



Bivalve aquaculture in estuaries: Review and synthesis of oyster cultivation effects

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ABSTRACT

Oyster farming in estuaries is a globally important industry based primarily around the Pacific oyster *Crassostrea gigas*, for which a common technique is elevated culture on racks, trestles and other structures. We review literature on cultivation impacts, revealing a research focus and state of knowledge that largely parallels that for other aquaculture species and cultivation methods. Ecological studies of elevated culture effects have focused on changes to the benthos from biodeposition, and largely show that impacts are localized and minor by comparison with many other forms of aquaculture. The broader ecological issues associated with elevated oyster culture include the effects of pests (fouling pests, toxic/noxious microalgae, disease), creation of novel habitat (e.g. by fouling of farm structures and accumulation of shell), alteration to nutrient cycling, depletion of suspended particulate matter by oyster crops, and related effects on higher trophic level animals including fish, seabirds and marine mammals. These issues are less well understood for elevated culture systems, but ecological effects can be inferred from the few studies that have been conducted, from other forms of bivalve aquaculture (e.g. mussels), and to some extent from fundamental knowledge of the role of oysters as 'ecosystem engineers'. We use a risk ranking method to evaluate ecological risks (and associated uncertainty intervals) for each of the issues associated with estuarine oyster culture, based on subjective assessment of the likelihood and consequences (severity, spatial extent and duration) of adverse effects. Our assessment reveals that the introduction and spread of pest species are potentially important but often overlooked consequences of oyster cultivation. By comparison with most other sources of impact, the spread of pests by aquaculture activities can occur at regional scales, potentially leading to ecologically significant and irreversible changes to coastal ecosystems. We suggest that future studies of cultivation effects redress the balance of effort by focusing more on these significant issues and less on the effects of biodeposition in isolation. Furthermore, the acceptability of aquaculture operations or new developments should recognize the full range of effects, since adverse impacts may be compensated to some extent by the nominally 'positive' effects of cultivation (e.g. habitat creation), or may be reduced by appropriate planning and management. Even more broadly, aquaculture developments should be considered in relation to other sources of environmental risk and cumulative impacts to estuarine systems at bay-wide or regional scales, so that the effects of cultivation are placed in context.

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1. Introduction

Intertidal oyster cultivation is one of the most important aquaculture industries globally (FAO, 2006a). While this industry sector is based on a range of species, Pacific oysters (*Crassostrea gigas*) are by far the most dominant (>96% by value and tonnage; FAO, 2006a,b,c), having been spread either deliberately or inadvertently (e.g. via shipping) to many countries (Kaiser et al., 1998; Dumbauld et al., 2009). Oyster cultivation takes place primarily on the tidal flats of estuaries, using farming methods that differ among localities according to environmental conditions, the type of product marketed, and tradition (FAO, 2006a). A common technique is elevated (off-ground) culture, which typically involves laying oysters on sticks, in mesh bags or trays across wooden racks or steel trestles (~0.3–1 m high) that are fixed in the intertidal zone and exposed during low tide, or uses stakes or long-lines (e.g. Forrest and Creese, 2006; Dubois et al., 2007; Leguerrier et al., 2004; McKindsey et al., 2006). Depending on region and the reliability of natural settlement, seed-stock may be derived from seabed populations, from wild-caught spat on artificial collectors, and increasingly from hatchery brood-stock (McKindsey et al., 2006; Dumbauld et al., 2009).

The occupation of space by intertidal structures means that oyster cultivation can conflict with a range of other environmental, social and economic values (DeFur and Rader, 1995; Simenstad and Fresh, 1995; Kaiser et al., 1998; Read and Fernandes, 2003). The literature on environmental effects is dominated by papers that describe changes to sediments and associated infaunal assemblages beneath cultivation

areas (e.g. Ito and Imai, 1955; Kusuki, 1981; Mariojouis and Sorin, 1986; Castel et al., 1989; Nugues et al., 1996; Spencer et al., 1997; De Grave et al., 1998; Kaiser et al., 1998; Forrest and Creese, 2006; Dubois et al., 2007; Bouchet and Sauriau, 2008). In addition to benthic effects, there are a range of broader ecological issues associated with elevated oyster aquaculture that are less well-recognized or need to be considered in a comparative context (Fig. 1). These include the introduction of pests (fouling pests, toxic/noxious microalgae, disease), creation of novel habitat, alteration to water flows and nutrient cycles, and depletion of suspended particulate matter (especially phytoplankton) by oyster crops (ICES, 2005a; McKindsey et al., 2006). Related considerations are the wider ecosystem consequences of such changes, for example implications for fish, seabirds and marine mammals.

