquaculture has not yet been examined at a landscape scale
1248 on the West Coast of the U.S. and new work will need to be done to address such landscape-level
1249 features as patch size, connectivity, and the population response of organisms. Managers and
1250 regulators rightly suggested a general “no net loss” policy for estuarine wetlands which include
1251 eelgrass. This constraint has focused their efforts to date on protecting existing eelgrass as
1252 valued structured benthic habitat without much consideration of other forms of habitat or the
1253 location and scale of eelgrass habitat. Studies to date have also mostly examined organism
1254 presence and density in a given habitat and not broad scale spatial pattern or functional roles of
1255 these habitats. It could be that some habitats are more important than others at a broader
1256 landscape scale (e.g., as protective cover near channel edges for juvenile salmon) and that the
1257 configuration of both shellfish and submerged aquatic vegetation as habitat is also important
1258 because it provides food for larger more mobile organisms at that scale (e.g., for juvenile salmon,
1259 English sole, or shorebirds and waterfowl as discussed above) and protective cover and food for
1260 others (e.g for juvenile crab). Applications might be gleaned from work in the terrestrial
1261 environment where agricultural field margins and forest edges have been considered and
1262 managed as valuable habitat (New, 2005).

1263
1264 Despite the generally negative results of disturbance to eelgrass from aquaculture on small
1265 spatial and short temporal scales discussed above, eelgrass is generally present and intermingles
1266 with shellfish on all aquaculture beds at the tidal elevation where it is found naturally in Willapa
1267 Bay, Washington. Studies conducted to date have not evaluated historical records to indicate
1268 either loss or gains in eelgrass habitat over time, nor whether eelgrass would have been present
1269 regardless of subsequent aquaculture activity. Across Willapa Bay as a whole, shellfish
1270 aquaculture currently occupies about 13% of the estuary (4625 ha) and 20% of the tideflat (B.R.
1271 Dumbauld, unpubl. data; Feldman et al., 2000). It has likely historically replaced at least two
1272 other habitat types: monospecific eelgrass (*Zostera marina*) and burrowing shrimp (*Neotrypaea*
1273 *californiensis* and/or *Upogebia pugettensis*). Interestingly, the application of carbaryl to remove
1274 burrowing shrimp may actually enhance eelgrass (both the native species and a non-native
1275 congener *Zostera japonica*, Dumbauld and Wyllie-Echeverria, 2003). With the exception of
1276 changes in practices like switching from on-bottom culture to off-bottom culture in some
1277 locations, the press (oyster addition) and pulse (planting and harvest operations) disturbances of
1278 oyster culture have not changed materially for decades (Ruesink et al., 2006), so there is no
1279 reason eelgrass would necessarily be worse off now than in the recent past. Indeed, there is
1280 scientific evidence that eelgrass fluctuates with environmental conditions (Thom et al., 2003) and
1281 compelling evidence that it has been expanding its distribution in Willapa Bay (Ruesink et al. in
1282 review) and other estuaries along the open coast of the western U.S. even though it is declining
1283 elsewhere in the world (Orth et al., 2006) and in isolated locations on the U.S. West Coast (e.g.
1284 Hood Canal and San Juan Archipelago in Puget Sound, Gaeckle et al., 2007; Mumford Jr.,
1285 2007). Based simply on tidal elevation, Willapa Bay was estimated to contain 3,139 ha suitable
1286 for *Z. marina* (0 to -1.2 m MLLW) in the 1850s, increasing to 4,845 ha in the 1950s as the
1287 bathymetry became shallower (Borde et al. 2003). A recent estimate based on aerial photography
1288 (3,424 ha) may be slightly lower than the potential area because other habitat types (e.g.

1289 aquaculture, burrowing shrimp) also occur at the same elevations (Ruesink et al. 2006). The two
1290 *Zostera* species together may cover 4,935 ha (B.R. Dumbauld unpubl. data) or 6,162 ha (Ruesink
1291 et al. 2006). Despite their chemical control for aquaculture, burrowing shrimp currently also
1292 occupy a very large intertidal area in Willapa Bay (3,060 ha = 13.5% of the intertidal; B.R.
1293 Dumbauld unpubl. data). They have probably fluctuated in abundance and would have the
1294 potential to occupy a much larger area if shrimp control had not occurred, with attendant effects
1295 on both native and non-native species of *Zostera* and associated benthic community. Simenstad
1296 and Fresh (1995) estimated 12.6% of an area near Stony Point in Willapa Bay was highly
1297 disturbed due to aquaculture with little to no eelgrass present. Despite the obvious signature
1298 from oyster culture disturbance however, when we re-examined the proportion of area with
1299 eelgrass present in oyster culture beds and compared it to that area at a similar tidal elevation just
1300 outside oyster culture (where eelgrass would be expected to occur) in the same Stony Point
1301 vicinity (2005 data, Figure 7), we found little difference in eelgrass cover (46 versus 50 %). Such
1302 comparisons are merely one-time snapshots of the presence of vegetative cover and more
1303 thorough analyses of a larger area over a slightly longer temporal scale with more descriptive
1304 categorizations of bed use will reflect the importance of vegetative recovery processes and
1305 perhaps other details discussed in above sections. In contrast, historical estimates do not account
1306 for occupation by other species, for instance, based on crude maps from the late 1800's, native
1307 oyster *Ostrea lurida* beds occupied 2,700 ha (12 % of the low intertidal and shallow subtidal)
1308 that now consists of relatively undisturbed and dense native eelgrass meadows (Collins, 1892;
1309 Townsend, 1896; Sayce, 1976). Thus shell habitat has always been present in Willapa Bay,
1310 although its current distribution is at a higher tidal elevation than would be assumed from a
1311 contemporary projection, or than is present at other important West Coast locations (Tables 2
1312 and 3). These spatial analyses have rarely been conducted in West Coast estuaries (but see
1313 Carswell et al., 2006 for Baynes Sound, British Columbia, Canada and Ward et al., 2003 for
1314 Bahia San Quentin, Mexico).

1315

1316 **8. Resilience - Management Implications and Research Needs**

1317

1318 Shellfish aquaculture has been an important activity and has supported local economies along the
1319 West Coast of the U.S. for at least 100 years. At present temporal and spatial scales in West
1320 Coast estuaries, our review suggests that the practice of shellfish aquaculture viewed as an
1321 ecological disturbance seems much more sustainable than other human activities such as
1322 freshwater diversion, coastal development and pollution, which continue to degrade estuarine
1323 function. On a global scale however, aquaculture is expanding and so may pressure to increase
1324 regional use of estuaries for bivalve culture. We end this review with some conclusions, caveats,
1325 and research needs which we hope will be useful to managers and decision-makers.

1326

1327 From a manager or land-use planner's perspective, the first consideration in evaluating shellfish
1328 aquaculture in a given estuary should be an answer to the question: What are we and/or should
1329 we be managing for? Estuaries have a wide range of potential functions, have been and will
1330 continue to be influenced by many human activities, and similarly are influenced by many
1331 natural disturbances in addition to shellfish aquaculture. While the current paradigm for most
1332 managers is whole "ecosystem based" management (Grumbine, 1997), in reality managers have
1333 only progressed to varying degrees down this path especially for marine systems. Thus the
1334 answer to "what are we managing for?" is driven by a wide variety of stakeholders and societal

1335 values (social historical, political, moral and aesthetic as well as economic; Leslie and McLeod,
1336 2007; Weinstein, 2007; Ruckelshaus et al., 2008). Although these values are outside the
1337 purview of our intended review, we found it instructive to at least classify West Coast estuaries
1338 by the current level of aquaculture and other anthropogenic disturbance as Weinstein et al.
1339 (2007) propose. Willapa Bay and Humboldt Bay might therefore be considered “production”
1340 estuaries with greater than 10% of the area occupied by shellfish aquaculture, while numerous
1341 other smaller estuaries with little aquaculture could be classified as other types (though the
1342 proportion of total estuarine area leased for aquaculture in some of these systems is also greater
1343 than 10%, leased does not necessarily mean actively used, Table 3). Portions of estuaries might
1344 also be classified or zoned separately this way (e.g. the South Slough portion of Coos Bay,
1345 Oregon or South Bay portion of Humboldt Bay, California). These classifications would then
1346 further help set goals and priorities for management and restoration, an activity which also
1347 involves social decisions about what should be “restored” (Simenstad et al., 2006).
1348 Classifications of production and production/conservation would be compatible with sustainable
1349 aquaculture, whereas areas classed as conservation or conservation marine within estuaries might
1350 not include aquaculture depending on the level of anthropogenic influence and goals for
1351 sustaining traditional commercial and recreational products desired. These decisions would
1352 obviously vary by jurisdiction. In Washington state for example, a critical societal decision was
1353 made in 1895 with passage of the Bush and Callow Acts which deeded 18,932 h of tidelands to
1354 private ownership specifically for the purpose of commercial shellfish culture. This set the stage
1355 for continued industry involvement and emphasis as a priority activity. Within such a
1356 framework which simply recognizes the current status and constraints on these systems, we offer
1357 the following conclusions specific to bivalve aquaculture as disturbance, its relevance to
1358 resilience in West Coast estuaries, and suggestions for future research:

- 1359
1360 1. Bivalves process phytoplankton and alter the forms and distribution of nitrogen in a
1361 system. In typical U.S. West Coast systems evaluated to date water column and sediment
1362 nutrient concentrations are generally relatively high and greatly influenced by the
1363 proximity to deeper nearshore ocean waters where upwelling controls production during
1364 summer months. The situation may be different for small systems such as coastal lagoons
1365 or portions of large fjords like Hood Canal in Puget Sound, Washington where circulation
1366 is restricted. Very little modeling of whole-system energy and nutrient budgets, including
1367 aquaculture, has been done regionally, although the methods are well worked out in
1368 Europe. We suspect, however, that terrestrial and anthropogenic nutrients will figure less
1369 prominently than in many other places where bivalves are grown. Studies that expand on
1370 work like that completed for Willapa Bay, Washington showing the potential for bivalves
1371 in one part of the estuary to limit production in another part (Banas et al., 2007), and
1372 comparisons with other systems including portions of fjords like Puget Sound,
1373 Washington would be extremely useful research avenues. Intermediate bed scale studies
1374 such as those conducted using flow models and benthic nutrient flux estimations within
1375 given estuaries (Newell et al., 1998; Porter et al., 2004) will still be necessary to calibrate
1376 the larger landscape scale estimations, particularly with new species or culture techniques
1377 (e.g. geoducks in tubes, oysters on longlines).
- 1378 2. Some bivalves and culture practices modify estuarine habitat at local community and at
1379 landscape scales. The effect of aquaculture is most often evaluated against existing
1380 structured habitat in the form of submerged aquatic vegetation. While bivalve

1381 aquaculture might be viewed as a press disturbance over the long term in a given area, the
1382 individual activities act as pulse disturbances and *Zostera marina* in U.S. West Coast
1383 estuaries can recover to pre-disturbance levels relatively rapidly (within a period of 2
1384 years in some systems). This is usually before the next planting or harvest disturbance
1385 occurs, but depends on conditions and the aquaculture practice (e.g. oyster fattening beds
1386 might be rotated on a yearly basis and thus disturbance is frequent, while seed-harvest
1387 beds are left undisturbed for 2 to 4 years). Furthermore, the extent of the effect depends
1388 on the practice (hand harvest versus dredge harvest, longlines versus on-bottom culture.
1389 The current distribution of eelgrass reflects a balance of space competition, pulse
1390 disturbance and recovery, and is therefore at dynamic equilibrium on aquaculture beds
1391 (albeit generally lower than in undisturbed eelgrass meadows). Research is still needed
1392 on factors that cause plants to alter their reproductive strategy and enhance seedling
1393 production (Wisehart et al. 2007), whether plants respond differently to disturbance
1394 across seasons, particularly since densities vary naturally over the year (Ruesink et al. in
1395 review) and finally on the effect this has at larger spatial scales (growing areas to estuary)
1396 and over relevant temporal scales (at least the lifetime of a shellfish crop = 3 or 4 years).

1397 3. The role of aquaculture (organisms themselves and support structures) as estuarine
1398 habitat should also be considered. For small benthic infauna and mobile epibenthic
1399 fauna, structure provided by aquaculture appears functionally similar to eelgrass, based
1400 on invertebrate abundances and composition measured to date in West Coast estuaries.
1401 For larger benthic invertebrates and fish, use of habitat depends on mobility and varies
1402 with life history stage and taxon being evaluated, so temporal and spatial scales are
1403 important considerations. Though less is known about habitat function for these larger
1404 more mobile organisms, they can use structure for protection from even larger predators
1405 (juvenile salmon in eelgrass and 0+ Dungeness crab in oyster), but still rely on other
1406 habitats for foraging (1+ Dungeness crab in unstructured open habitat). Given the
1407 presence of mixed habitats (i.e. eelgrass within aquaculture beds), it would be valuable to
1408 determine relationships between eelgrass density and its ecosystem function, effective
1409 habitat patch sizes, and corridor use at a larger landscape scale. This may be an area
1410 where best management plans can be designed and implemented since the shellfish
1411 industry would likely be supportive of maintaining habitat corridors (e.g. eelgrass along
1412 channel edges) and timing windows (e.g. limited harvest operations in some areas during
1413 fish spawning or bird migration periods) should they prove necessary.

1414 4. Finally, it is important to consider estuarine changes not simply in terms of departure
1415 from baseline, but as they influence resilience, that is, capacity of the system to withstand
1416 or recover from other shocks. Aquaculture as disturbance is generally within the scope of
1417 existing “natural” disturbances to the system (e.g. winter storms) and other ecosystem
1418 engineers (e.g. eelgrass and burrowing shrimp) are also inherently adapted to this scale of
1419 disturbance. Certain anthropogenic disturbances have reduced estuarine resilience, for
1420 instance habitat removal via wetland diking and filling, hardening of surfaces in the
1421 watershed, nutrient additions, invasive species such as *Spartina*, and possibly food web
1422 modifications like removal (sharks, skates and sturgeon) or protection (harbor seals and
1423 sea lions) of large predators. In contrast, bivalve aquaculture does not remove area from
1424 the estuary or degrade water quality, and thus is less likely to undermine resilience.
1425 Though local and short term effects are clearly evident in U.S. West Coast estuaries,
1426 bivalve aquaculture has not been implicated in shifts to alternate states or reduced

1427 adaptive capacity of the larger ecological system. Typical thresholds that might be
1428 involved in such catastrophic change would likely be reached first with other human
1429 disturbances (e.g. nutrients and predator removal), although location and scale remain
1430 important management considerations (e.g. small inlets with stratified water columns and
1431 less routine physical disturbance might exhibit lower thresholds to large scale aquaculture
1432 operations).
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Acknowledgements

The authors sincerely thank numerous contributors to aquaculture studies in Willapa Bay, Puget Sound and Humboldt Bay including especially Alan Trimble, Lee McCoy, Sally Hacker, Lorena Wisheart, Victoria Poulton, Geoff Hosack, Heather Tallis, Bruce Kauffman, Beth Wheat, Kirsten Rowell, Kirsten Holsman, Dan Cheney, and Andy Suhrbier. Lee McCoy was instrumental in conducting mapping efforts and producing GIS results for Willapa Bay. Shellfish growers in all of these locations provided access to their tidelands to conduct studies, logistical support, and invaluable practical insight about local conditions and history. Funding for these studies was provided by the Western Regional Aquaculture Center (2001-38500-10495 and 2003-38500-13198), Grant #NA 16R1044, Project R/ ES42 from NOAA to Washington Sea Grant, the Andrew W. Mellon Foundation, Washington Dept. of Fish and Wildlife, and USDA-ARS. The authors also thank Gary Banowetz, Dan Cheney, Chris Langdon and three anonymous reviewers for their comments on the manuscript.

1452 **Literature Cited**

- 1453
- 1454 Able, K.W., 1999. Measures of juvenile fish habitat quality: Examples from a national estuarine
1455 research reserve. In: Benaka, L.R. (Ed.), *Fish Habitat: Essential Fish Habitat and*
1456 *Rehabilitation*. American Fisheries Society, Bethesda, Maryland, pp. 134-147.
- 1457 Ahern, J., 2005. Integration of landscape ecology and landscape architecture: an evolutionary
1458 and reciprocal process. In: Wiens, J.A., Moss, M.R. (Eds.), *Issues and Perspectives in*
1459 *Landscape Ecology*. Cambridge University Press, New York, pp. 365-373.
- 1460 Alexandre, A., Santos, R., Serrao, E., 2005. Effects of clam harvesting on sexual reproduction of
1461 the seagrass *Zostera noltii*. *Mar. Ecol. Prog. Ser.* 298, 115-122.
- 1462 Alheit, J., Scheibel, W., 1982. Benthic harpacticoids as a food source for fish. *Mar. Biol.* 70,
1463 141-147.
- 1464 Araujo, F.G., de Azevedo, M.C.C., 2001. Assemblages of southeast-south Brazilian coastal
1465 systems based on the distribution of fishes. *Estuar. Coast. Shelf Sci.* 52, 729-738.
- 1466 Armstrong, D.A., Rooper, C., Gunderson, D., 2003. Estuarine production of juvenile Dungeness
1467 crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery.
1468 *Estuaries* 26, 1174-1188.
- 1469 Armstrong, J.L., Armstrong, D.A., Mathews, S.B., 1994. Food habits of estuarine staghorn
1470 sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab,
1471 *Cancer magister*. *Fish. Bull.* 93, 456-470.
- 1472 Asmus, H., Asmus, R.M., 2005. Significance of suspension-feeders systems on different spatial
1473 scales. In: Dame, R.F., Olenin, S. (Eds.), *The Comparative Roles of Suspension-Feeders*
1474 *in Ecosystems*. Springer Verlag, Netherlands, pp. 199-219.
- 1475 Attrill, M.J., Strong, J.A., Rowden, A.A., 2000. Are macroinvertebrate communities influenced
1476 by seagrass structural complexity? *Ecography* 23, 114-121.
- 1477 Atwater, B.F., 1987. Evidence for great Holocene earthquakes along the outer coast of
1478 Washington State. *Science* 236, 942-944.
- 1479 Babson, A.L., Kawase, A., MacCready, P., 2006. Seasonal and interannual variability in the
1480 circulation of Puget Sound, Washington: A box model study. *Atmosphere-Ocean* 44, 29-
1481 45.
- 1482 Bacher, C., Duarte, P., Ferreira, J.G., Heral, M., Raillard, O., 1998. Assessment and comparison
1483 of the Marennes-Oleron Bay (France) and Carlingford Lough (Ireland) carrying capacity
1484 with ecosystem models. *Aquat. Ecol.* 31, 379-394.
- 1485 Bahr, L.M., Lanier, W.P., 1981. The ecology of intertidal oyster reefs of the South Atlantic
1486 coast: A community profile. U.S. Fish and Wildlife Service, Office of Biological
1487 Sciences, FWS/OBS-81/15, Washington, D.C.
- 1488 Baker, P., 1995. Review of ecology and fishery of the Olympia oyster, *Ostrea lurida* with
1489 annotated bibliography. *J. Shellfish Res.* 14, 501-518.
- 1490 Baldwin, J.R., Lovvorn, J.R., 1994. Habitats and tidal accessibility of the marine foods of
1491 dabbling ducks and brant in Boundary Bay, British Columbia. *Mar. Biol.* 120, 627-638.
- 1492 Banas, N.S., Hickey, B.M., Newton, J.A., Ruesink, J.L., 2007. Tidal exchange, bivalve grazing,
1493 and patterns of primary production in Willapa Bay, Washington, USA. *Mar. Ecol. Prog.*
1494 *Ser.* 341, 123-139.
- 1495 Bando, K.J., 2006. The roles of competition and disturbance in a marine invasion. *Biol.*
1496 *Invasions* 8, 755-763.

- 1497 Barnhart, R.A., Boyd, M.J., Pequegnat, J.E., 1992. The ecology of Humboldt Bay, California:
1498 An estuarine profile. U.S. Fish and Wildlife Service, Washington, D.C., pp. 1-121.
- 1499 Barrett, E.M., 1963. The California oyster industry. Calif. Fish Game 123, 1-103.
- 1500 Beadman, H.A., Kaiser, M.J., Galanidi, M., Shucksmith, R., Willows, R.I., 2004. Changes in
1501 species richness with stocking density of marine bivalves. J. Appl. Ecol. 41, 464-475.
- 1502 Beal, B.F., Kraus, M.G., 2002. Interactive effects of initial size, stocking density, and type of
1503 predator deterrent netting on survival and growth of cultured juveniles of the soft-shell
1504 clam, *Mya arenaria* L., in eastern Maine. Aquaculture 208, 81-111.
- 1505 Beattie, J.H., 1992. Geoduck enhancement in Washington State. Bull. Aqua. Assoc. Can. 92, 18-
1506 24.
- 1507 Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M.,
1508 Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein,
1509 M.R., 2001. The identification, conservation, and management of estuarine and marine
1510 nurseries for fish and invertebrates. Bioscience 51, 633-641.
- 1511 Bell, S.S., Kern, K., Walters, J.C., 1984. Meiofauna from seagrass habitats: a review and
1512 prospectus for future research. Estuaries 7, 331-338.
- 1513 Beninger, P.G., Veniot, A., Poussart, Y., 1999. Principles of pseudofeces rejection on the bivalve
1514 mantle: integration in particle processing. Mar. Ecol. Prog. Ser. 178, 259-269.
- 1515 Berkenbusch, K., Rowden, A.A., 2007. An examination of the spatial and temporal generality of
1516 the influence of ecosystem engineers on the composition of associated assemblages.
1517 Aquat. Ecol. 41, 129-147.
- 1518 Berkenbusch, K., Rowden, A.A., Probert, P.K., 2000. Temporal and spatial variation in
1519 macrofauna community composition imposed by ghost shrimp *Callinassa filholi*
1520 bioturbation. Mar. Ecol. Prog. Ser. 192, 249-258.
- 1521 Bird, E.M., 1982. Population dynamics of thalassinidean shrimps and community effects through
1522 sediment modification. Ph.D. dissertation, University of Maryland, College Park,
1523 Maryland.
- 1524 Boese, B.L., 2002. Effects of recreational clam harvesting on eelgrass (*Zostera marina*) and
1525 associated infaunal invertebrates: in situ manipulative experiments. Aquat. Bot. 73, 63-
1526 74.
- 1527 Boese, B.L., Alayan, K.E., Gooch, E.F., Robbins, B.D., 2003. Dessication index: a measure of
1528 damage caused by adverse aerial exposure on intertidal eelgrass (*Zostera marina*) in and
1529 Oregon (USA) estuary. Aquat. Bot. 76, 329-337.
- 1530 Borde, A.B., Thom, R.M., Rumrill, S., Miller, L.M., 2003. Geospatial habitat change analysis in
1531 Pacific Northwest coastal estuaries. Estuaries 26, 1104-1106.
- 1532 Bostrom, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on
1533 associated fauna: A review. Estuar. Coast. Shelf Sci. 68, 383-403.
- 1534 Bottom, D.L., Jones, K.K., Cornwell, T.J., Gray, A., Simenstad, C.A., 2005. Patterns of Chinook
1535 salmon migration and residency in the Salmon River estuary (Oregon). Estuar. Coast.
1536 Shelf Sci. 64, 79-93.
- 1537 Bougrier, S., Hawkins, A.J.S., Heral, M. 1997. Preingestive selection of differential microalgal
1538 mixtures in *Crassostrea gigas* and *Mytilus edulis*, analysed by flow cytometry.
1539 Aquaculture 150, 123-134.
- 1540 Bowden, D.A., Rowden, A.A., Attrill, M.J., 2001. Effect of patch size and in-patch location on
1541 the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. J. Exp.
1542 Mar. Biol. Ecol. 259, 133-154.

- 1543 Breitberg, D.L., 1999. Are three dimensional structure and healthy oyster populations the keys to
1544 an ecologically interesting and important fish community? In: Luckenbach, M.W.,
1545 Wesson, J. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis of Approaches*. Virginia
1546 Institute of Marine Sciences Press, Williamsburg, Virginia, pp. 239-250.
- 1547 Brilliant, M.G.S., MacDonald, B.A., 2002. Post-ingestive selection in the sea scallop
1548 (*Placopecten magellanicus*) on the basis of chemical properties of particles. *Mar. Biol.*
1549 141, 457-465.
- 1550 Brilliant, M.G.S., MacDonald, B.A., 2003. Post-ingestive sorting of living and heat-killed
1551 *Chlorella* within the sea scallop, *Placopecten magellanicus* (Gmelin). *J. Exp. Mar. Biol.*
1552 *Ecol.* 290, 81-91.
- 1553 Brooks, K.M., 2000. Literature review and model evaluation describing the environmental
1554 effects and carrying capacity associated with intensive culture of mussels (*Mytilus edulis*
1555 *galloprovincialis*). Pacific Shellfish Institute, Unpublished technical report, Olympia,
1556 Washington, pp. 1-125.
- 1557 Brooks, K.M., 2004. The fouling community found in association with the intensive raft culture
1558 of *Mytilus edulis galloprovincialis* in Totten Inlet, Washington. Report to the National
1559 Oceanic and Atmospheric Administration., Seattle, WA.
- 1560 Brooks, R.A., Bell, S.S., 2001. Mobile corridors in marine landscapes: enhancement of faunal
1561 exchange at seagrass / sand ecotones. *J. Exp. Mar. Biol. Ecol.* 264, 67-84.
- 1562 Brugere, C., Ridler, N., 2004. Global aquaculture outlook in the next decades: An analysis of
1563 national aquaculture production forecasts to 2030. Food and Agriculture Organization of
1564 the United Nations, FAO Fisheries Circular 1001, FIPP/C1001, Rome, Italy, pp. 1-47.
- 1565 Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine
1566 communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community*
1567 *Ecology*. Sinauer Associates, Sunderland, MA, pp. 201-219.
- 1568 Buhle, E.R., Margolis, M., Ruesink, J.L., 2005. Bang for buck: cost-effective control of invasive
1569 species with different life histories. *Ecol. Econ.* 52, 355-366.
- 1570 Burdick, D.M., Short, F.T., 1999. The effects of boat docks on eelgrass beds in coastal waters of
1571 Massachusetts. *Environ. Manag.* 23, 231-240.
- 1572 Cabaco, S., Alexandre, A., Santos, R., 2005. Population-level effects of clam harvesting on the
1573 seagrass *Zostera noltii*. *Mar. Ecol. Prog. Ser.* 298, 123-129.
- 1574 Caldow, R.W.G., Beadman, H.A., McGroarty, S., Kaiser, M.J., Goss-Custard, J.D., Mould, K.,
1575 Wilson, A., 2003. Effects of intertidal mussel cultivation on bird assemblages. *Mar. Ecol.*
1576 *Prog. Ser.* 259, 173-183.
- 1577 Caldow, R.W.G., Beadman, H.A., McGroarty, S., Stillman, R.A., Goss-Custard, J.D., Durell,
1578 S.E.A.L., West, A.D., Kaiser, M.J., Mould, K., Wilson, A., 2004. A behavior-based
1579 modeling approach to reducing shorebird-shellfish conflicts. *Ecol. Appl.* 14, 1411-1427.
- 1580 Callier, M.D., Weise, A.M., McKindsey, C.W., Desrosiers, G., 2006. Sedimentation rates in a
1581 suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and
1582 dispersion. *Mar. Ecol. Prog. Ser.* 322, 129-141.
- 1583 Cannon, A., 2000. Settlement and sea-levels on the central coast of British Columbia: Evidence
1584 from shell midden cores. *Amer. Antiquity* 65, 67-77.
- 1585 Carlton, J.T., Mann, R.H., 1996. Transfers and world wide introductions. In: Kennedy, V.S.,
1586 Newell, R.I.E., Eble, A.F. (Eds.), *The eastern oyster *Crassostrea virginica**. Maryland Sea
1587 Grant, College Park, Maryland, pp. 691-705.

- 1588 Carlton, J.T., Ruiz, G.M., Everett, R.A., 1991. The structure of benthic estuarine communities
1589 associated with dense suspended populations of the introduced Japanese oyster
1590 *Crassostrea gigas*: Years 1 and 2. South Slough National Estuarine Research Reserve,
1591 Final Report to NOAA, Charleston, Oregon, pp. 1-45.
- 1592 Carswell, B., Cheesman, S., Anderson, J., 2006. The use of spatial analysis for environmental
1593 assessment of shellfish aquaculture in Baynes Sound, Vancouver Island, British
1594 Columbia, Canada. *Aquaculture* 253, 408-414.
- 1595 Castel, J., Labourg, P.J., Escaravage, V., Auby, I., Garcia, M.E., 1989. Influence of seagrass beds
1596 and oyster parks on the abundance and biomass patterns of meiobenthos and
1597 macrobenthos in tidal flats. *Estuar. Coast. Shelf Sci.* 28, 71-85.
- 1598 Cerco, C.F., Noel, M.R., 2007. Can oyster restoration reverse cultural eutrophication in
1599 Chesapeake Bay? *Estuaries Coasts* 30, 331-343.
- 1600 Chamberlain, J., Fernandes, T.F., Read, P., Nickell, T.D., Davies, I.M., 2001. Impacts of
1601 biodeposits from suspended mussel (*Mytilus edulis* L) culture on the surrounding surficial
1602 sediments. *ICES J. Mar. Sci.* 58, 411-416.
- 1603 Chapelle, A., Menesguen, A., Deslous-Paoli, J.M., Souchu, P., Mazouni, N., Vaquer, A., Millet,
1604 B., 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon.
1605 Impact of oyster farming and inputs from the watershed. *Ecol. Model.* 127, 161-181.
- 1606 Chauvaud, L., Jean, F., Ragueneau, O., Thouzeau, G., 2000. Long-term variation of the Bay of
1607 Brest ecosystem: benthic-pelagic coupling revisited. *Mar. Ecol. Prog. Ser.* 200, 35-48.
- 1608 Chew, K.K., 1990. Global bivalve shellfish introductions. *World Aquaculture* 21, 9-22.
- 1609 Chew, K.K., 2001. A changing scene for oyster aquaculture in Humboldt, Bay, California.
1610 *Aquaculture Magazine* 27, 87-91.
- 1611 Christensen, P.B., Glud, R.N., Dalsgaard, T., Gillespie, P., 2003. Impacts of longline mussel
1612 farming on oxygen and nitrogen dynamics and biological communities of coastal
1613 sediments. *Aquaculture* 218, 567-588.
- 1614 Cigarria, J., Fernandez, J.M., 2000. Management of Manila clam beds I. Influence of seed size,
1615 type of substratum and protection on initial mortality. *Aquaculture* 182, 173-182.
- 1616 Clynick, B.G., McKindsey, C.W., Archambault, P., 2008. Distribution and productivity of fish
1617 and macroinvertebrates in mussel aquaculture sites in the Magdalen Islands (Quebec,
1618 Canada). *Aquaculture* 283, 203-210.
- 1619 Coen, L., Grizzle, R.E., 2007. The importance of habitat created by molluscan shellfish to
1620 managed species along the Atlantic coast of the United States. *Atlantic States Marine*
1621 *Fisheries Commission, Habitat Management Series*, Washington, D.C., pp. 1-108.
- 1622 Coen, L.D., Luckenbach, M.W., Breitberg, D.L., 1999. The role of oyster reefs as essential fish
1623 habitat: A review of current knowledge and some new perspectives. In: Benaka, L.R.
1624 (Ed.), *Fish Habitat: Essential Fish Habitat and Rehabilitation*. American Fisheries
1625 Society, Bethesda, Maryland, pp. 438-454.
- 1626 Cognie, B., Barille, L., Rince, W., 2001. Selective feeding of the oyster *Crassostrea gigas* fed on
1627 a natural microphytobenthos assemblage. *Estuaries* 24, 126-131.
- 1628 Cognie, B., Barille, L., Masse, G., Beninger, P.G., 2003. Selection and processing of large
1629 suspended algae in the oyster *Crassostrea gigas*. *Mar. Ecol. Prog. Ser.* 250, 145-152.
- 1630 Cohen, R.R.H., Dresler, P.V., Phillips, E.J.P., Cory, R.L., 1984. The effect of the asiatic clam,
1631 *Corbicula fluminea*, on phytoplankton in the Potomac River, Maryland. *Limnol.*
1632 *Oceanogr.* 29, 170-180.

- 1633 Cole, V.J., Chapman, M.G., Underwood, A.J., 2007. Landscapes and life-histories influence
1634 colonisation of polychaetes to intertidal biogenic habitats. *J. Exp. Mar. Biol. Ecol.* 348,
1635 191-199.
- 1636 Collins, J.W., 1892. Report on the fisheries of the Pacific coast of the United States. United
1637 States Commission of Fish and Fisheries, Report of the Commissioner for 1888,
1638 Washington, D.C., pp. 3-2xx.
- 1639 Comeau, L.A., Drapeau, A., Landry, T., Davidson, J., 2008. Development of longline mussel
1640 farming and the influence of sleeve spacing in Prince Edward Island Canada.
1641 *Aquaculture* 281, 56-62.
- 1642 Connolly, L.M., Colwell, M.A., 2005. Comparative use of longline oysterbeds and adjacent tidal
1643 flats by waterbirds. *Bird Conserv. Int.* 15, 237-255.
- 1644 Connolly, R.M., Hindell, J.S., 2006. Review of nekton patterns and ecological processes in
1645 seagrass landscapes. *Estuar. Coast. Shelf Sci.* 68, 433-444.
- 1646 Conte, F.S., Harbell, S.C., RaLonde, R.L., 1994. Oyster Culture: Fundamentals and technology
1647 of the West Coast industry. Western Regional Aquaculture Center WRAC 94-101,
1648 Seattle, Washington, pp. 1-150.
- 1649 Cortright, R., Weber, J., Bailey, R., 1987. The Oregon estuary plan book. Oregon Dept. Land
1650 Conservation and Development.
- 1651 Costa-Pierce, B., 2002. Ecology as the paradigm for the future of aquaculture. In: Costa-Pierce,
1652 B. (Ed.), *Ecological Aquaculture: The evolution of the blue revolution*. Blackwell
1653 Science, Oxford, UK, pp. 339-372.
- 1654 Costa-Pierce, B.A., Desbonnet, A., Edwards, P., Baker, D., 2005. *Urban Aquaculture*. CABI
1655 Publishing, Cambridge, Massachusetts.
- 1656 Cranford, P.J., Strain, P.M., Dowd, M., Hargrave, B.T., Grant, J., Archambault, M.C., 2007.
1657 Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal
1658 embayment. *Mar. Ecol. Prog. Ser.* 347, 61-78.
- 1659 Crawford, C.M., Macleod, C.K.A., Mitchell, I.M., 2003. Effects of shellfish farming on the
1660 benthic environment. *Aquaculture* 224, 117-140.
- 1661 Daehler, C.C., Strong, D.R., 1996. Status, prediction and prevention of introduced cordgrass
1662 *Spartina spp.* invasions in Pacific estuaries, USA. *Biol. Conserv.* 78, 51-58.
- 1663 Dahlback, B., Gunnarsson, L.A.H., 1981. Sedimentation and sulfate reduction under mussel
1664 culture. *Mar. Biol.* 63, 269-275.
- 1665 Dame, R.F., 1996. *Ecology of Marine bivalves: An Ecosystem Approach*. CRC Press, Boca
1666 Raton, Florida.
- 1667 Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. *Aquat. Ecol.* 31,
1668 409-421.
- 1669 Dame, R.F., Spurrier, J.D., Zingmark, R.G., 1992. In situ metabolism of an oyster reef. *J. Exp.*
1670 *Mar. Biol. Ecol.* 164, 147-159.
- 1671 D'Amours, O., Archambault, P., McKindsey, C.W., Johnson, L.E., 2008. Local enhancement of
1672 epibenthic macrofauna by aquaculture activities. *Mar. Ecol. Prog. Ser.* 371, 73-84.
- 1673 Darcy, M.C., Eggleston, D.B., 2005. Do habitat corridors influence animal dispersal and
1674 colonization in estuarine systems? *Landsc. Ecol.* 20, 841-855.
- 1675 Dawes, C.J., Andorfer, J., Rose, C., Uranowski, C., Ehringer, N., 1997. Regrowth of the seagrass
1676 *Thalassia testudinum* into propeller scars. *Aquat. Bot.* 59, 139-155.
- 1677 De Casabianca, M.-L., Laugier, T., Collart, D., 1997. Impact of shellfish farming eutrophication
1678 on benthic macrophyte communities in the Thau lagoon, France. *Aquac. Int.* 5, 301-314.