With some exceptions, knowledge of this broad range of ecological effects from oyster aquaculture is limited. Furthermore, where the ecological effects of elevated culture methods are specifically addressed, the complexity of some of the ecosystem issues and interactions depicted in Fig. 1 means they are often described in the literature only superficially (e.g. Crawford, 2003). Alternatively more thorough assessments have usually focused on a subset of the broad range of potential issues (e.g. McKindsey et al., 2006; Dumbauld et al., 2009). We propose that to understand and manage ecological risks from elevated culture systems, there is a need for a more integrated and in-depth assessment in which the relative significance of each issue is considered within the context of the full range of actual or potential ecological effects.

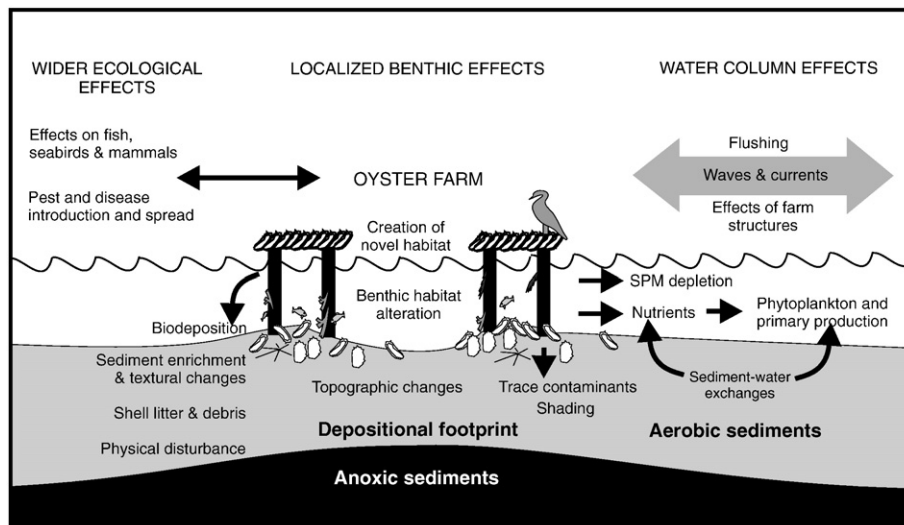


Fig. 1. Schematic of actual and potential ecological effects from elevated intertidal oyster cultivation. SPM=suspended particulate matter.

As a contribution to such a goal, this paper provides a synthesis of the ecological impacts that can arise with the development of elevated oyster cultivation in estuaries, and assesses the relative importance of the different effects. To provide insight into effects for which little is known, we expand our synthesis to include other types of aquaculture (especially of other bivalves) for which the suite of ecological issues is qualitatively similar. We also draw on the literature on aquaculture effects more broadly (i.e. for different culture methods or species) where this assists in placing in context the magnitude of effects from oyster cultivation. Similarly, where valid comparisons can be made, we refer to the substantial body of knowledge for natural or restored oyster reefs that describes the functional role of oysters as 'ecosystem engineers'; such comparisons can facilitate understanding of the potential for wider ecosystem changes from cultivation. We then discuss the relative ecological importance of the different ecological issues, and highlight key knowledge gaps or uncertainties. Based on these findings, research and management implications are then discussed. While we recognize that a range of short-term ecological effects may arise as a result of oyster farm construction, and in relation to other aspects of farming operations such as off-site spat catching and product processing (McKindsey et al., 2006), we restrict discussion in this paper to the sea grow-out stage of oyster aquaculture.

2. Local benthic effects

2.1. Biodeposition and enrichment

Oyster farms act as biological filters that concentrate suspended particulate matter from the water column as it flows through the culture, producing waste particles in the form of faeces and pseudofaeces. These wastes (generally referred to as 'biodeposits') are heavier than their constituent particles, and readily settle on the seabed beneath culture areas (Haven and Morales-Alamo, 1966; Kusuki, 1981; Mitchell, 2006). Since biodeposits are organic-rich and consist of a substantial proportion of fine particles (i.e. silt and clay), seabed sediments beneath oyster cultures can become organically enriched and fine-textured relative to surrounding areas, and have anoxic sediments closer to the sediment surface (Forrest and Creese, 2006).