- 1679 De Grave, S., Moore, S.J., Burnell, G., 1998. Changes in benthic macrofauna associated with
1680 intertidal oyster, *Crassostrea gigas* (Thunberg) culture. J. Shellfish Res. 17, 1137-1142.
- 1681 Dealteris, J.T., Kilpatrick, B.D., Rheault, R.B., 2004. A comparative evaluation of the habitat
1682 value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated
1683 seabed. J. Shellfish Res. 23, 867-874.
- 1684 Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments.
1685 Conserv. Biol. 14, 342-355.
- 1686 Defossez, J.M., Hawkins, A.J.S., 1997. Selective feeding in shellfish: size-dependent rejection of
1687 large particles within pseudofaeces from *Mytilus edulis*, *Ruditapes philippinarum* and
1688 *Tapes decussatus*. Mar. Biol. 129, 139-147.
- 1689 Dennison, W.C., Aller, R.C., Alberte, R.S., 1987. Sediment ammonium availability and eelgrass
1690 (*Zostera marina*) growth. Mar. Biol. 94, 469-477.
- 1691 Dernie, K.M., Kaiser, M.J., Richardson, E.A., Warwick, R.M., 2003. Recovery of soft sediment
1692 communities and habitats following physical disturbance. J. Exp. Mar. Biol. Ecol. 285-
1693 286, 415-434.
- 1694 Deslous-Paoli, J.M., Lannou, A.M., Geairon, P., Bougrier, S., Raillard, O., Heral, M., 1992.
1695 Effects of the feeding behaviour of *Crassostrea gigas* (bivalve molluscs) on
1696 biosedimentation of natural particulate matter. Hydrobiologia 231, 85-91.
- 1697 Dittmann, S., 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal
1698 flats. Mar. Ecol. Prog. Ser. 134, 119-130.
- 1699 Drapeau, A., Comeau, L.A., Landry, T., Stryhn, H., Davidson, J., 2006. Association between
1700 longline design and mussel productivity in Prince Edward Island, Canada. Aquaculture
1701 261, 879-889.
- 1702 Duarte, P., Hawkins, A.J.S., Pereira, A., 2005. How does estimation of environmental carrying
1703 capacity for bivalve culture depend upon spatial and temporal scales? In: Dame, R.F.,
1704 Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in Ecosystems. Springer
1705 Verlag, Netherlands, pp. 121-135.
- 1706 Dubois, S., Orvain, F., Marin-Leal, J.C., Ropert, M., Lefebvre, S., 2007. Small-scale spatial
1707 variability of food partitioning between cultivated oysters and associated suspension-
1708 feeding species, as revealed by stable isotopes. Mar. Ecol. Prog. Ser. 336, 151-160.
- 1709 Dumbauld, B., Visser, E., Armstrong, D.A., Cole-Warner, L., Feldman, K., Kauffman, B., 2000.
1710 Use of oyster shell to create habitat for juvenile Dungeness crab in Washington coastal
1711 estuaries: Status and prospects. J. Shellfish Res. 19, 379-386.
- 1712 Dumbauld, B.R., Wyllie-Echeverria, S., 2003. The influence of burrowing thalassinid shrimps on
1713 the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. Aquat. Bot.
1714 77, 27-42.
- 1715 Dumbauld, B.R., Brooks, K.M., Posey, M.H., 2001. Response of an estuarine benthic
1716 community to application of the pesticide carbaryl and cultivation of Pacific oysters
1717 (*Crassostrea gigas*) in Willapa Bay, Washington. Mar. Pollut. Bull. 42, 826-844.
- 1718 Dumbauld, B.R., Feldman, K., Armstrong, D., 2004. A comparison of the ecology and effects of
1719 two species of thalassinidean shrimps on oyster aquaculture operations in the eastern
1720 North Pacific. Nagasaki University, Proceedings of the symposium on "ecology of large
1721 bioturbators in tidal flats and shallow sublittoral sediments-from individual behavior to
1722 their role as ecosystem engineers", Nagasaki, Japan, pp. 53-61.
- 1723 Dumbauld, B.R., Ruesink, J.L., Rumrill, S., 2005. The ecological role and potential impacts of
1724 molluscan shellfish culture in the estuarine environment. US Department of Agriculture,

- 1725 Agricultural Research Service, Final Report to the Western Regional Aquaculture Center
1726 Newport, Oregon, pp. 1-31.
- 1727 Eckrich, C.E., Holmquist, J.G., 2000. Trampling in a seagrass assemblage: direct effects,
1728 response of associated fauna, and the role of substrate characteristics. *Mar. Ecol. Prog.*
1729 *Ser.* 201, 199-209.
- 1730 Edgar, G.J., Barrett, N.S., Graddon, D.J., Last, P.R., 2000. The conservation significance of
1731 estuaries: a classification of Tasmanian estuaries using ecological, physical and
1732 demographic attributes as a case study. *Biol. Conserv.* 92, 383-397.
- 1733 Eggleston, D.B., Armstrong, D.A., 1995. Pre- and post-settlement determinants of estuarine
1734 Dungeness crab recruitment. *Ecol. Monogr.* 65, 193-216.
- 1735 Emmett, R., Llanso, R., Newton, J., Thom, R., Hornberger, M., Morgan, C., Levings, C.,
1736 Copping, A., Fishman, P., 2000. Geographic signatures of North American West Coast
1737 estuaries. *Estuaries* 23, 765-792.
- 1738 Erbland, P.J., Ozbay, G., 2008. Comparison of the macrofaunal communities inhabiting a
1739 *Crassostrea virginica* oyster reef and oyster aquaculture gear in Indian River Bay,
1740 Delaware. *J. Shellfish Res.* 27, 757-768.
- 1741 Erftemeijer, P.L.A., Lewis, R.R.R., 2006. Environmental impacts of dredging on seagrasses: A
1742 review. *Mar. Pollut. Bull.* 52, 1553-1572.
- 1743 Everett, R.A., Ruiz, G.M., Carlton, J.T., 1995. Effect of oyster mariculture on submerged aquatic
1744 vegetation: an experimental test in a Pacific Northwest estuary. *Mar. Ecol. Prog. Ser.*
1745 125, 205-217.
- 1746 Feist, B.E., Simenstad, C.A., 2000. Expansion rates and recruitment frequency of exotic smooth
1747 cordgrass, *Spartina alterniflora* (Loisel), colonizing unvegetated littoral flats in Willapa
1748 Bay, Washington. *Estuaries* 23, 267-274.
- 1749 Feldman, K.L., Armstrong, D.A., Dumbauld, B.R., DeWitt, T.H., Doty, D.C., 2000. Oysters,
1750 crabs, and burrowing shrimp: Review of an environmental conflict over aquatic resources
1751 and pesticide use in Washington State's (USA) coastal estuaries. *Estuaries* 23, 141-176.
- 1752 Ferraro, S.P., Cole, F.A., 2007. Benthic macrofauna-habitat associations in Willapa Bay,
1753 Washington, USA. *Estuar. Coast. Shelf Sci.* 71, 491-507.
- 1754 Ferreira, J.G., Hawkins, A.J.S., Bricker, S.B., 2007. Management of productivity, environmental
1755 effects and profitability of shellfish aquaculture - the Farm Aquaculture Resource
1756 Management (FARM) model. *Aquaculture* 264, 160-174.
- 1757 Ferrell, D.J., Bell, J.D., 1991. Differences among assemblages of fish associated with *Zostera*
1758 *capricorni* and bare sand over a large spatial scale. *Mar. Ecol. Prog. Ser.* 72, 15-24.
- 1759 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S.,
1760 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev.*
1761 *Ecol. Evol. Syst.* 35, 557-581.
- 1762 Fonseca, M., Whitfield, P.E., Kelly, N.M., Bell, S.S., 2002. Modeling seagrass landscape pattern
1763 and associated ecological attributes. *Ecol. Appl.* 12, 218-237.
- 1764 Fonseca, M.S., Thayer, G.W., Chester, A.J., Foltz, C., 1984. Impact of scallop harvesting on
1765 eelgrass (*Zostera marina*) meadows: implications for management. *N. Am. J. Fish.*
1766 *Manag.* 4, 286-293.
- 1767 Forman, R.T., 1995. *Land Mosaics: the Ecology of Landscapes and Regions.* Cambridge
1768 University Press, New York.
- 1769 Forrest, B.M., Creese, R.G., 2006. Benthic impacts of intertidal oyster culture, with
1770 consideration of taxonomic sufficiency. *Environ. Monit. Assess.* 112, 159-176.

- 1771 Gaeckle, J., Dowty, P., Reeves, B., Berry, H.D., Wyllie-Echeverria, S., Mumford Jr., T.F., 2007.
1772 Puget Sound Vegetation Monitoring Project 2005 Monitoring Report. Washington
1773 Department of Natural Resources, Olympia, WA, pp. 1-94.
- 1774 Gangnery, A., Bacher, C., Buestel, D., 2001. Assessing the production and the impact of
1775 cultivated oysters in the Thau lagoon (Mediterranean, France) with a population
1776 dynamics model. *Can. J. Fish. Aquat. Sci.* 58, 1012-1020.
- 1777 Gangnery, A., Chabirand, J.M., Lagarde, F., LeGall, P., Oheix, J., Bacher, C., Buestel, D., 2003.
1778 Growth model of the Pacific oyster, *Crassostrea gigas*, cultured in Thau Lagoon
1779 (Mediterranean, France). *Aquaculture* 215, 267-290.
- 1780 Ganter, B., 2000. Seagrass (*Zostera spp.*) as food for brent geese (*Branta bernicla*): an overview.
1781 *Helgol. Mar. Res.* 54, 63-70.
- 1782 Gee, J.M., 1989. An ecological and economic review of meiofauna as food for fish. *Zool. J.*
1783 *Linn. Soc.* 96, 243-261.
- 1784 Gerritsen, J., Holland, A.F., Irvine, D.E., 1994. Suspension-feeding bivalves and the fate of
1785 primary production - an estuarine model applied to Chesapeake Bay. *Estuaries* 17, 403-
1786 416.
- 1787 Gibbs, M.T., 2004. Interactions between bivalve shellfish farms and fishery resources.
1788 *Aquaculture* 240, 267-296.
- 1789 Giles, H., Pilditch, C.A., 2006. Effects of mussel (*Perna canaliculus*) biodeposit decomposition
1790 on benthic respiration and nutrient fluxes. *Mar. Biol.* 150, 261-271.
- 1791 Glancy, T.P., Frazer, T.K., Cichra, C.E., Lindberg, W.J., 2003. Comparative patterns of
1792 occupancy by decapod crustaceans in seagrass, oyster, and marsh-edge habitats in a
1793 northeast Gulf of Mexico estuary. *Estuaries* 26, 1291-1301.
- 1794 Glasby, T.M., Underwood, A.J., 1996. Sampling to differentiate between pulse and press
1795 perturbations. *Environ. Monit. Assess.* 42, 241-252.
- 1796 Glasoe, S., Christy, A., 2004. Coastal urbanization and microbial contamination of shellfish
1797 growing areas: Literature review and analysis. Puget Sound Action Team, PSAT04-09,
1798 Olympia, Washington, pp. 1-28.
- 1799 Good, T.P., Beechie, T.J., McElhany, P., McClure, M.M., Ruckelshaus, M.H., 2007. Recovery
1800 planning for endangered species act listed Pacific salmon: Using science to inform goals
1801 and strategies. *Fisheries* 32, 426-440.
- 1802 Goodwin, C.L., 1976. Observations of spawning and growth of subtidal geoducks (*Panope*
1803 *generosa*, Gould). *Proceedings of the National Shellfisheries Association* 65, 49-58.
- 1804 Goodwin, C.L., Pease, B.C., 1991. Geoduck *Panopea abrupta* (Conrad 1849) size, density, and
1805 quality as related to various environmental parameters in Puget Sound, Washington. *J.*
1806 *Shellfish Res.* 10, 65-77.
- 1807 Gouleau, D., Jouanneau, J.M., Weber, O., Sauriau, P.G., 2000. Short- and long-term
1808 sedimentation on Montportail-Brouage intertidal mudflat, Marennes-Oleron Bay
1809 (France). *Cont. Shelf Res.* 20, 1513-1530.
- 1810 Grabowski, J.H., Hughes, R.A., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting
1811 influences restored oyster reef communities. *Ecology* 86, 1926-1935.
- 1812 Grant, J., Hatcher, A., Scott, D.B., Pocklington, P., Schafer, C.T., Winters, G.V., 1995. A
1813 multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic
1814 communities. *Estuaries* 18, 124-144.
- 1815 Grant, J., Bugden, G., Horne, E., Archambault, M.C., Carreau, M., 2007. Remote sensing of
1816 particle depletion by coastal suspension-feeders. *Can. J. Fish. Aquat. Sci.* 64, 387-390.

- 1817 Grant, J., Bacher, C., Cranford, P.J., Guyondet, T., Carreau, M., 2008. A spatially explicit
1818 ecosystem model of seston depletion in dense mussel culture. *Journal of Marine Systems*
1819 73, 155-168.
- 1820 Griffiths, J., Dethier, M.N., Newsom, A., Byers, J.E., Meyer, J.J., Oyarzun, F., Lenihan, H.,
1821 2006. Invertebrate community responses to recreational clam digging. *Mar. Biol.* 149,
1822 1489-1497.
- 1823 Grizzle, R.E., Greene, J.K., Coen, L.D., 2008. Seston removal by natural and constructed
1824 intertidal Eastern oyster (*Crassostrea virginica*) reefs: A comparison with previous
1825 laboratory studies, and the value of in situ methods. *Estuaries Coasts* in press.
- 1826 Groffman, P., Baron, J., Blett, T., Gold, A., Goodman, I., Gunderson, L., Levinson, B., Palmer,
1827 M., Paerl, H., Peterson, G., Poff, N., Rejeski, D., Reynolds, J., Turner, M., Weathers, K.,
1828 Wiens, J., 2006. Ecological thresholds: The key to successful environmental management
1829 or an important concept with no practical application? *Ecosystems* 9, 1-13.
- 1830 Groot, C., Margolis, L., 1991. *Pacific Salmon Life Histories*. University of British Columbia
1831 Press, Vancouver, British Columbia.
- 1832 Gruet, Y., Heral, M., Robert, J.-M., 1976. Premieres observations sur l'introduction de la faune
1833 associee au naissan d'huitres Japonaises *Crassostrea gigas* (Thunberg), importe sur la
1834 cote Atlantique Francaise. *Cah. Biol. Mar.* 17, 173-184.
- 1835 Grumbine, R.E., 1997. Reflections on "what is ecosystem management?". *Conserv. Biol.* 11, 41-
1836 47.
- 1837 Gunderson, L.H., 2000. Ecological resilience - in theory and application. *Annu. Rev. Ecol. Syst.*
1838 31, 425-439.
- 1839 Gutierrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem
1840 engineers: the role of shell production in aquatic habitats. *Oikos* 101, 79-90.
- 1841 Haedrich, R.L., 1983. Estuarine fishes. In: Ketchum, B.H. (Ed.), *Ecosystems of the World:*
1842 *Estuaries and Enclosed Seas*. Elsevier, New York, pp. 183-207.
- 1843 Haertel-Borer, S.S., Allen, D.M., Dame, R.F., 2004. Fishes and shrimps are significant sources
1844 of dissolved inorganic nutrients in intertidal salt marsh creeks. *J. Exp. Mar. Biol. Ecol.*
1845 311, 79-99.
- 1846 Hagstrum, J.T., Atwater, B.F., Sherrod, B.L., 2004. Paleomagnetic correlation of late Holocene
1847 earthquakes among estuaries in Washington and Oregon. *Geochemistry Geophysics*
1848 *Geosystems* 5,[online] URL:
1849 <http://www.agu.org/pubs/crossref/2004/2004GC000736.shtml>.
- 1850 Harbin-Ireland, A.C., 2004. Effects of oyster mariculture on the benthic invertebrate community
1851 in Drakes Estero, Pt. Reyes Peninsula, California. M.S. thesis, University of California,
1852 Davis, California.
- 1853 Hargrave, B.T., Doucette, L.I., Cranford, P.J., Law, B.A., Milligan, T.G., 2008. Influence of
1854 mussel aquaculture on sediment organic enrichment in a nutrient-rich coastal embayment.
1855 *Mar. Ecol. Prog. Ser.* 365, 137-149.
- 1856 Harrington, E., 2005. Assessment of the oyster market distribution chain and its implications for
1857 cooperative formation in the Alaskan mariculture industry. M.S. thesis, University of
1858 Alaska, Fairbanks, Alaska.
- 1859 Harrison, T.D., Whitfield, A.K., 2006. Estuarine typology and the structuring of fish
1860 communities in South Africa. *Environ. Biol. Fishes* 75, 269-293.

- 1861 Hartstein, N.D., Rowden, A.A., 2004. Effect of biodeposits from mussel culture on
1862 macroinvertebrate assemblages at sites of different hydrodynamic regime. *Mar. Environ.*
1863 *Res.* 57, 339-357.
- 1864 Harvey, D.J., 2006. *Aquaculture Outlook*. U.S. Department of Agriculture, Electronic Outlook
1865 Report from the Economic Research Service, LDP-AQS-23 . [online] URL:
1866 <http://www.ers.usda.gov>.
- 1867 Harwell, H.D., 2004. Landscape aspects of oyster reefs: fragmentation and habitat utilization.
1868 M.S. thesis, University of North Carolina Wilmington, North Carolina.
- 1869 Hatcher, A., Grant, J., Schofield, B., 1994. Effects of suspended mussel culture (*Mytilus spp.*) on
1870 sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Mar.*
1871 *Ecol. Prog. Ser.* 115, 219-235.
- 1872 Hauxwell, J., Cebrian, J., Valiela, I., 2003. Eelgrass *Zostera marina* loss in temperate estuaries:
1873 relationship to land-derived nitrogen loads and effect of light limitation imposed by
1874 algae. *Mar. Ecol. Prog. Ser.* 247, 59-73.
- 1875 Hauxwell, J., Cebrian, J., Furlong, C., Valiela, I., 2001. Macroalgal canopies contribute to
1876 eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82, 1007-
1877 1022.
- 1878 Hawkins, A.J.S., Bayne, B.L., Bougrier, S., Heral, M., Iglesias, J.I.P., Navarro, E., Smith,
1879 R.F.M., Urrutia, M.B., 1998. Some general relationships in comparing the feeding
1880 physiology of suspension-feeding bivalve molluscs. *J. Exp. Mar. Biol. Ecol.* 219, 87-103.
- 1881 Healey, M.C., 1982. Juvenile Pacific salmon in estuaries: The life support system. In: Kennedy,
1882 V.S. (Ed.), *Estuarine Comparisons*. Academic Press, New York, pp. 315-341.
- 1883 Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for
1884 seagrass meadows. *Mar. Ecol. Prog. Ser.* 253, 123-136.
- 1885 Heck, K.L., Jr., Thoman, T.A., 1984. The nursery role of seagrass meadows in upper and lower
1886 reaches of the Chesapeake Bay. *Estuaries* 7, 70-92.
- 1887 Hedgepeth, J., Obrebski, S., 1981. Willapa Bay: A historical perspective and a rationale for
1888 research. Office of Biological Services U.S. Fish and Wildlife Service, FWS/OBS-81/03,
1889 pp. 1-52.
- 1890 Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middleburg, J., Soetaert, K., 1995.
1891 Production and consumption of biological particles in temperate tidal estuaries. *Annu.*
1892 *Rev. Ocean. Mar. Biol.* 33, 1-149.
- 1893 Heral, M., 1993. Why carrying capacity models are useful tools for management of bivalve
1894 molluscs culture. In: Dame, R.F. (Ed.), *Bivalve Filter Feeders in Estuarine and Coastal*
1895 *Ecosystem Processes*. Springer-Verlag, Berlin, Heidelberg, pp. 455-477.
- 1896 Hickey, B.M., Banas, N.S., 2003. Oceanography of the U.S. Pacific Northwest coastal ocean and
1897 estuaries with application to coastal ecology. *Estuaries* 26, 1010-1031.
- 1898 Hilgerloh, G., O' Halloran, J., Kelly, T.C., Burnell, G.M., 2001. A preliminary study on the
1899 effects of oyster culturing structures on birds in a sheltered Irish estuary. *Hydrobiologia*
1900 465, 175-180.
- 1901 Hinchey, E.K., Nicholson, M.C., Zajac, R.N., Irlandi, E.A., 2008. Marine and coastal
1902 applications in landscape ecology. *Landsc. Ecol.* 23, 1-5.
- 1903 Hoffmann, A., Bradbury, A., Goodwin, C.L., 2000. Modeling geoduck, *Panopea abrupta*
1904 (Conrad, 1849) population dynamics. I. Growth. *J. Shellfish Res.* 19, 57-62.
- 1905 Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1-
1906 23.

- 1907 Holmer, M., Frederiksen, M.S., Mollegaard, H., 2005. Sulfur accumulation in eelgrass (*Zostera*
1908 *marina*) and effect of sulfur on eelgrass growth. *Aquat. Bot.* 81, 367-379.
- 1909 Holsman, K.K., McDonald, P.S., Armstrong, D.A., 2006. Intertidal migration and habitat use by
1910 subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Mar. Ecol. Prog. Ser.*
1911 308, 183-195.
- 1912 Holsman, K.K., Armstrong, D.A., Beauchamp, D.A., Ruesink, J.L., 2003. The necessity for
1913 intertidal foraging by estuarine populations of subadult dungeness crab, *Cancer magister*:
1914 evidence from a bioenergetics model. *Estuaries* 26, 1155-1173.
- 1915 Horinouchi, M., 2007. Review of the effects of within-patch scale structural complexity on
1916 seagrass fishes. *J. Exp. Mar. Biol. Ecol.* 350, 111-129.
- 1917 Horn, M.H., Allen, L.G., 1976. Numbers of species and faunal resemblance of marine fishes in
1918 California bays and estuaries. *Bull. Southern Cal. Acad. Sci.* 75, 159-170.
- 1919 Hosack, G.R., Dumbauld, B.R., Ruesink, J.L., Armstrong, D.A., 2006. Habitat associations of
1920 estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*), and
1921 oyster (*Crassostrea gigas*) habitats. *Estuaries Coasts* 29, 1150-1160.
- 1922 Hovel, K.A., Fonseca, M.S., 2005. Influence of seagrass landscape structure on the juvenile blue
1923 crab habitat-survival function. *Mar. Ecol. Prog. Ser.* 300, 179-181.
- 1924 Huang, C.H., Lin, H.J., Huang, T.C., Su, H.M., Hung, J.J., 2008. Responses of phytoplankton
1925 and periphyton to system-scale removal of oyster-culture racks from a eutrophic tropical
1926 lagoon. *Mar. Ecol. Prog. Ser.* 358, 1-12.
- 1927 Hughes, A.R., Bando, K.J., Rodriguez, L.F., Williams, S.L., 2004. Relative effects of grazers and
1928 nutrients on seagrasses: a meta-analysis approach. *Mar. Ecol. Prog. Ser.* 282, 87-99.
- 1929 ICES, 2005. ICES Code of Practice on the Introductions and Transfers of Marine Organisms
1930 2005.[online] Url:
1931 <http://www.ices.dk/reports/general/2004/ices%20code%20of%20practice%202005.pdf>.
- 1932 Inglis, G.J., Gust, N., 2003. Potential indirect effects of shellfish culture on the reproductive
1933 success of benthic predators. *J. Appl. Ecol.* 40, 1077-1089.
- 1934 Iribarne, O., Armstrong, D., Fernandez, M., 1995. Environmental impact of intertidal juvenile
1935 Dungeness crab habitat enhancement: Effects on bivalves and crab foraging rate. *J. Exp.*
1936 *Mar. Biol. Ecol.* 192, 173-194.
- 1937 Irlandi, E.A., Crawford, M.K., 1997. Habitat linkages: The effect of intertidal saltmarshes and
1938 adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish.
1939 *Oecologia* 110, 222-230.
- 1940 Irlandi, E.A., Ambrose, W.G., Orlando, B.A., 1995. Landscape ecology and the marine-
1941 environment - How spatial configuration of seagrass habitat influences growth and
1942 survival of the bay scallop. *Oikos* 72, 307-313.
- 1943 Jackson, E.L., Attrill, M.J., Jones, M.B., 2006. Habitat characteristics and spatial arrangement
1944 affecting the diversity of fish and decapod assemblages of seagrass (*Zostera marina*) beds
1945 around the coast of Jersey (English Channel). *Estuar. Coast. Shelf Sci.* 68, 421-432.
- 1946 Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S.J., Jones, M.B., 2001. The importance of
1947 seagrass beds as a habitat for fishery species. *Ocean. Mar. Biol.* 39, 269-303.
- 1948 Jacobs, D.K., Haney, T.A., Louie, K.D., 2004. Genes, diversity, and geologic process on the
1949 Pacific coast. *Annu. Rev. Earth Planetary Sci.* 32, 601-652.
- 1950 Jamieson, G., Chew, L., Gillespie, G., Robinson, A., Bendell-Young, L., Heath, W., Bravender,
1951 B., Tompkins, A., Nishimura, D., Doucette, P., 2001. Phase 0 review of the

- 1952 environmental impacts of intertidal shellfish aquaculture in Baynes Sound. Canadian
1953 Science Advisory Secretariat, 2001/125, Ottawa, pp. 1-103.
- 1954 Jenkins, G.P., Walker-Smith, G.K., Hamer, P.A., 2002. Elements of habitat complexity that
1955 influence harpacticoid copepods associated with seagrass beds in a temperate bay.
1956 *Oecologia* 131, 598-605.
- 1957 Jenkins, G.P., May, H.M.A., Wheatley, M.J., Holloway, M.G., 1997. Comparison of fish
1958 assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip
1959 Bay and Corner Inlet, Victoria, Australia with emphasis on commercial species. *Estuar.
1960 Coast. Shelf Sci.* 44, 569-588.
- 1961 Jiang, W., Gibbs, M.T., 2005. Predicting the carrying capacity of bivalve shellfish culture using a
1962 steady, linear food web model. *Aquaculture* 244, 171-185.
- 1963 Jie, H., Zhinan, Z., Zishan, Y., Widdows, a.J., 2001. Differences in the benthic-pelagic particle
1964 flux biodeposition and sediment erosion at intertidal sites with and without clam
1965 (*Ruditapes philippinarum*) cultivation in eastern China. *J. Exp. Mar. Biol. Ecol.* 261, 245-
1966 261.
- 1967 Johnson, M.W., Heck, K.L.J., 2006. Effects of habitat fragmentation per se on decapods and
1968 fishes inhabiting seagrass meadows in the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.*
1969 306, 233-246.
- 1970 Jones, C.G., Lawton, J.H., Shackak, M., 1997. Positive and negative effects of organisms as
1971 physical ecosystem engineers. *Ecology* 78, 1946-1957.
- 1972 Kaiser, M.J., Laing, I., Utting, S.D., Burnell, G.M., 1998. Environmental impacts of bivalve
1973 mariculture. *J. Shellfish Res.* 17, 59-66.
- 1974 Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J., Karakassis, I., 2006.
1975 Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog.
1976 Ser.* 311, 1-14.
- 1977 Kaldy, J.E., 2006. Carbon, nitrogen, phosphorus and heavy metal budgets: How large is the
1978 eelgrass (*Zostera marina* L.) sink in a temperate estuary? *Mar. Pollut. Bull.* 52, 332-356.
- 1979 Kareiva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature*
1980 326, 388-390.
- 1981 Kareiva, P., Marvier, M., McClure, M., 2000. Recovery and management options for
1982 spring/summer chinook salmon in the Columbia River Basin. *Science* 290, 977-979.
- 1983 Kaspar, H.F., Gillespie, P.A., Boyer, I.C., MacKenzie, A.L., 1985. Effects of mussel aquaculture
1984 on the nitrogen cycle and benthic communities in Kenerupu Sound, Marlborough Sounds,
1985 New Zealand. *Mar. Biol.* 85, 127-136.
- 1986 Kautsky, N., Evans, S., 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter
1987 and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.* 38, 201-212.
- 1988 Kelly, J.P., Evens, J.G., Stallcup, R.W., Wimpfheimer, D., 1996. Effects of aquaculture on
1989 habitat use by wintering shorebirds in Tomales Bay, California. *Calif. Fish Game* 82,
1990 160-174.
- 1991 Kelly, J.R., Volpe, J.R., 2007. Native eelgrass (*Zostera marina* L.) survival and growth adjacent
1992 to non-native oysters (*Crassostrea gigas* Thunberg) in the Strait of Georgia, British
1993 Columbia. *Bot. Mar.* 50, 143-150.
- 1994 Kelly, J.R., Proctor, H., Volpe, J.P., 2008. Intertidal community structure differs significantly
1995 between substrates dominated by native eelgrass (*Zostera marina* L.) and adjacent to the
1996 introduced oyster *Crassostrea gigas* (Thunberg) in British Columbia, Canada.
1997 *Hydrobiologia* 596, 57-66.

- 1998 Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwell,
1999 J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., Houde, E.D., Kimmel, D.G.,
2000 Miller, W.D., Newell, R.I.E., Roman, M.R., Smith, E.M., Stevenson, J.C., 2005.
2001 Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar.
2002 Ecol. Prog. Ser. 303, 1-29.
- 2003 Kirby, M.X., 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries
2004 along continental margins. Proc. Natl. Acad. Sci. U. S. A. 101, 13096-13099.
- 2005 Kirk, M., Esler, D., Boyd, W.S., 2007. Morphology and density of mussels on natural and
2006 aquaculture structure habitats: implications for sea duck predators. Mar. Ecol. Prog. Ser.
2007 346, 179-187.
- 2008 Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A., van der Meer, J., 2007. Dredging for edible
2009 cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-
2010 choice decisions for target and non-target benthic fauna. ICES J. Mar. Sci. 64, 1735-
2011 1742.
- 2012 Kraeuter, J.N., Castagna, M., 1985. The effects of seed size, shell bags, crab traps, and netting on
2013 the survival of the northern hard clam *Mercenaria mercenaria* (Linne). J. Shellfish Res. 5
2014 69-72.
- 2015 Kurokura, H., 2004. The importance of seaweeds and shellfishes in Japan. Bulletin of Fisheries
2016 Research Agency Supplement #1, 1-4.
- 2017 Laffargue, P., Begout, M.L., Lagardere, F., 2006. Testing the potential effects of shellfish
2018 farming on swimming activity and spatial distribution of sole (*Solea solea*) in a
2019 mesocosm. ICES J. Mar. Sci. 63, 1014-1028.
- 2020 Langdon, C., Newell, R.I.E., 1996. Digestion and nutrition of larvae and adults. In: Kennedy,
2021 V.S., Newell, R.I.E., Able, A. (Eds.), The Eastern Oyster, *Crassostrea virginica*.
2022 Maryland Sea Grant, College Park, Maryland, pp. 231-270.
- 2023 Largier, J.L., Hollibaugh, J.T., Smith, S.V., 1997. Seasonally hypersaline estuaries in
2024 Mediterranean-climate regions. Estuar. Coast. Shelf Sci. 45, 789-797.
- 2025 Larned, S.T., 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient
2026 fluxes between the water column and benthos in a NE Pacific estuary. Mar. Ecol. Prog.
2027 Ser. 254, 69-80.
- 2028 LeGall, S., Hassen, M.B., LeGall, P., 1997. Ingestion of a bacterivorous ciliate by the oyster
2029 *Crassostrea gigas*: Protozoa as a trophic link between picoplankton and benthic
2030 suspension-feeders. Mar. Ecol. Prog. Ser. 152, 301-306.
- 2031 Leguerrier, D., Niquil, N., Petiau, A., Bodoy, A., 2004. Modeling the impact of oyster culture on
2032 a mudflat food web in Marennes-Oleron Bay (France). Mar. Ecol. Prog. Ser. 273, 147-
2033 161.
- 2034 Lehane, C., Davenport, J., 2006. A 15-month study of zooplankton ingestion by farmed mussels
2035 (*Mytilus edulis*) in Bantry Bay, Southwest Ireland. Estuar. Coast. Shelf Sci. 67, 645-652.
- 2036 Lehnert, R.L., Allen, D.M., 2002. Nekton use of subtidal oyster shell habitat in a southeastern
2037 US estuary. Estuaries 25, 1015-1024.
- 2038 Lenihan, 1999. Physical-biological coupling on oyster reefs: How habitat structure influences
2039 individual performance. Ecol. Monogr. 697840, 251-275.
- 2040 Lenihan, H.S., Micheli, F., 2001. Soft-sediment communities. In: Bertness, M.D., Gaines, S.D.,
2041 Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland,
2042 Massachusetts, pp. 253-287.

- 2043 Lenihan, H.S., Peterson, C.H., 2004. Conserving oyster reef habitat by switching from dredging
2044 and tonging to diver-harvesting. *Fish. Bull.* 102, 298-305.
- 2045 Lenihan, H.S., Peterson, C.H., Allen, J.M., 1996. Does flow speed also have a direct effect on
2046 growth of active suspension-feeders: An experimental test on oysters. *Limnol. Oceanogr.*
2047 41, 1359-1366.
- 2048 Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001.
2049 Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress.
2050 *Ecol. Appl.* 11, 764-782.
- 2051 Leslie, H.M., McLeod, K.L., 2007. Confronting the challenges of implementing marine
2052 ecosystem-based management. *Front. Ecol. Environ.* 5, 540-548.
- 2053 Levin, S.A., Lubchenco, J., 2008. Resilience, robustness, and marine ecosystem-based
2054 management. *Bioscience* 58, 27-32.
- 2055 Lindahl, O., Hart, R. Hernroth, B., Kollberg, S., Lars-Ove, L., Olrog, L. Rehnstrom-Holm, A.,
2056 Svensson, J. Svensson, S. Syversen, U., 2005. Improving water quality by mussel
2057 farming: A profitable solution for Swedish society. *Ambio* 34, 131-138.
- 2058 Lindenmayer, D.B., Fischer, J., 2006. Habitat fragmentation and landscape change: an ecological
2059 and conservation synthesis. Island Press, Washington, D.C.
- 2060 Lindsay, C.E., Simons, D., 1997. The fisheries for Olympia oysters, *Ostreola conchaphila*;
2061 Pacific oysters, *Crassostrea gigas*; and Pacific razor clams, *Siliqua patula*, in the State of
2062 Washington. In: Mackenzie, C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.),
2063 The history, present condition, and future of the molluscan fisheries of North and Central
2064 America and Europe. Vol. 2, Pacific Coast and Supplemental Topics., pp. 89-113.
- 2065 Lonsdale, D.J., Cerrato, R.M., Caron, D.A., Schaffner, R.A., 2007. Zooplankton changes
2066 associated with grazing pressure of northern quahogs (*Mercenaria mercenaria* L.) in
2067 experimental mesocosms. *Estuar. Coast. Shelf Sci.* 73, 101-110.
- 2068 Lovatelli, A., 2006. Bivalve farming: An overview of world production, World Aquaculture
2069 Society Meeting, Florence, Italy. [online] URL:<http://www.fao.org/fishery/sofia/en>.
- 2070 Lovvorn, J.R., Baldwin, J.R., 1996. Intertidal and farmland habitats of ducks in the Puget Sound
2071 region: A landscape perspective. *Biol. Conserv.* 77, 97-114.
- 2072 Lu, L., Grant, J., 2008. Recolonization of intertidal infauna in relation to organic deposition at an
2073 oyster farm in Atlantic Canada - A field experiment. *Estuaries Coasts* 31, 767-775.
- 2074 Luckenbach, M.W., 1984. Biogenic structure and foraging by five species of shorebirds
2075 (Charadrii). *Estuar. Coast. Shelf Sci.* 19, 691-696.
- 2076 MacKenzie, C.L.J., Burrell, V.G.J., 1997. Trends and status of molluscan fisheries in North and
2077 Central America and Europe. In: Mackenzie, C.L.J., Burrell, V.G.J., Rosenfield, A.,
2078 Hobart, W.L. (Eds.), The history, present condition, and future of the molluscan fisheries
2079 of North and Central America and Europe. Vol. 1, Atlantic and Gulf Coasts., pp. 1-14.
- 2080 Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction
2081 between water movement, sediment dynamics and submersed macrophytes.
2082 *Hydrobiologia* 444, 71-84.
- 2083 Magnusson, A., Hilborn, R., 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus*
2084 *kisutch*) and Chinook Salmon (*Oncorhynchus tshawytscha*) released from hatcheries on
2085 the U.S. Pacific coast. *Estuaries* 26, 1094-1103.
- 2086 Malet, N., Sauriau, P.G., Faury, N., Soletchnik, P., Guillou, G., 2007. Effect of seasonal
2087 variation in trophic conditions and the gametogenic cycle on delta C-13 and delta N-15