Changes in physico-chemical characteristics beneath oyster cultures can lead to a displacement of large-bodied macrofauna (e.g. heart urchins, brittle stars, large bivalves) and the proliferation of small-bodied disturbance-tolerant 'opportunistic' species (e.g. capitellid polychaetes and other marine worms). In some instances an associated reduction in the richness of the infaunal assemblage has been described for elevated cultures (e.g. Castel et al., 1989; Nugues et al., 1996), consistent with moderate organic enrichment in terms of the classic conceptual model of Pearson and Rosenberg (1978). However, in many case studies the response of the infaunal assemblage has been less pronounced, for example evident as a change in species composition and dominance without an appreciable effect on richness (Forrest and Creese, 2006). Yet other studies have revealed little or no discernible enrichment effect on infauna (e.g. Crawford et al., 2003). In fact, extreme enrichment effects as a result of oyster farming have been described historically only for suspended culture systems in Japan, and been attributed to repeated culturing and overstocking (Ito and Imai, 1955; Kusuki, 1981). Hence, it is apparent that the magnitude of benthic enrichment from elevated intertidal culture is generally relatively minor by comparison with suspended subtidal culture of fish (e.g. Brown et al., 1987; Karakassis et al., 2000; Forrest et al., 2007a) and, to a lesser extent, other bivalves (e.g. Mattsson and Lindén, 1983; Kaspar et al., 1985; Grant et al., 1998). Irrespective of the magnitude of the effect, without exception it is apparent that direct benthic effects associated with oyster cultivation are highly localized to farmed areas (extending tens of metres or less from

structures) and can be greater directly beneath cultivation structures than in the space between them (Forrest and Creese, 2006).

The magnitude of effects from enrichment will depend primarily on stocking density and biomass in relation to the flushing characteristics of the environment (Pearson and Black, 2001). Additionally, the level of biodeposition for a given stocking density, and the assimilative capacity of the environment, may vary seasonally (Kusuki, 1981; Souchu et al., 2001; Mitchell, 2006). To our knowledge, however, the relative role of these different attributes has not been quantified for oyster farms. In the case of intertidal culture, the capacity of the environment to assimilate and disperse farm wastes will mainly depend on water current velocity and wave action (Souchu et al., 2001), as these factors control the size and concentration of the depositional 'footprint'. Increased flushing from currents and waves will reduce biodeposit accumulation and increase oxygen delivery to the sediments, thus allowing for greater assimilation of farm wastes (Findlay and Watling, 1997; Mitchell, 2006). Negligible enrichment from elevated oyster farms in Tasmania has been attributed to a combination of low stocking densities and adequate flushing (Crawford, 2003; Crawford et al., 2003; Mitchell, 2006). Generally, well-flushed aquaculture sites can be expected to have depositional footprints that are less intense but more widely dispersed than shallow or poorly flushed sites (Pearson and Black, 2001).

Recovery rates of seabed communities from oyster farm biodeposition and enrichment are not well understood, but in some localities (e.g. where coarse sandy sediments are prevalent) appears to be relatively rapid (time periods of months) once farming ceases (Martin et al., 1991). Rapid recovery can also be inferred from seasonal or temporal reductions in the severity of benthic enrichment effects over time scales of months in unvegetated soft-sediment habitats (Forrest, 1991). By comparison, time scales of recovery in strongly enriched (sometimes near-azoic) muddy sediments beneath fish farms can be highly variable, but may be many years at poorly flushed subtidal sites (Karakassis et al., 1999; Pereira et al., 2004; Forrest et al., 2007a).