- 2088 levels of diploid and triploid Pacific oysters *Crassostrea gigas*. Mar. Ecol. Prog. Ser. 346,
2089 203-217.
- 2090 Mallet, A.L., Carver, C.E., Landry, T., 2006. Impact of suspended and off-bottom Eastern oyster
2091 culture on the benthic environment in eastern Canada. Aquaculture 255, 362-373.
- 2092 Marba, N., Duarte, C.M., 1995. Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to
2093 subaqueous dune migration. J. Ecol. 83, 381-389.
- 2094 Marinov, D., Galbiati, L., Giordani, G., Viarogi, P., Norro, A., Bencivelli, S., Zaldivar, J.M.,
2095 2007. An integrated modelling approach for the management of clam farming in coastal
2096 lagoons. Aquaculture 269, 306-320.
- 2097 Mattsson, J., Linden, O., 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L.
2098 (*Bivalvia*), cultured on hanging long-lines. Sarsia 68, 97-102.
- 2099 Mazerolle, M.J., Villard, M.A., 1999. Patch characteristics and landscape context as predictors of
2100 species presence and abundance: A review. Ecoscience 6, 117-124.
- 2101 Mazouni, N., 2004. Influence of suspended oyster cultures on nitrogen regeneration in a coastal
2102 lagoon (Thau, France). Mar. Ecol. Prog. Ser. 276, 103-113.
- 2103 McGlathery, K.J., 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-
2104 enriched coastal waters. J. Phycol. 37, 453-456.
- 2105 McKindsey, C.W., Thetmeyer, H., Landry, T., Silvert, W., 2006. Review of recent carrying
2106 capacity models for bivalve culture and recommendations for research and management.
2107 Aquaculture 261, 451-462.
- 2108 McKindsey, C.W., Landry, T., O'Beirn, F.X., Davies, I.N., 2007. Bivalve aquaculture and exotic
2109 species: A review of ecological considerations and management issues. J. Shellfish Res.
2110 26, 281-294.
- 2111 Melia, P., Gatto, M., 2005. A stochastic bioeconomic model for the management of clam
2112 farming. Ecol. Model. 184, 163-174.
- 2113 Mesnage, V., Ogier, S., Bally, G., Disnar, J.R., Lottier, N., Dedieu, K., Rabouille, C., Copard,
2114 Y., 2007. Nutrient dynamics at the sediment-water interface in a Mediterranean lagoon
2115 (Thau, France): Influence of biodeposition by shellfish farming activities. Mar. Environ.
2116 Res. 63, 257-277.
- 2117 Metzger, E., Simonucci, C., Viollier, E., Sarazin, G., Prevot, F., Jezequel, D., 2007. Benthic
2118 response to shellfish farming in Thau lagoon: Pore water signature. Estuar. Coast. Shelf
2119 Sci. 72, 406-419.
- 2120 Miller, B.A., Sadro, S., 2003. Residence time and seasonal movements of juvenile coho salmon
2121 in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Trans. Am.
2122 Fish. Soc. 132, 546-559.
- 2123 Miller, J.A., Simenstad, C.A., 1997. A comparative assessment of a natural and created estuarine
2124 slough as rearing habitat for juvenile chinook and coho salmon. Estuaries 20, 792-806.
- 2125 Minchin, D., 2007. Aquaculture and transport in a changing environment: Overlap and links in
2126 the spread of alien biota. Mar. Pollut. Bull. 55, 302-313.
- 2127 Miron, G., Landry, T., Archambault, P.F., Bruno, 2005. Effects of mussel culture husbandry
2128 practices on various benthic characteristics. Aquaculture 250, 138-154.
- 2129 Mirto, S., La Rosa, T., Danovaro, R., Mazzola, A., 2000. Microbial and meiofaunal response to
2130 intensive mussel-farm biodeposition in coastal sediments of the Western Mediterranean.
2131 Mar. Pollut. Bull. 40, 244-252.
- 2132 Mojica, R., Nelson, W.G., 1993. Environmental-effects of a hard clam (*Mercenaria-mercenaria*)
2133 aquaculture site in the Indian River Lagoon, Florida. Aquaculture 113, 313-329.

- 2134 Monaco, M.E., Lowery, T.A., Emmett, R.L., 1992. Assemblages of U.S. west coast estuaries
2135 based on the distribution of fishes. *J. Biogeogr.* 19, 251-267.
- 2136 Moore, J.E., Black, J.M., 2006. Slave to the tides: Spatiotemporal foraging dynamics of spring
2137 staging black brant. *Condor* 108, 661-677.
- 2138 Moore, J.E., Colwell, M.A., Mathis, R.L., Black, J.M., 2004. Staging of Pacific flyway brant in
2139 relation to eelgrass abundance and site isolation, with special consideration of Humboldt
2140 Bay, California. *Biol. Conserv.* 115, 475-486.
- 2141 Muir, J., 2005. Managing to harvest? Perspectives on the potential of aquaculture. *Philos. Trans.*
2142 *R. Soc. Lond. B Biol. Sci.* 360, 191-218.
- 2143 Muller-Feuga, A., 2000. The role of microalgae in aquaculture: situation and trends. *J. Appl.*
2144 *Phycol.* 12, 527-534.
- 2145 Mumford Jr., T.F., 2007. Kelp and eelgrass in Puget Sound. Seattle District, U.S. Army Corps of
2146 Engineers, Puget Sound Nearshore Partnership Report, 2007-5, Seattle, WA, pp. 1-27
- 2147 Munroe, D., McKinley, R.S., 2007a. Commercial Manila clam (*Tapes philippinarum*) culture in
2148 British Columbia, Canada: The effects of predator netting on intertidal sediment
2149 characteristics. *Estuar. Coast. Shelf Sci.* 72, 319-328.
- 2150 Munroe, D., Mckinley, R.S., 2007b. Effect of predator netting on recruitment and growth of
2151 Manila clams (*Venerupis philippinarum*) on soft substrate intertidal plots in British
2152 Columbia, Canada. *J. Shellfish Res.* 26, 1035-1044.
- 2153 Murray, L.G., Newell, C.R., Seed, R., 2007. Changes in the biodiversity of mussel assemblages
2154 induced by two methods of cultivation. *J. Shellfish Res.* 26, 153-162.
- 2155 Nacken, N., Reise, K., 2000. Effects of herbivorous birds on intertidal seagrass beds in the
2156 northern Wadden Sea. *Helgol. Mar. Res.* 54, 87-94.
- 2157 Navedo, J.G., Masero, J.A., 2008. Effects of traditional clam harvesting on the foraging ecology
2158 of migrating curlews (*Numenius arquata*). *J. Exp. Mar. Biol. Ecol.* 255, 59-65.
- 2159 Neckles, H.A., Short, F.T., Barker, S., Kopp, B.S., 2005. Disturbance of eelgrass *Zostera marina*
2160 by commercial mussel *Mytilus edulis* harvesting in Maine: dragging impacts and habitat
2161 recovery. *Mar. Ecol. Prog. Ser.* 285, 57-73.
- 2162 Nelson, D.M., Monaco, M.E., 2000. National overview and evolution of NOAA's estuarine
2163 living marine resources (ELMR) Program. NOAA Technical Memorandum,
2164 NOSNCCOSCCMA 144, Silver Spring, MD, pp. 1-60.
- 2165 New, T.R., 2005. Invertebrate Conservation and Agricultural Systems. Cambridge University
2166 Press, New York.
- 2167 Newell, C.R., Campbell, D.E., Gallagher, S.M., 1998. Development of the mussel aquaculture
2168 lease site model MUSMOD (c): A field program to calibrate model formulations. *J. Exp.*
2169 *Mar. Biol. Ecol.* 219, 143-169.
- 2170 Newell, R., Fisher, T., Holyoke, R., Cornwell, J., 2005. Influence of eastern oysters on nitrogen
2171 and phosphorus regeneration in Chesapeake Bay, USA. In: Dame, R.F., Olenin, S. (Eds.),
2172 *The Comparative Roles of Suspension-Feeders in Ecosystems*. Springer Verlag,
2173 Netherlands, pp. 93-120.
- 2174 Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: Are they the result of
2175 overharvesting the American oyster, *Crassostrea virginica*? In: Lynch, M.P., Krome,
2176 E.C. (Eds.), *Understanding the estuary: Advances in Chesapeake Bay research*.
2177 Chesapeake Research Consortium, Solomons, Maryland, pp. 379-388.
- 2178 Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-
2179 feeding bivalve molluscs: a review. *J. Shellfish Res.* 23, 51-62.

- 2180 Newell, R.I.E., Langdon, C., 1996. Mechanisms and physiology of larval and adult feeding. In:
2181 Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), *The Eastern Oyster, Crassostrea*
2182 *virginica*. Maryland Sea Grant, College Park, Maryland, pp. 185-230.
- 2183 Newell, R.I.E., Koch, E.W., 2004. Modeling seagrass density and distribution in response to
2184 changes to turbidity stemming from bivalve filtration and seagrass sediment stabilization.
2185 *Estuaries* 27, 793-806.
- 2186 Newell, R.I.E., Cornwell, J.C., Owens, M.S., 2002. Influence of simulated bivalve biodeposition
2187 and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnol.*
2188 *Oceanogr.* 47, 1367-1379.
- 2189 Nizzoli, D., Welsh, D.T., Fano, E.A., Viaroli, P., 2006. Impact of clam and mussel farming on
2190 benthic metabolism and nitrogen cycling, with emphasis on nitrate reduction pathways.
2191 *Mar. Ecol. Prog. Ser.* 315, 151-165.
- 2192 NOAA, 2006. Interim 10- Year plan for the NOAA Aquaculture Program. Silver Springs, MD,
2193 pp. 1-20.
- 2194 Nosh, T.Y., Chew, K.K., 1991. Remote Setting and Nursery Culture for Shellfish Growers.
2195 Washington Sea Grant, Seattle, Washington.
- 2196 Nugues, M.M., Kaiser, M.J., Spencer, B.E., Edwards, D.B., 1996. Benthic community changes
2197 associated with intertidal oyster cultivation. *Aquac. Res.* 27, 913-924.
- 2198 Olafsson, E.B., Peterson, C.H., Ambrose, W.G.J., 1994. Does recruitment limitation structure
2199 populations and communities of macro-invertebrates in marine soft sediments: The
2200 relative significance of pre- and post-settlement processes. *Annu. Rev. Ocean. Mar. Biol.*
2201 32, 65-109.
- 2202 Olesen, B., Marba, N., Duarte, C.M., Savelle, R.S., Fortes, M.D., 2004. Recolonization dynamics
2203 in a mixed seagrass meadow: the role of clonal versus sexual processes. *Estuaries* 27,
2204 770-780.
- 2205 Oliveira, A., Himelbloom, B., Crapo, C.A., Vorholt, C., Fong, Q., RaLonde, R., 2006. Quality of
2206 Alaskan maricultured oysters (*Crassostrea gigas*): A one-year survey. *J. Food Sci.* 71,
2207 c532-c543.
- 2208 Onuf, C.P., 1994. Seagrasses, dredging and light in Laguna madre, Texas, USA. *Estuar. Coast.*
2209 *Shelf Sci.* 39, 75-91.
- 2210 Orensanz, J.M., Hand, C.M., Parma, A.M., J., V., Hilborn, R., 2004. Precaution in the harvest of
2211 Methuselah's clams- the difficulty of getting timely feedback from slow- paced dynamics.
2212 *Can. J. Fish. Aquat. Sci.* 61, 1355-1372.
- 2213 Orth, R.J., Heck, K.L., Jr., Montfrans, J.v., 1984. Faunal communities in seagrass beds: A review
2214 of the influence of plant structure and prey characteristics on predator-prey relationships.
2215 *Estuaries* 7, 339-350.
- 2216 Orth, R.J., Fishman, J.R., Wilcox, D.J., Moore, K.A., 2002. Identification and management of
2217 fishing gear impacts in a recovering seagrass system in the coastal bays of the Delmarva
2218 peninsula. *J. Coast. Res.* 37, 111-129.
- 2219 Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L.,
2220 Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M.,
2221 Williams, S.L., 2006. A global crisis for seagrass ecosystems. *Bioscience* 56, 987-996.
- 2222 Paerl, H.W., Valdes, L.M., Peierls, B.L., Adolf, J.E., Harding, L.W., 2006. Anthropogenic and
2223 climatic influences on the eutrophication of large estuarine ecosystems. *Limnol.*
2224 *Oceanogr.* 51, 448-462.

- 2225 Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological
2226 surprises. *Ecosystems* 1, 535-545.
- 2227 Palacios, R., Armstrong, D., Orensanz, J., 2000. Fate and legacy of an invasion: extinct and
2228 extant populations of the soft-shell clam *Mya arenaria* in Grays Harbor, Washington.
2229 *Aquatic Conservation: Mar. Fresh. Ecosystems* 10, 279-303.
- 2230 PCSGA, 2001. Environmental Policy. Pacific Coast Shellfish Growers Association, Olympia,
2231 Washington, pp. 1-12.
- 2232 Pearcy, W.G., Myers, S.M., 1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for
2233 marine fishes. *Fish. Bull.* 72, 201-213.
- 2234 Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment
2235 and pollution of the marine environment. *Annu. Rev. Ocean. Mar. Biol.* 16, 229-311.
- 2236 Peterken, C., Conacher, C., 1997. Seed germination and recolonization of *Zostera capricorni*
2237 after grazing by dugongs. *Aquat. Bot.* 59, 333-340.
- 2238 Peterson, B.J., Heck Jr., K.L., 1999. The potential for suspension feeding bivalves to increase
2239 seagrass productivity. *J. Exp. Mar. Biol. Ecol.* 240, 37-52.
- 2240 Peterson, B.J., Heck Jr., K.L., 2001. Positive interactions between suspension-feeding bivalves
2241 and seagrass—a facultative mutualism. *Mar. Ecol. Prog. Ser.* 213, 143-155.
- 2242 Peterson, C.H., Summerson, H., Fegley, S.R., 1987. Ecological consequences of mechanical
2243 harvesting of clams. *Fish. Bull.* 85, 281-298.
- 2244 Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production
2245 resulting from restoring oyster reef habitat: quantitative valuation. *Mar. Ecol. Prog. Ser.*
2246 264, 249-264.
- 2247 Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale.
2248 *Ecosystems* 1, 6-18.
- 2249 Phelps, H.L., 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological
2250 change in the Potomac River estuary near Washington, D.C. *Estuaries* 17, 614-621.
- 2251 Pickett, S.T.A., White, P.S., 1985. The ecology of natural disturbance and patch dynamics.
2252 Academic Press, New York.
- 2253 Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term
2254 indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden
2255 Sea. *J. Appl. Ecol.* 38, 976-990.
- 2256 Pihl, L., Cattrijsse, A., Codling, I., Mathieson, S., McClusky, D.S., Roberts, C., 2002. Habitat
2257 use by fishes in estuaries and other brackish areas. In: Elliott, M., Hemingway, K.L.
2258 (Eds.), *Fishes in estuaries*. Blackwell Science, London, pp. 10-53.
- 2259 Pillay, D., Branch, G.M., Forbes, A.T., 2007. Experimental evidence for the effects of the
2260 thalassinidean sandprawn *Callinassa kraussi* on macrobenthic communities. *Mar. Biol.*
2261 152, 611-618.
- 2262 Pinnix, W.D., Shaw, T.A., Acker, K.C., Hetrick, N.J., 2005. Fish communities in eelgrass, oyster
2263 culture, and mudflat habitats of north Humboldt Bay, California. U.S. Fish and Wildlife
2264 Service, Arcata Fisheries Technical Report TR2005-02, Arcata, California, pp. 1-55.
- 2265 Pitman, R.W., 1995. Wastewater bacteria and shellfish. *Bull. Southern Cal. Acad. Sci.* 94, 92-
2266 102.
- 2267 Plus, M., Deslous-Paoli, J.-M., Dagault, F., 2003. Seagrass (*Zostera marina* L.) bed
2268 recolonisation after anoxia-induced full mortality. *Aquat. Bot.* 77, 121-134.
- 2269 Pohle, G., Frost, B., Findlay, R., 2001. Assessment of regional benthic impact of salmon
2270 mariculture within the Letang Inlet, Bay of Fundy. *ICES J. Mar. Sci.* 58, 417-426.

- 2271 Pomeroy, L.R., D'Elia, C.F., Schaffner, L.C., 2006. Limits to top-down control of phytoplankton
2272 by oysters in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 325, 301-309.
- 2273 Porter, E.T., Cornwell, J.C., Sanford, L.P., 2004. Effect of oysters *Crassostrea virginica* and
2274 bottom shear velocity on benthic-pelagic coupling and estuarine water quality. *Mar. Ecol.*
2275 *Prog. Ser.* 271, 61-75.
- 2276 Posey, M.H., 1986. Changes in a benthic community associated with dense beds of a burrowing
2277 deposit feeder, *Callianassa californiensis*. *Mar. Ecol. Prog. Ser.* 313171, 15-22.
- 2278 Posey, M.H., 1990. Functional approaches to soft-substrate communities: how useful are they?
2279 *Aquat Sci* 2, 343-356.
- 2280 Posey, M.H., Dumbauld, B.R., Armstrong, D.A., 1991. Effects of a burrowing mud shrimp,
2281 *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *J. Exp. Mar. Biol. Ecol.*
2282 148, 283-294.
- 2283 Posey, M.H., Alphin, T.D., Powell, C.M., Townsend, E., 1999. Oyster reefs as habitat for fish
2284 and decapods. In: Luckenbach, M.W., Wesson, J. (Eds.), *Oyster reef habitat restoration: A synopsis of approaches* Virginia Institute of Marine Sciences Press, Williamsburg,
2285 Virginia, pp. 229-237.
- 2287 Potter, I.C., Hyndes, G.A., 1999. Characteristics of the ichthyofaunas of southwestern Australian
2288 estuaries, including comparisons with holartic estuaries and estuaries elsewhere in
2289 temperate Australia: A review. *Aust. J. Ecol.* 24, 395-421.
- 2290 Powers, M.J., Peterson, C.H., Summerson, H.C., Powers, S.P., 2007. Macroalgal growth on
2291 bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and
2292 juvenile fishes. *Mar. Ecol. Prog. Ser.* 339, 109-122.
- 2293 Pregnall, M.M., 1993. Regrowth and recruitment of eelgrass (*Zostrea marina*) and recovery of
2294 benthic community structure in areas disturbed by commercial oyster culture in the South
2295 Slough National Estuarine Research Reserve. M.S. thesis, Bard College, Annandale-on-
2296 Hudson, New York.
- 2297 Prins, T.C., Escaravage, V., 2005. Can bivalve suspension-feeders affect pelagic food web
2298 structure? In: Dame, R.F., Olenin, S. (Eds.), *The Comparative Roles of Suspension-Feeders in Ecosystems*. Springer Verlag, Netherlands, pp. 31-51.
- 2299 Prins, T.C., Smaal, A.C., Dame, R.F., 1998. A review of the feedbacks between bivalve grazing
2300 and ecosystem processes. *Aquat. Ecol.* 31, 349-359.
- 2302 PSI, 2005. North American West Coast Shellfish Industry 2015 Goals: Research and Initiative
2303 Priorities. Pacific Shellfish Institute, Olympia, WA, pp. 1-28.
- 2304 Putland, J.N., Iverson, R.L., 2007. Microzooplankton: major herbivores in an estuarine
2305 planktonic food web. *Mar. Ecol. Prog. Ser.* 345, 63-73.
- 2306 Quayle, D.B., 1941. The Japanese "little neck" clam accidentally introduced into British
2307 Columbia waters. Fisheries Research Board of Canada, Pacific Coast Station, Progress
2308 Reports, 48, pp. 17-18.
- 2309 Quayle, D.B., 1988. Pacific Oyster Culture in British Columbia. *Can. J. Fish. Aquat. Sci.* 218, 1-
2310 241.
- 2311 Quinn, T.P., 2004. *The Behavior and Ecology of Pacific Salmon and Trout*. University of
2312 Washington Press, Seattle, Washington.
- 2313 Ragnarsson, S.A., Raffaelli, D., 1999. Effects of the mussel *Mytilus edulis* L. on the invertebrate
2314 fauna of sediments. *J. Exp. Mar. Biol. Ecol.* 241, 31-43.

- 2315 Raillard, O., Deslous-Paoli, J.M., Heral, M., Rajet, D., 1993. Modeling growth and feeding of the
2316 Japanese oyster *Crassostrea gigas* in Marennes-Oleron Bay (France). *Oceanologica Acta*
2317 16, 73-82.
- 2318 Reusch, T.B.H., Williams, S.L., 1998. Variable responses of native eelgrass *Zostera marina* to a
2319 non-indigenous bivalve *Musculista senhousia*. *Oecologia* 113, 428-441.
- 2320 Reusch, T.B.H., Chapman, A.R.O., Groger, J.P., 1994. Blue mussels *Mytilus edulis* do not
2321 interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition.
2322 *Mar. Ecol. Prog. Ser.* 108, 265-282.
- 2323 Richard, M., Archambault, P., Thozeau, G., McKindsey, C.W., Desrosiers, G., 2007. Influence
2324 of suspended scallop cages and mussel lines on pelagic and benthic biogeochemical
2325 fluxes in havre-aux-Maisons lagoon, Iles-de-la-Madelaine (Quebec, Canada). *Can. J.*
2326 *Fish. Aquat. Sci.* 64, 1491-1505.
- 2327 Richardson, N.F., Ruesink, J.L., Naeem, S., Hacker, S.D., Tallis, H.M., Dumbauld, B.R.,
2328 Wisheart, L.M., 2008. Bacterial abundance and aerobic microbial activity across natural
2329 and oyster aquaculture habitats during summer conditions in a Northern Pacific estuary.
2330 *Hydrobiologia* 596, 269-278.
- 2331 Riisgard, H.U., 2001. On measurement of filtration rates in bivalves-the stony road to reliable
2332 data: Review and interpretation. *Mar. Ecol. Prog. Ser.* 211, 275-291.
- 2333 Rivers, D.O., Short, F.T., 2007. Effect of grazing by Canada geese *Branta canadensis* on an
2334 intertidal eelgrass *Zostera marina* meadow. *Mar. Ecol. Prog. Ser.* 333, 271-279.
- 2335 Robinson, A.M., 1997. Molluscan fisheries in Oregon: Past, present and future. In: Mackenzie,
2336 C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.), *The history, present*
2337 *condition, and future of the molluscan fisheries of North and Central America and*
2338 *Europe. Vol. 2, Pacific Coast and Supplemental Topics.*, pp. 75-87.
- 2339 Rodhouse, P.G., Roden, C.M., 1987. Carbon budget for a coastal inlet in relation to intensive
2340 cultivation of suspension-feeding bivalve molluscs. *Mar. Ecol. Prog. Ser.* 36, 225-236.
- 2341 Rodney, W.S., Paynter, K.T., 2006. Comparisons of macrofaunal assemblages on restored and
2342 non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *J. Exp.*
2343 *Mar. Biol. Ecol.* 335, 39-51.
- 2344 Roegner, C.G., Hickey, B.M., Newton, J.A., Shanks, A.L., Armstrong, D.A., 2002. Wind-
2345 induced plume and bloom intrusions into Willapa Bay, Washington. *Limnol. Oceanogr.*
2346 47, 1033-1042.
- 2347 Ruckelshaus, M.H., Levin, P., Johnson, J.B., Kareiva, P.M., 2002. The Pacific salmon wars:
2348 What science brings to the challenge of recovering species. *Annu. Rev. Ecol. Syst.* 33,
2349 665-706.
- 2350 Ruckelshaus, M.H., Klinger, T., Knowlton, N., De Master, D.P., 2008. Marine ecosystem-based
2351 management in practice: Scientific and governance challenges. *Bioscience* 58, 53-63.
- 2352 Ruesink, J.L., Roegner, G.C., Dumbauld, B.R., Newton, J.A., Armstrong, D.A., 2003.
2353 Contributions of coastal and watershed energy sources to secondary production in a
2354 Northeastern Pacific estuary. *Estuaries* 26, 1079-1093.
- 2355 Ruesink, J.L., Feist, B.E., Harvey, C.J., Hong, J.S., Trimble, A.C., Wisheart, L.M., 2006.
2356 Changes in productivity associated with four introduced species: ecosystem
2357 transformation of a "pristine" estuary. *Mar. Ecol. Prog. Ser.* 311, 203-215.
- 2358 Ruesink, J.L., Lenihan, H.S., Trimble, A.C., Heiman, K.W., Micheli, F., Byers, J.E., Kay, M.C.,
2359 2005. Introduction of non-native oysters: ecosystem effects and restoration implications.
2360 *Annu. Rev. Ecol. Syst.* 36, 643-689.

- 2361 Ruesink, J.L., Hong, J.S., Wisehart, L.M., Hacker, S.D., Dumbauld, B.R., Trimble, A.C.,
2362 Hessing-Lewis, M., in review. Congener comparison of native (*Zostera marina*) and
2363 introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary,
2364 Biol. Invasions.
- 2365 Rumrill, S., 2006. The Ecology of the South Slough Estuary: Site Profile of the South Slough
2366 National Estuarine Research Reserve. NOAA / Oregon Department of State Lands, pp.
2367 1-238.
- 2368 Rumrill, S., Christy, J., 1996. Ecological impacts of oyster ground culture within estuarine
2369 tidelands: South Slough National Estuarine Research Reserve. South Slough National
2370 Estuarine Research Reserve, Final Report to The Oregon Dept. of Land Conservation
2371 and Development, Charleston, Oregon, pp. 1-12.
- 2372 Rumrill, S., Sowers, D., 2008. Concurrent assessment of eelgrass beds (*Zostera marina*) and
2373 saltmarsh communities along the estuarine gradient of the South Slough, Oregon. J.
2374 Coast. Res. 55, 121-134.
- 2375 Rumrill, S.S., Poulton, V.K., 2004. Ecological role and potential impacts of molluscan shellfish
2376 culture in the estuarine environment of Humboldt Bay, Ca. Oregon Department of State
2377 Lands, Final Annual Report to the Western Regional Aquaculture Center, pp. 1-22.
- 2378 Rysgaard, S., Christensen, P.B., Nielsen, L.P., 1995. Seasonal variation in nitrification and
2379 denitrification in estuarine sediment colonized by benthic microalgae and bioturbating
2380 infauna. Mar. Ecol. Prog. Ser. 126, 111-121.
- 2381 Salita, J.T., Ekau, W., Saint-Paul, U., 2003. Field evidence on the influence of seagrass
2382 landscapes on fish abundance in Bolinao, Northern Philippines. Mar. Ecol. Prog. Ser.
2383 247, 183-195.
- 2384 Sara, G., 2007. A meta-analysis on the ecological effects of aquaculture on the water column:
2385 Dissolved nutrients. Mar. Environ. Res. 63, 390-408.
- 2386 Sara, G., Mazzola, A., 2004. The carrying capacity for Mediterranean bivalve suspension
2387 feeders: evidence from analysis of food availability and hydrodynamics and their
2388 integration into a local model. Ecol. Model. 179, 281-296.
- 2389 Sauriau, P.G., Mouret, V., Rince, J., 1989. Organisation trophique de la malacofaune benthique
2390 non cultivée du bassin ostréicole de Marennes-Oleron. Oceanologica Acta 12, 193-204.
- 2391 Sayce, C.S., 1976. The oyster industry of Willapa Bay, Proceedings of a symposium on
2392 terrestrial and ecological studies of the Northwest. Eastern Washington State College
2393 Press, Cheney, WA, pp. 347-356.
- 2394 Sayce, C.S., Larson, C.C., 1966. Willapa oyster studies--use of the pasture harrow for the
2395 cultivation of oysters. Comm. Fish. Rev. 28, 1-21.
- 2396 Scheffer, M., Carpenter, S., de Young, B., 2005. Cascading effects of overfishing marine
2397 systems. Trends Ecol. Evol. 20, 579-581.
- 2398 Scholz, A.J., Jones, C., Westley, R.E., Tufts, D.F., 1984. Improved techniques for culturing
2399 Pacific oysters, *Crassostrea gigas*: A summary of studies conducted by the Washington
2400 Department of Fisheries since 1955. Washington Department of Fisheries, Olympia,
2401 Washington.
- 2402 Schreffler, D., Griffen, K., 2000. Ecological interactions among eelgrass oysters and burrowing
2403 shrimp in Tillamook Bay, Oregon. Tillamook County Performance Partnership, Report
2404 to the Tillamook County Performance Partnership, pp. 1-43
- 2405 Selgrath, J.C., Hovel, K.A., Wahle, R.A., 2007. Effects of habitat edges on American lobster
2406 abundance and survival. J. Exp. Mar. Biol. Ecol. 353, 253-264.

- 2407 Semmens, B.X., 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon
2408 (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. *Can.*
2409 *J. Fish. Aquat. Sci.* 65, 2053-2062.
- 2410 Sequeira, A., Ferreira, J.G., Hawkins, A.J.S., Nobre, A., Lourenco, P., Zhang, X.L., Yan, X.,
2411 Nickell, T., 2008. Trade-offs between shellfish aquaculture and benthic biodiversity: A
2412 modelling approach for sustainable management. *Aquaculture* 274, 313-328.
- 2413 Serchuk, F.M., Murawski, S.A., 1997. The offshore molluscan resources of the northeastern
2414 coast of the United States: Surfclams, ocean quahogs, and sea scallops. In: Mackenzie,
2415 C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.), *The history, present*
2416 *condition, and future of the molluscan fisheries of North and Central America and*
2417 *Europe*. Vol. 1, Atlantic and Gulf Coasts, pp. 45-62.
- 2418 Shaul, W., Goodwin, C.L., 1982. Geoduck (*Panope generosa*: Bivalvia) age determined by
2419 internal growth lines in the shell. *Can. J. Fish. Aquat. Sci.* 39, 632-636.
- 2420 Shaw, W.N., 1997. The shellfish industry of California- Past, present and future. In: Mackenzie,
2421 C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.), *The history, present*
2422 *condition, and future of the molluscan fisheries of North and Central America and*
2423 *Europe*. Vol. 2, Pacific Coast and Supplemental Topics, pp. 57-74.
- 2424 Shumway, S.E., Cucci, T.L., Newell, R.C., Yentsch, C.M., 1985. Particle selection, ingestion and
2425 absorption in filter-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 91, 77-92.
- 2426 Simenstad, C., Reed, D., Ford, M., 2006. When is restoration not? Incorporating landscape-scale
2427 processes to restore self-sustaining ecosystems in coastal wetland restoration. *Ecol.*
2428 *Engineer.* 26, 27-39.
- 2429 Simenstad, C.A., Fresh, K.L., 1995. Influence of intertidal aquaculture on benthic communities
2430 in Pacific Northwest estuaries: Scales of disturbance. *Estuaries* 18, 43-70.
- 2431 Simenstad, C.A., Cordell, J.R., 2000. Ecological assessment criteria for restoring anadromous
2432 salmonid habitat in Pacific Northwest estuaries. *Ecol. Engineer.* 15, 283-302.
- 2433 Simenstad, C.A., Fresh, K.L., Salo, E.A., 1982. The role of Puget Sound and Washington coastal
2434 estuaries in the life history of Pacific salmon: An unappreciated function. In: Kennedy,
2435 V.S. (Ed.), *Estuarine Comparisons*. Academic Press, New York, pp. 343-364.
- 2436 Smith, V.H., Joye, S.B., Howarth, R.W., 2006. Eutrophication of freshwater and marine
2437 ecosystems. *Limnol. Oceanogr.* 51, 351-355.
- 2438 Sorokin, I.I., Giovanardi, O., Pranovi, F., Sorokin, P.I., 1999. Need for restricting bivalve culture
2439 in the southern basin of the Lagoon of Venice. *Hydrobiologia* 400, 141-148.
- 2440 Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J.M., Bibent, B., 2001. Influence
2441 of shellfish farming activities on the biogeochemical composition of the water column in
2442 Thau lagoon. *Mar. Ecol. Prog. Ser.* 218, 141-152.
- 2443 Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15,
2444 353-391.
- 2445 Sousa, W.P., 2001. Natural disturbance and the dynamics of marine benthic communities. In:
2446 Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer,
2447 Sunderland, MA, pp. 85-130.
- 2448 Spencer, B.E., Kaiser, M., Edwards, D.B., 1997. Ecological effects of intertidal Manila clam
2449 cultivation: Observations at the end of the cultivation phase. *J. Appl. Ecol.* 34, 444-452.
- 2450 Stenton-Dozey, J., Probyn, T., Busby, A., 2001. Impact of mussel (*Mytilus galloprovincialis*)
2451 raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha
2452 Bay, South Africa. *Can. J. Fish. Aquat. Sci.* 58, 1021-1031.

- 2453 Strayer, D.L., Caraco, N.F., Cole, J.J., Findlay, S., Pace, M.L., 1999. Transformation of
2454 freshwater ecosystems by bivalves - A case study of zebra mussels in the Hudson River.
2455 *Bioscience* 49, 19-27.
- 2456 Steele, E.N., 1964. The Immigrant Oyster (*Ostrea gigas*) Now Known as the Pacific Oyster.
2457 Warrens Quick Print, Olympia, Washington.
- 2458 Subasinghe, R., 2006. State of World Aquaculture 2006. FAO Fisheries Technical Paper Rome,
2459 Italy.
- 2460 Swanberg, I.L., 1991. The influence of the filter-feeding bivalve *Cerastoderme edule* L. on
2461 microphytobenthos, a laboratory study. *J. Exp. Mar. Biol. Ecol.* 151, 93-111.
- 2462 Tallis, H.M., Ruesink, J.L., Dumbauld, B.R., Hacker, S.D., Wisheart, L.M., in press. Oysters and
2463 aquaculture practices affect eelgrass density and productivity in a Pacific Northwest
2464 estuary. *J. Shellfish Res.*
- 2465 Tallman, J.C., Forrester, G.E., 2007. Oyster grow-out cages function as artificial reefs for
2466 temperate fishes. *Trans. Am. Fish. Soc.* 136, 790-799.
- 2467 Tanner, J.E., 2005. Edge effects on fauna in fragmented seagrass meadows. *Austral. Ecol.* 30,
2468 210-218.
- 2469 Tanner, J.E., 2006. Landscape ecology of interactions between seagrass and mobile epifauna:
2470 The matrix matters. *Estuar. Coast. Shelf Sci.* 68, 404-412.
- 2471 Taylor, J., Bushek, D., 2008. Intertidal oyster reefs can persist and function in a temperate
2472 North American Atlantic estuary. *Mar. Ecol. Prog. Ser.* 361, 301-306.
- 2473 Thom, R.M., Albright, R.G., 1990. Dynamics of benthic vegetation standing stock, irradiance,
2474 and water properties in Central Puget Sound. *Mar. Biol.* 104, 129-141.
- 2475 Thom, R.M., Williams, G.W., Diefenderfer, H.L., 2005. Balancing the need to develop coastal
2476 areas with the desire for an ecologically functioning coastal environment: Is net
2477 ecosystem improvement possible? *Restor. Ecol.* 13, 193-203.
- 2478 Thom, R.M., Parkwell, T.L., Niyogi, D.K., Shreffler, D.K., 1994. Effects of graveling on the
2479 primary productivity, respiration and nutrient flux of 2 estuarine tidal flats. *Mar. Biol.*
2480 118, 329-341.
- 2481 Thom, R.M., Southard, S.L., Borde, A.B., Stoltz, P., 2008. Light requirements for growth and
2482 survival of eelgrass (*Zostera marina* L.) in Pacific Northwest (USA) estuaries. *Estuaries*
2483 *Coasts* 31, 969-980.
- 2484 Thom, R.M., Borde, A.B., Rumrill, S., Woodruff, D.L., Williams, G.D., Southard, J.A.,
2485 Sargeant, S.L., 2003. Factors influencing spatial and annual variability in eelgrass
2486 (*Zostera marina* L.) meadows in Willapa Bay, Washington and Coos Bay, Oregon, USA.
2487 *Estuaries* 26, 1117-1129.
- 2488 Thom, R.M., Antrim, L.D., Borde, A.B., Gardiner, W.W., Shreffler, D.K., Farley, P.G., Norris,
2489 J.G., Wyllie-Echeverria, S., McKenzie, T.P., 1998. Puget Sound's eelgrass meadows:
2490 Factors contributing to depth distribution and spatial patchiness, Puget Sound Research
2491 1998. Puget Sound Action Team, Seattle, Wa., pp. 363-370.
- 2492 Thompson, D.S., 1995. Substrate additive studies for the development of hardshell clam habitat
2493 in Washington State: An analysis of effects on recruitment, growth and survival of the
2494 Manila clam, *Tapes philippinarum*, and on the species diversity and abundance of
2495 existing benthic organisms. *Estuaries* 18, 91-107.
- 2496 Thompson, J.K., 2005. One estuary, one invasion, two responses: phytoplankton and benthic
2497 community dynamics determine the effect of an estuarine invasive suspension-feeder. In:

- 2498 Dame, R.F., Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in
2499 Ecosystems. Springer Verlag, Netherlands, pp. 291-316.
- 2500 Thomsen, M.S., McGlathery, K., 2006. Effects of accumulations of sediments and drift algae on
2501 recruitment of sessile organisms associated with oyster reefs. *J. Exp. Mar. Biol. Ecol.*
2502 328, 22-34.
- 2503 Toba, D.R., Chew, K.K., Thompson, D.S., Anderson, G.J., Miller, M.B., 1992. Guide to Manila
2504 clam culture. Washington Sea Grant, University of Washington, Seattle Washington.
- 2505 Tokeshi, M., Romero, A., 1995. Filling a gap: dynamics of space occupancy on a mussel
2506 dominated sub-tropical rocky shore. *Mar. Ecol. Prog. Ser.* 119, 167-176.
- 2507 Toole, C., 1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery
2508 areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). *Environ. Biol. Fishes*
2509 5, 383-390.
- 2510 Townsend, C.H., 1896. The transplanting of eastern oysters to Willapa Bay, Washington with
2511 notes on the native oyster industry. U.S. Commissioner of Fisheries, pp. 193-202.
- 2512 Trianni, M.S., 1995. The influence of commercial oyster culture activities on the benthic infauna
2513 of Arcata Bay. M.S. thesis, Humboldt State University, Arcata, California.
- 2514 Trigger, B.G., 1986. Native Shell Mounds of North America: Early Studies. Garland Press, New
2515 York.
- 2516 Trimble, A.C., Ruesink, J. L., Dumbauld, B.R. in press. Factors preventing the recovery of a
2517 historically overexploited shellfish species. *J. Shellfish Res.*
- 2518 Trotter, A., Roy, S., Tamigneaux, E., Lovejoy, C., 2007. Importance of heterotrophic planktonic
2519 communities in a mussel culture environment: the Grande Entree lagoon, Magdalen
2520 Islands (Quebec, Canada). *Mar. Biol.* 151, 377-392.
- 2521 US COP, 2004. An ocean blueprint for the 21st century. US Commission on Ocean Policy,
2522 Washington, D.C.
- 2523 Verhulst, S., Oosterbeek, K., Rutten, A.L., Ens, B.J., 2004. Shellfish fishery severely reduces
2524 condition and survival of oystercatchers despite creation of large marine protected areas.
2525 *Ecol. Soc.* 9,[online] Url: <http://www.ecologyandsociety.org/vol9/iss1/art17/>.
- 2526 Viaroli, P., Bartoli, M., Giordani, G., Azzoni, R., Nizzoli, D., 2003. Short term changes of
2527 benthic fluxes during clam harvesting in a coastal lagoon (Sacca Di Goro, Po River
2528 Delta). *Chem. Ecol.* 19, 189-206.
- 2529 Vinther, H.F., Holmer, M., 2008. Experimental test of biodeposition and ammonium excretion
2530 from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. *J. Exp.*
2531 *Mar. Biol. Ecol.* 364, 72-79.
- 2532 Vinther, H.F., Laursen, J.S., Holmer, M., 2008. Negative effects of blue mussel (*Mytilus edulis*)
2533 presence in eelgrass (*Zostera marina*) beds in Flensborg fjord, Denmark. *Estuar. Coast.*
2534 *Shelf Sci.* 77, 91-103.
- 2535 Visser, E.P., McDonald, P.S., Armstrong, D.A., 2004. The impact of yellow shore crabs,
2536 *Hemigrapsus oregonensis*, on early benthic phase dungeness crabs, *Cancer magister*, in
2537 intertidal oyster shell mitigation. *Estuaries* 27, 699-715.
- 2538 Waddell, J.E., 1964. The effect of oyster culture on eelgrass (*Zostera marina* L.) growth. M.S.
2539 thesis, Humboldt State College, Arcata, California.
- 2540 Walker, B., Gunderson, L., Kinzig, A., Folke, C., Carpenter, S., Schultz, L., 2006. A handful of
2541 heuristics and some propositions for understanding resilience in social-ecological
2542 systems. *Ecol. Soc.* 11,[online] Url: <http://www.ecologyandsociety.org/vol11/iss1/art13/>.

- 2543 Walker, D.I., Lukatelich, R.J., Bastyan, G., McComb, A.J., 1989. Effect of boat moorings on
2544 seagrass beds near Perth, Western Australia. *Aquat. Bot.* 36, 69-77.
- 2545 Wall, C.C., Peterson, B.J., Gobler, C.J., 2008. Facilitation of seagrass *Zostera marina*
2546 productivity by suspension-feeding bivalves. *Mar. Ecol. Prog. Ser.* 357, 165-174.
- 2547 Wang, H., Huang, W., Harwell, M.A., Edmiston, L., Johnson, E., Hsieh, P., Milla, K.,
2548 Christensen, J., Stewart, J., Liu, X., 2008. Modeling oyster growth rate by coupling
2549 oyster population and hydrodynamic models for Apalachicola Bay, Florida, USA. *Ecol.*
2550 *Model.* 211, 77-89.
- 2551 Ward, D.H., Morton, A., Tibbitts, T.L., Douglas, D.C., Carrera-Gonzalez, E., 2003. Long-term
2552 change in eelgrass distribution at Bahia San Quintin, Baja California, Mexico, using
2553 satellite imagery. *Estuaries* 26, 1529-1539.
- 2554 Ward, E.J., Shumway, S.E., 2004. Separating the grain from the chaff: particle selection in
2555 suspension- and deposit- feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 300, 83-130.
- 2556 Ward, J., Sanford, L.P., Newell, R.I.E., MacDonald, B.A., 1998a. A new explanation of particle
2557 capture in suspension-feeding bivalve molluscs. *Limnol. Oceanogr.* 43, 741-752.
- 2558 Ward, J.E., Levinton, J.S., Shumway, S.E., Cucci, T., 1997. Site of particle selection in a bivalve
2559 mollusc. *Nature* 390, 131-132.
- 2560 Ward, J.E., Levinton, J.S., Shumway, S.E., Cucci, T., 1998b. Particle sorting in bivalves: in vivo
2561 determination of the pallial organs of selection. *Mar. Biol.* 131, 283-292.
- 2562 Weinstein, M.P., 2007. Linking restoration ecology and ecological restoration in estuarine
2563 landscapes. *Estuaries Coasts* 30, 365-370.
- 2564 Weinstein, M.P., Reed, D.J., 2005. Sustainable coastal development: The dual mandate and a
2565 recommendation for "commerce managed areas". *Restor. Ecol.* 13, 174-182.
- 2566 Weschler, J.F., 2004. Assessing the relationship between the ichthyofauna and oyster mariculture
2567 in a shallow embayment, Drakes Estero, Point Reyes National Seashore. M.S. thesis,
2568 University of California, Davis, California.
- 2569 Wetz, M.S., Lewitus, A.J., Koepfler, E.T., Hayes, K.C., 2002. Impact of the Eastern oyster
2570 *Crassostrea virginica* on microbial community structure in a salt marsh estuary. *Aquat.*
2571 *Microb. Ecol.* 28, 87-97.
- 2572 Whiteley, J., Bendell-Young, L., 2007. Ecological implications of intertidal mariculture:
2573 observed differences in bivalve community structure between farm and reference sites. *J.*
2574 *Appl. Ecol.* 44, 495-505.
- 2575 Widdows, J., Brinsley, M.D., Salkeld, P.N., Elliott, M., 1998. Use of annular flumes to
2576 determine the influence of current velocity and bivalves on material flux at the sediment-
2577 water interface. *Estuaries* 21, 552-559.
- 2578 Wiens, J., 2005. Towards a unified landscape ecology. In: Wiens, J.A., Moss, M.R. (Eds.), *Issues*
2579 *and Perspectives in Landscape Ecology*. Cambridge University Press, New York, pp.
2580 365-373.
- 2581 Williams, S.L., Ruckelshaus, M.H., 1993. Effects of nitrogen availability and herbivory on
2582 eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74 904-918.
- 2583 Williamson, K.J., 2006. Relationships between eelgrass (*Zostera marina*) habitat characteristics
2584 and juvenile Dungeness crab (*Cancer magister*) and other invertebrates in Southern
2585 Humboldt Bay, California, USA. M.S. thesis, Humboldt State University, Arcata,
2586 California.
- 2587 Wilson, U.W., Atkinson, J.B., 1995. Black brant winter and spring-staging use at two
2588 Washington coastal areas in relation to eelgrass abundance. *Condor* 97, 91-98.

- 2589 Wisehart, L.M., Ruesink, J.L., Hacker, S.D., Dumbauld, B.R., 2007. Importance of eelgrass early
2590 life history stages in response to oyster aquaculture disturbance. *Mar. Ecol. Prog. Ser.*
2591 344, 71-80.
- 2592 Wisehart, L.M., 2006. Impacts of oysters on eelgrass (*Zostera marina* L.): Importance of early
2593 life history stages in response to aquaculture disturbance. M.Sc., Oregon State University,
2594 Corvallis, Oregon.
- 2595 Wynberg, R.P., Branch, G.M., 1994. Disturbance associated with bait-collection for sandprawns
2596 (*Callinassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the
2597 biota of intertidal sandflats. *J. Mar. Res.* 52, 523-558.
- 2598 Zhang, G.F., Yan, X.W., 2006. A new three-phase culture method for Manila clam, *Ruditapes*
2599 *philippinarum*, farming in northern China. *Aquaculture* 258, 452-461.
- 2600 Zieman, J.C., 1976. The ecological effects of physical damage from motor boats on turtle grass
2601 beds in Southern Florida. *Aquat. Bot.* 2, 127-139.
- 2602 Zimmerman, R., Minello, T., Baumer, T., Castiglione, M., 1989. Oyster reef as habitat for
2603 estuarine macrofauna. USDC, NOAA, NOAA Technical Memorandum, NMFS-SEFC-
2604 249, Silver Springs, Maryland.
- 2605 Zydels, R., Esler, D., Boyd, W.S., LaCroix, D.L., Kirk, M., 2006. Habitat use by wintering surf
2606 and white-winged scoters: Effects of environmental attributes and shellfish aquaculture.
2607 *J. Wildl. Manag.* 70, 1754-1762.
- 2608
- 2609

2610 Figure Legends

2611

2612 Figure 1. Conceptual diagram of 3 pathways of shellfish aquaculture interaction with the
2613 environment. This simplistic view is of course more complex when broken down into
2614 component parts such as those for material processes including both benthic pelagic
2615 coupling and biodeposition (inset).

2616

2617 Figure 2. Preliminary results from field surveys in Willapa Bay, Washington using drifting
2618 sensors (YSI® instruments) which moved over long-line oyster aquaculture areas and
2619 displayed a negative slope indicating phytoplankton (measured as chlorophyll *a*
2620 fluorescence) was being removed from the water column. Two separate drifts with
2621 instruments in the field are shown (top) and separate instrument calibration
2622 measurements taken with water bottles at start and end of drifts and measured on
2623 laboratory fluorometer (bottom).

2624

2625 Figure 3. A) Competition between eelgrass and oysters can be viewed on a continuum from
2626 overyielding, in which total production is larger than expected from averaging the 2
2627 species because individuals perform better in combination, to underyielding, in which
2628 total production is lower than expected. B) Results of a field experiment in Willapa Bay,
2629 Washington where oysters were added to 2m x 2m plots at two locations (Mill Channel
2630 and Peterson Station). Measurements taken after 2 years indicated that eelgrass had
2631 entirely disappeared when oyster cover was greater than 20% (E.L. Wagner unpubl.
2632 data). C) Measurements taken after 3 years showed showed some recovery and almost a
2633 1:1 tradeoff between oysters and eelgrass.

2634

2635 Figure 4. Canonical correlation biplot of catch per unit effort data from fyke nets deployed
2636 over three intertidal habitats: oyster aquaculture (OYS), eelgrass, *Zostera marina* (EEL),
2637 and open mud (MUD) in Willapa Bay, Washington in 2001. Species close to vectors and
2638 far from the midpoint are closely associated with that habitat. Many commonly collected
2639 species (box and circle) show no association with habitat, but some others like tubesnout
2640 and smelt in eelgrass, and rock crab and hippolytid shrimp in oyster show loose
2641 association with habitat.

2642

2643 Figure 5. Mean catch per unit water flow of juvenile Chinook salmon smolts by area fished with
2644 a modified two boat trawl net in Willapa Bay, Washington during 2003-2005. Catch
2645 varied by location (top), and over time (bottom), but no difference was evident between
2646 habitats.

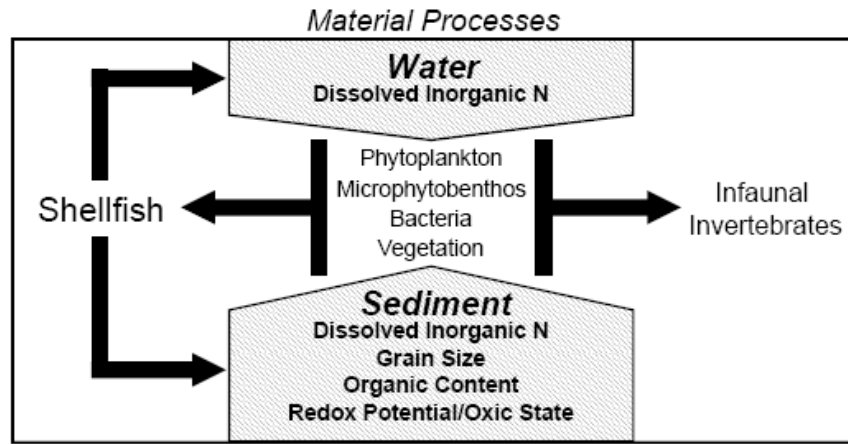
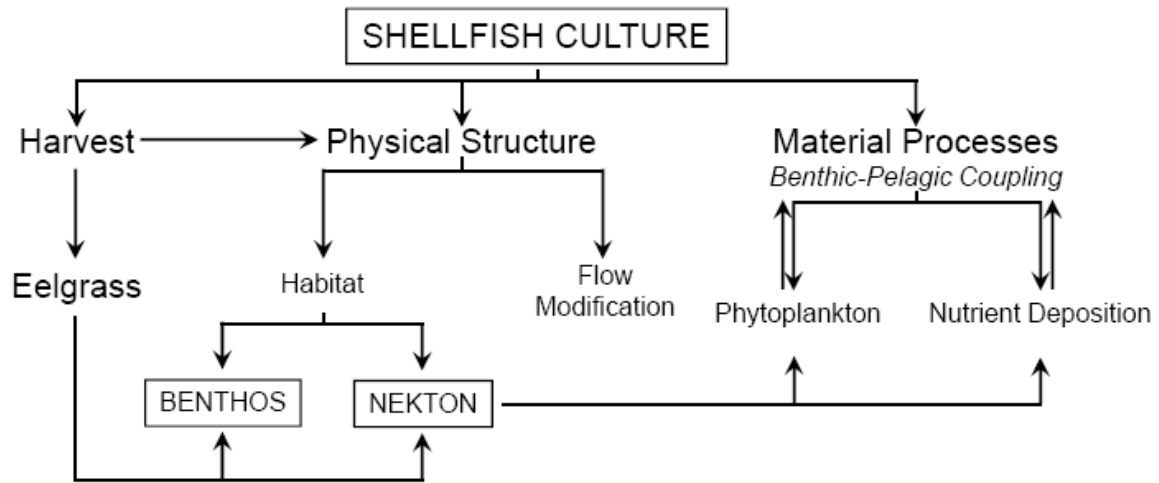
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2648 Figure 6. Eelgrass spatial cover (top) and density of shoots (bottom) measured in experimental
2649 oyster long-line plots (1.5 to 10 ft spacing) in Humboldt Bay, California just before
2650 harvest at the end of the experiment compared to an eelgrass reference area nearby,
2651 ground culture plot (ground), a control plot with stakes but no lines (control) and 5 distant
2652 reference eelgrass beds (Mad River, Sand Island, East Bay, and Arcata Channel).