2.2. Accumulation of shell litter, debris and associated organisms

The accumulation of live oysters, shell litter and farm debris (e.g. oyster growing sticks), and fouling or epibenthic organisms beneath grow-out structures can be a highly visible effects of oyster farms during low tide (Fig. 2). The extent of drop-off to the seabed is likely to depend on the type of cultivation system (e.g. stick culture is likely to deposit more debris than basket or cage culture) and may be exacerbated periodically during harvesting. The degree of fouling accumulation will depend on the degree to which structures become fouled, and patterns of natural drop-off or active defouling by farm personnel. Subsequent effects to benthic community composition, for example aggregation of carnivorous and deposit feeding species in response to the food supply (e.g. sea stars) and competition between deposited shellfish and benthic filter-feeders, are indicated for other forms of bivalve aquaculture (Inglis and Gust, 2003; Smith and Shackley, 2004; Amours et al., 2008; Hartstein and Rowden, 2008) and conceivably occur in the case of elevated oyster culture. Excessive deposition and decay of fouling biomass may also exacerbate the organic enrichment described above, although such effects would likely be patchy beneath cultivation areas and were not evident in a recent study at a well-flushed location in eastern Canada (Mallet et al., 2009).

Hard surfaces on the seabed such as live and dead oysters, calcareous debris (e.g. bivalve shells, serpulid polychaete tubes) and farm materials potentially provide novel habitats for fouling organisms and associated mobile biota, which would otherwise not occur (or be at reduced densities) in the absence of oyster growing. Such effects have been widely documented in the case of on-ground shellfish culture (Dumbauld et al., 2001; Hosack et al., 2006; Powers



Fig. 2. Fouling by oysters and other organisms on derelict oyster racks. Altered topography and rows of accumulated shell and debris are visible in the background (photo courtesy of B. Howse, Northland Regional Council, New Zealand).

et al., 2007; Ysebaert et al., 2009) and oyster reefs (Peterson et al., 2003; Escapa et al., 2004; Ruesink et al., 2005; Coen et al., 2007). The structured habitat provided by oyster reefs can support a diversity of taxa (macroalgae, sessile and mobile invertebrate epifauna, infauna, fish, birds) that may be absent or at reduced densities in adjacent unvegetated soft-sediment habitats (Ruesink et al., 2005 and references therein). Similarly, oyster shell has been used to successfully enhance estuarine habitat for juvenile Dungeness crabs (*Cancer magister*), to compensate for habitat loss caused by dredging (Dumbauld et al., 2000). Probably the main factors that would limit the value of hard substrata deposited beneath operational oyster farms would be the effect of enhanced sedimentation beneath structures, or sediment resuspension and physical disturbance from farming activities (see below). Nonetheless, the introduction of novel habitats could result in fundamental or long-term shifts in benthic community composition after cessation of farming, depending on site-specific variation in environmental conditions, oyster species and density, and the extent and persistence of accumulated material. Dumbauld et al. (2000) observed that transplanted oyster shell could sink or become covered in sediment in a matter of months. However, in long-established cultivation areas the longer term persistence of shell and other inorganic material is often evident (Fig. 2), although regulatory authorities in many countries are increasingly stipulating management practices to mitigate such effects (e.g. requiring removal and land disposal of accumulated material).

2.3. Changes in seabed topography and sedimentation

Changes in seabed topography (in the order of a few tens of centimetres at maximum) have been described beneath oyster farms in several studies (Ottmann and Sornin, 1982; Everett et al., 1995; Forrest and Creese, 2006; see also Fig. 2). Such changes can result from the accumulation of shell and inorganic debris, and erosion or accretion of sediment beneath and between farm structures (Forrest and Creese, 2006). Sedimentation rates directly beneath cultures are generally elevated by comparison with non-culture areas (Mariojous and Sornin, 1986; Sornin et al., 1987; Nugues et al., 1996), being as much as three times greater directly beneath farm structures than at control sites (Forrest and Creese, 2006). However, effects on seabed topography are more likely to be related to changes in hydrodynamic conditions caused by the structures themselves rather than enhanced sedimentation (Kirby, 1994). Excessive sediment build-up within Pacific oyster leases can occur at sites where cultivation structures are

in high density or aligned perpendicular to tidal currents, resulting in the entrapment of suspended sediments (Kirby, 1994; Handley and Bergquist, 1997). In such instances oyster leases in New Zealand have become un-useable and farming abandoned, with shell litter and debris still evident many years later. Redistribution of sediments either into (Kirby, 1994) or out of (Mallet et al., 2009) culture sites may also occur in relation to events such as storms that lead to large scale sediment mobilisation.

2.4. Physical disturbance

Physical disturbance is obviously an issue with on-ground shellfish culture and harvest methods (Dumbauld et al., 2009). At least two studies of elevated oyster culture have also recognized physical disturbance, in particular from vessel movements (e.g. propeller wash) and farm personnel walking between cultivation structures, as having a strong influence on benthic changes beneath farm sites (De Grave et al., 1998; Forrest and Creese, 2006). Forrest and Creese (2006), for example, described a relatively strong association between benthic macrofaunal composition and decreased sediment shear strength beneath Pacific oyster cultures in New Zealand, which they suggested could reflect physical disturbance beneath racks. Impacts from physical disturbance are conceivably equally as important as enrichment within elevated cultivation areas, and perhaps more important where enrichment is negligible. Despite this, the relative importance of these two effects is yet to be rigorously evaluated in the case of elevated culture; hence the recovery rate of seabed communities from disturbance effects is unknown. Studies of on-ground culture systems have more clearly demonstrated physical effects during intermittent shellfish harvesting, and the recovery of soft-sediment communities in a matter of weeks to months in unvegetated habitats (McKindsey et al., 2006 and references therein). By contrast, recovery from physical disturbance by eelgrass (*Zostera marina*) may take several years (McKindsey et al., 2006; Dumbauld et al., 2009 and references therein).

2.5. Shading

Shading by farm structures could reduce the amount of light reaching the seafloor, with implications for the growth, productivity, survival and depth distribution of ecologically important primary producers such as benthic microalgae, macroalgae or seagrasses. In the context of studies that report negligible effects on seagrass beneath oyster farms (Crawford, 2003; Ward et al., 2003), we can infer that shading effects in such cases are of little significance. However, other studies have described adverse effects on seagrass beneath oyster racks and suggested shading as a possible cause (e.g. Everett et al., 1995). To our knowledge, however, the relative importance of shading versus other sources of seabed impact has never been conclusively established, and to do so would require targeted manipulative experiments. Despite the absence of clear evidence for adverse effects from shading, Hewitt et al. (2006) demonstrated that a small reduction in cover of New Zealand eelgrass (*Zostera muelleri*) was theoretically possible because of shading from planned long-line oyster cultures. Shading effects are conceivably important where oyster farms are placed across seagrass and algal habitats in environments of relatively high water clarity, and in locations (e.g. well-flushed systems) where other ecological effects (especially those from sedimentation and biodeposition) are minimal. Alternatively, the incremental reduction in incident light by shading may be more important in turbid systems where the depth distribution of benthic algae and macrophytes is already light limited. Clearly the potential for adverse effects is situation-specific, but can to a large extent be mitigated by appropriate site selection and management (Dumbauld et al., 2009).

2.6. Contaminant inputs

Operational oyster farms do not generally require the ongoing input of external materials that could introduce trace contaminants to the marine environment, as can occur for example as a result of synthetic feed inputs to sea-cage fish farms (Morrisey et al., 2000; Easton et al., 2002; Schendel et al., 2004). Possible exceptions to this situation arise in shellfish aquaculture where compounds such as hypochlorite and acetic acid have been used to mitigate the effects of biofouling (Carver et al., 2003; Forrest et al., 2007b); however, these tend to be non-persistent contaminants whose use is unlikely to lead to significant non-target effects (Locke et al., 2009). Historically, many oyster cultivation racks have been constructed from wood treated with preservatives (e.g. copper–chromium–arsenic, CCA; creosote) that could leach into surrounding waters. Highly localized effects on sediments have been described in the vicinity of marine pilings as a result of CCA leaching (Weis et al., 1993), consistent with expectations that trace metals that are released to the water column will rapidly bind to suspended sediments and organic material (Forstner, 2005). Such binding is likely to reduce the bioavailability and toxicity to associated biota, and the release of contaminants from treated timber in seawater is reported to decrease over time (Brooks, 1996; Breslin and Adler-Ivanbrook, 1998). Hence, this issue is probably of negligible significance in the case of oyster culture sites where wooden structures are used. We also note that there is an increasing trend to use alternative construction materials or develop strict regulatory guidelines around the use of treated timber (e.g. DPI, 2008).