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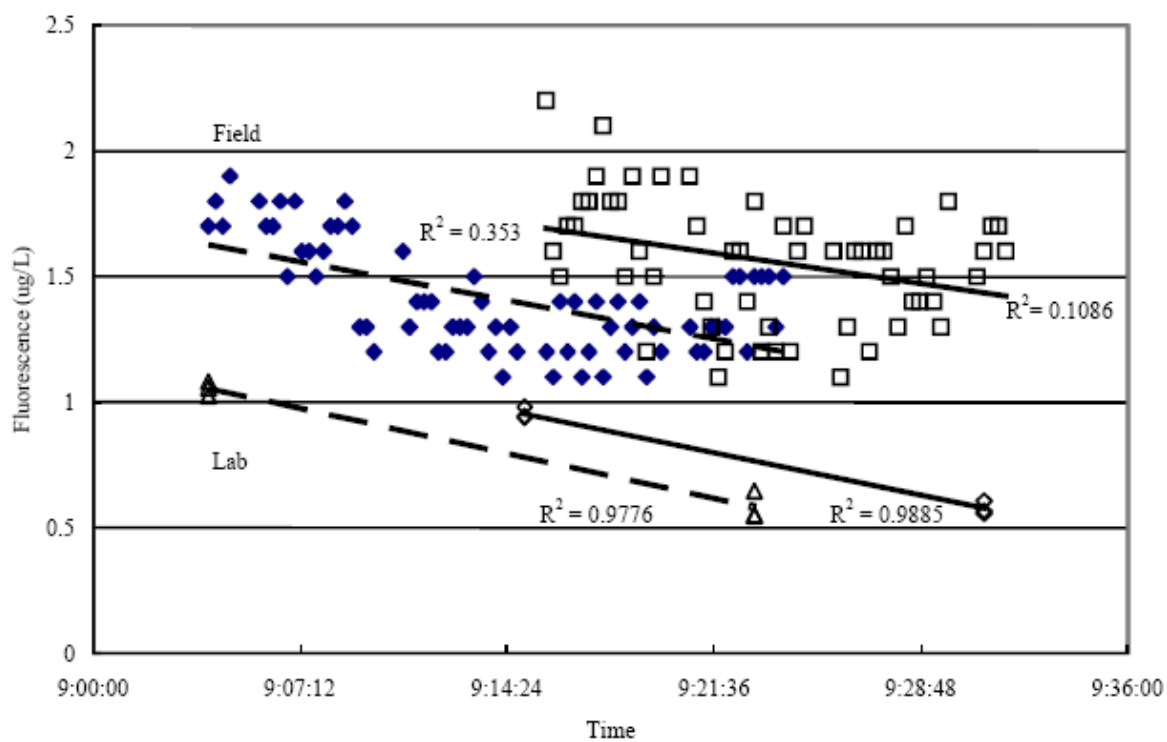
2654 Figure 7. Infrared aerial photography of an area near Stony Point in Willapa Bay, Washington
2655 was used to determine presence of intertidal vegetation (*Zostera* green shading, D). A

2656 separate layer was created which shows the distribution of active oyster aquaculture (A,
2657 top left) based on interviews with growers and both a 100 m and 200 m buffer zone
2658 around the edge of the culture areas (B and C). Estimates were then made of the
2659 proportion of the total area represented by *Zostera* in each of these zones (E, F, G).
2660 Although it represents a temporal snapshot (May 2005), the proportion of area covered by
2661 vegetation is comparable inside and outside aquaculture in these zones (46% inside
2662 aquaculture, 50% in 100m buffer, and 44% in 200m buffer).
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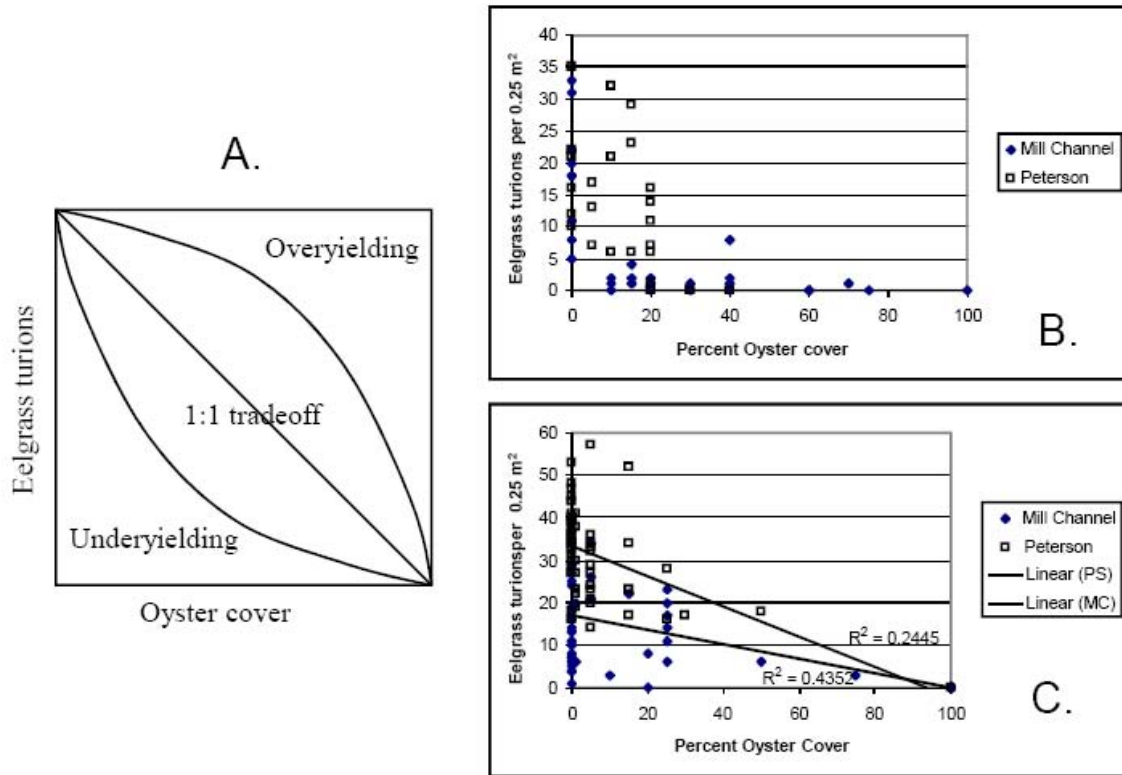


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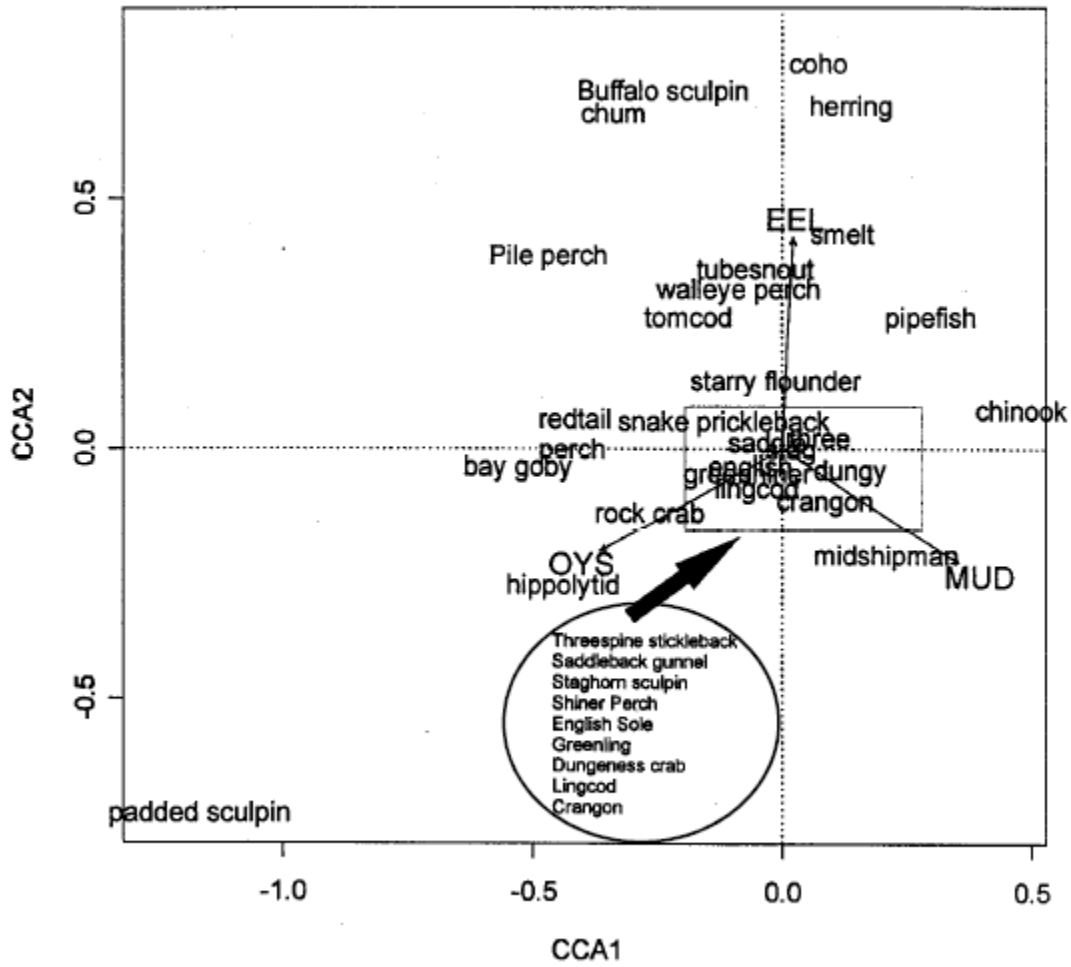
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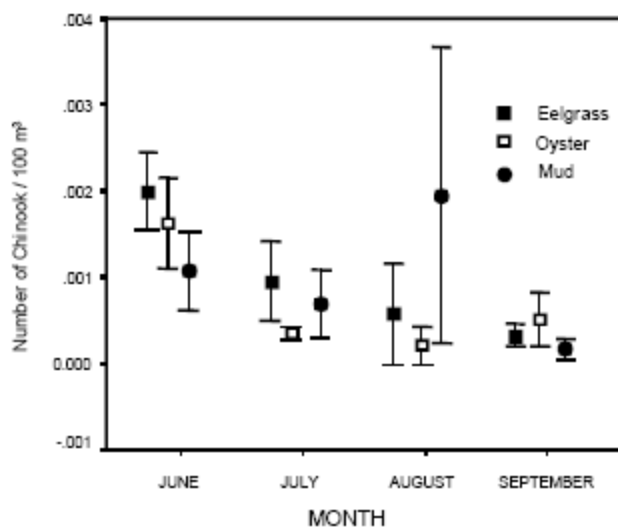
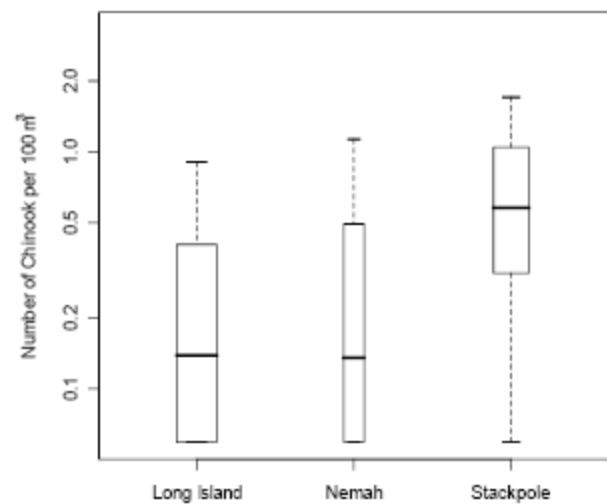


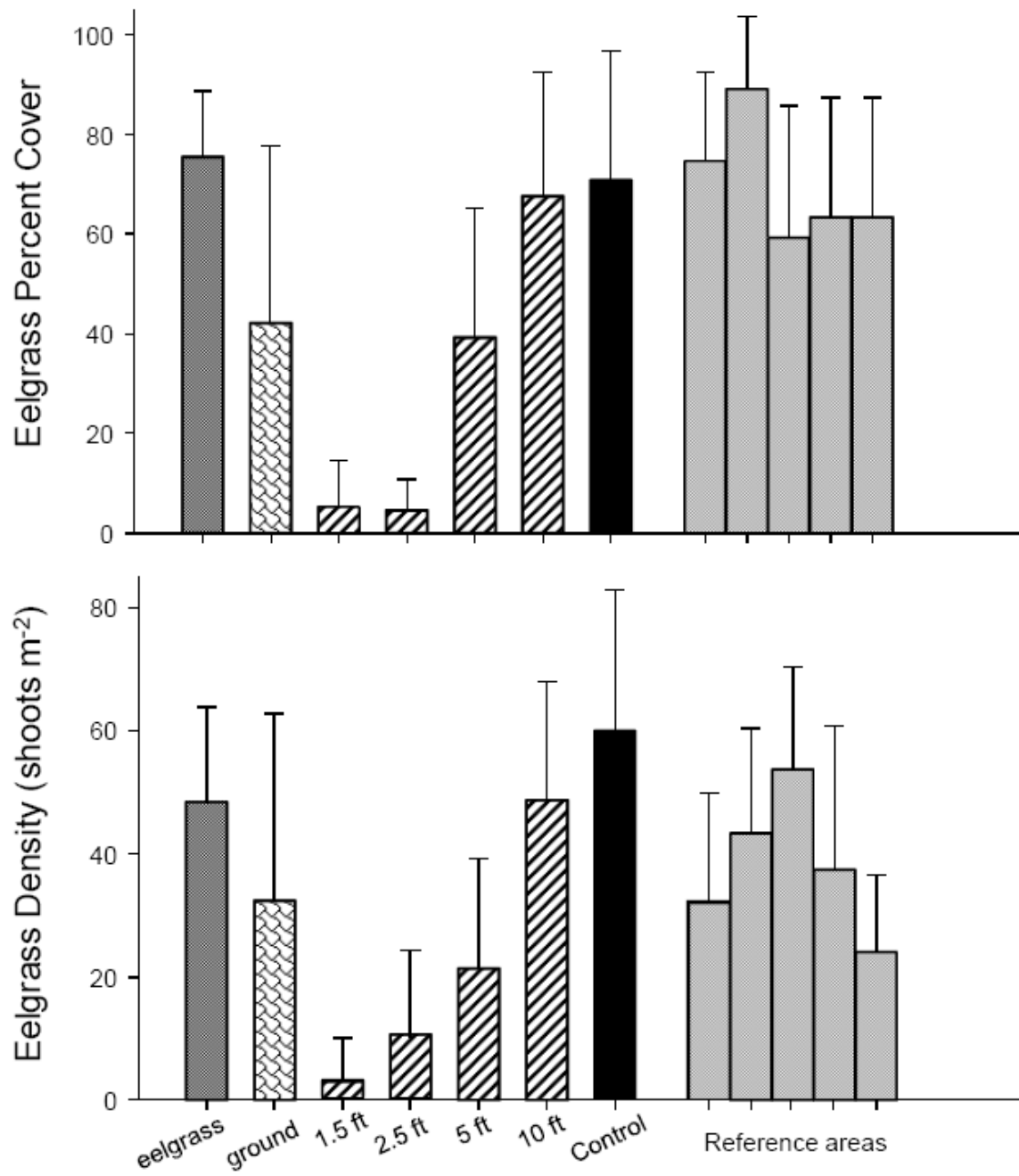
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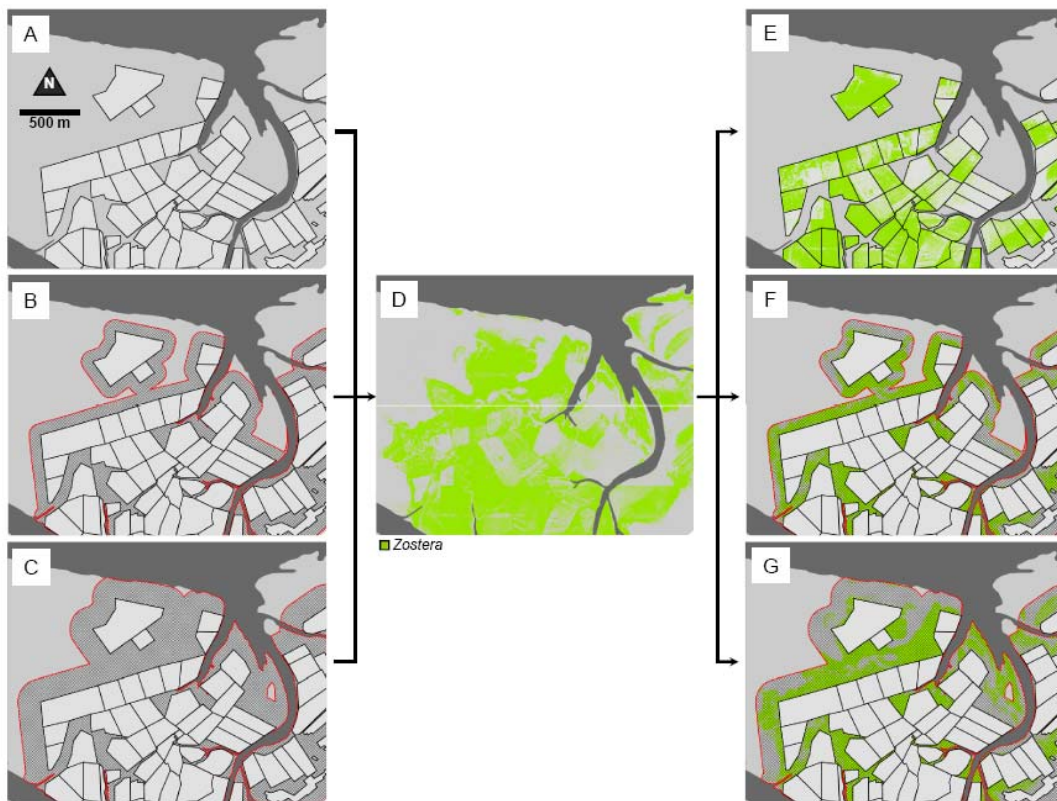


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2675 Table 1. Yields (thousand pounds) by bivalve species from the West Coast of North America
 2676 aquaculture (from PCSGA, 2006; BC Ministry of Environment, 2007)
 2677

	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	Humboldt Bay, Tomales Bay, Drakes Estero
<i>Crassostrea gigas</i> (Pacific oyster)	920	17,861	77,000	6,290	10,000
<i>Ruditapes philippinarum</i> (Manila clam)	41	3,528	8,500		14
<i>Mytilus galloprovincialis</i> (Mediterranean mussel)	3		2,100		600
<i>Panopea abrupta</i> (geoduck clam)			850		

2678

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 4.5m	Low wind, small tidal amplitude <1m	5 months	Two towns	Oysters on longlines (80%), Mussels (20%)	75 km ² / $<1\text{km}^2$	12,000t harvested, 14 – 20,000 t present, 15km ²	DeCasabianca 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 1.5m	FW flow regulated	1 – 25 days	Towns, flow highly managed with dredging	Clams, Mussels	26 km ² /0 km	15,000t Clams 1,000 t Mussels harvested, 8km 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 / 82km ²	30,000 t harvested 100,000t present, 32km 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, 8m	Very large rivers (e.g. Susquehana) small tidal amplitude (0.7m)	22 days	Large Cities and towns, dredging	Clams, native oyster fishery	9,900 km ²	940,000t oysters in their heyday	Newell, 1988; Gerritsen et al., 1994; Cerco and Noel, 2007
Totten Inlet, Puget Sound, WA	Portion of fjord 10 to >100m	6m tidal range, limited FW input	10 to 11 days	Rural, many waterfront residences	Clams, oysters, mussels and geoducks	24.7 km ² / 0.85km ²	1,136t oysters, clams and mussels	Brooks, 2000

Table 2(cont.)

Estuary	Type and Ave depth	Physical Conditions	Residence time	Development and Anthropogenic disturbance	Bivalves	Area Total/Intertidal	Biomass, Aquaculture Area	References
Willapa Bay, WA	Bay w/ relatively small rivers, 3.2m	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	1,468 t harvest, 46km ²	Hedgepeth and Obrebski, 1981; 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	Coos Bay, lumber mills, diked tidelands, dredging	Oysters on bottom and longlines	34 km ² /3.8 km ²	17t	Hickey and Banas, 2003; Rumrill, 2006
Humboldt Bay, CA	Bay w/ very small creeks, almost lagoonal, 3.5m	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, 260ha	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, 2,510 t oysters, 458 ha	Jamieson et al., 2001; Carswell et al., 2006

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. 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).

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	4,626	0.129	Oyster- longline, bottom Clams	Marsh fill	Production
Tillamook Bay, OR	37.3	1,014.8	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

Tomales Bay, CA	28.5	240	0.08	Clams	Nutrients	Production
San Francisco Bay	1,060	0	0	Historical oyster harvest	Diking and fill, Modified fw flow, nutrients	Zones: Urban Industrial, Conservation