3. Water column effects and interactions with the benthic environment

3.1. Altered currents and flushing

Currents and waves play an important role in ecosystem function. In relation to shellfish farming these include delivery of seston and dissolved oxygen, and the flushing of wastes and associated nutrients into and out of the localized environment. For example, excessive enrichment effects on benthos could occur if currents are not above a critical threshold to allow dispersion and resuspension of seabed sediments and shellfish farm biodeposits. Although there appears to be little published information, oyster farm structures and farm-related alterations to seabed topography (e.g. from shell accumulation) are likely to lead to effects on waves, currents and flushing characteristics in the vicinity of farm sites (Gouleau et al., 1982; Nagues et al., 1996; Hewitt et al., 2006). Literature for oyster reef habitats indicates that flow changes across the seabed may alter fluxes of materials (e.g. sediments) to adjacent habitats, and influence ecological processes such as patterns of dispersal and recruitment of invertebrates and fish (Breitburg et al., 1995; Ruesink et al., 2005). Effects of this general nature are also conceivable in the case of elevated oyster culture, although specific differences can be expected given that the extent to which flows are modified will differ for different types of habitat (e.g. because of differences in the 'porosity' of benthic reef versus elevated structures), and depend on attributes of the cultivation structures (e.g. height, density) and the extent to which cultivation physically alters the seabed (e.g. by shell accumulation).

3.2. Water quality

Natural oyster reefs are considered to have the potential to improve estuarine water quality by filtering sediments and other suspended particulate matter (SPM) from the water column (e.g. Gottlieb and Schweighofer, 1996; Ruesink et al., 2005; Grizzle et al., 2006). As a consequence, there is much interest in the restoration of degraded oyster reefs as a means of top-down control of phytoplank-

ton densities in eutrophic estuaries (Newell, 2004; Cerco and Noel, 2007; Newell et al., 2002, 2007). A recent study also suggests that elevated oyster cultures can have a comparable function (Lin et al., 2009; see below). The adverse effects of intertidal culture systems on water quality in estuarine environments are less well understood, but are likely to be relatively minor given that seabed enrichment is low and external contaminant inputs are minimal, as described above. The only published cases of adverse water quality from oyster aquaculture have arisen in suspended cultivation systems where farms have been over-stocked or located in poorly flushed environments. Early studies of suspended culture of Pacific oysters in Japan revealed adverse water column impacts that were related to excessive biodeposition (Ito and Imai, 1955; Kusuki, 1981). For example, Ito and Imai (1955) described seabed enrichment so severe that oyster culture areas became 'self-polluting' (i.e. leading to oyster mortality) as a result of dissolved oxygen depletion in the overlying water column and the associated release (from sediments) of hydrogen sulphide at toxic concentrations.

By contrast, a study in Marennes-Oléron Bay (a major Pacific oyster culture area in France) suggests that mortality can occur as a result of a range of factors, and not simply a negative feedback on water quality (Soletchnik et al., 2005). The findings of the latter study further indicate that the potential for adverse water quality-related effects in the case of elevated intertidal culture is low, which is perhaps not surprising considering that intertidal farm sites are substantially or completely flushed on every tidal cycle. Any water quality effects associated with elevated culture can undoubtedly be minimized by appropriate site selection and farm design (e.g. ensuring that farm structures are configured in a way that causes minimal retardation of flushing processes).

3.3. Nutrient cycling

The effect of elevated oyster cultivation on nutrient cycling in estuaries is incompletely understood, highly complex and situation-specific. Based on information from other bivalve culture systems, and natural or restored oyster reefs, it is evident that effects will be determined by processes involving filter-feeding and dissolved nutrient excretion, biodeposition and sediment remineralization of nutrients, and loss of nutrients through oyster harvest (Prins et al., 1998; Newell, 2004; Porter et al., 2004; Su et al., 2004). The production of dissolved (hence bioavailable) nutrients can occur directly via excretion by the oyster stock, or indirectly via remineralization and subsequent release from enriched sediments (Souchu et al., 2001; Dumbauld et al., 2009). The resultant effects of dissolved nutrient release on algal production involve complex interactions that are likely to be highly variable in relation to factors such as flushing, temperature, water clarity, stocking density, and the level of seabed enrichment. For example, although oysters may deplete phytoplankton, dissolved nutrients released from oyster excretion or sediment remineralization have the potential to offset this effect by simultaneously stimulating phytoplankton production at local scales (e.g. Prins et al., 1998; Pietros and Rice, 2003). Conversely, in the case of oyster reefs where filter-feeding leads to locally increased water clarity (Cerco and Noel, 2007), the production of benthic algae and seagrasses may be enhanced, thereby reducing the flux of dissolved nutrients to the water column and reducing phytoplankton production (Souchu et al., 2001; Newell, 2004; Porter et al., 2004). For example, increased water clarity resulting from restoration of oyster reefs is predicted to lead to an increased biomass of submerged aquatic vegetation (Newell and Koch, 2004; Cerco and Noel, 2007). For elevated culture systems, however, decreased sediment shear stress beneath grow-out areas (i.e. indicative of greater erosion potential), combined with turbulence induced by culture structures, may lead to enhanced sediment resuspension and high turbidity (Forrest and Creese, 2006; Leguerrier et al., 2004).

3.4. Suspended particulate matter depletion and ecological carrying capacity

Oysters can filter particles within the 4–100 μm size range (Hawkins et al., 1998; Dupuy et al., 2000), and hence can derive nutrition from suspended particulate matter (SPM) in the form of phytoplankton (predominantly), detritus, bacteria, protozoa, zooplankton, and resuspended benthic microalgae (Le Gall et al., 1997; Dame and Prins, 1998; Leguerrier et al., 2004). Cultured oysters may also contribute to the SPM pool during spawning. There has been considerable research into food depletion and modelling of carrying capacity for oyster culture (e.g. Ball et al., 1997; Bacher et al., 1998; Ferreira et al., 1998) as well as for other bivalves and polyculture systems (e.g. Carver and Mallet, 1990; Prins et al., 1998; Smaal et al., 1998; Gibbs et al., 2002; Nunes et al., 2003). Typically, this work has focused on phytoplankton depletion and maximum production capacity within growing regions. In this respect a number of indicators of carrying capacity have been used, in particular water residence time in relation to bivalve clearance and primary production time within a system (e.g. Dame and Prins, 1998; Gibbs, 2007). The literature in this field primarily addresses the role of natural or cultivated bivalve populations, whereas the filter-feeding activities of fouling organisms and other biota associated with shellfish cultures can also be functionally important (e.g. Mazouni et al., 2001; Mazouni, 2004; Decottignies et al., 2007).

Influences from oyster aquaculture on estuarine carrying capacity are inextricably linked to the issues of nutrient cycling, SPM depletion, and coupling between the seabed and water column. Interactions between shellfish cultivation and the water column and seabed environments are complex (see review by Dumbauld et al., 2009). However, there is compelling evidence that bivalve aquaculture can affect nutrient cycling and the quantity and quality of SPM across a range of spatial scales (Prins et al., 1998; Cerco and Noel, 2007; Coen et al., 2007; Lin et al., 2009). Empirically, phytoplankton depletion is certainly evident at local scales in the vicinity of oyster cultures (Dumbauld et al., 2009) or intensive culture zones (Lin et al., 2009), and serial depletion among multiple adjacent farms at larger spatial scales has been described for other types of suspended bivalve culture (Gibbs, 2007; Grant et al., 2007). Top-down control of phytoplankton has similarly been described or inferred for estuarine systems where indigenous oyster populations have declined (Newell, 2004) or non-indigenous bivalves have reached high densities (e.g. San Francisco Bay; Nichols, 1985).

There is some evidence that SPM depletion by cultivation can negatively affect oyster production. For example, control of Pacific oyster growth by phytoplankton availability has been described for subtidal floating culture systems in environments with long residence times such as Thau Lagoon in southern France (Souchu et al., 2001). In relation to elevated intertidal culture, Marennes-Oléron Bay has been described as "...one of the few systems where bivalve filter-feeders have on two occasions been over-stocked and overexploited" (Dame and Prins, 1998). Marennes-Oléron Bay is a highly turbid system where bivalve clearance times are shorter than primary production and water residence times, and where resuspended benthic microalgae are an important food source (Dame and Prins, 1998). There are anecdotal reports that Pacific oyster production in New Zealand estuaries has also been limited by carrying capacity, although this has not been definitively proven (Handley and Jeffs, 2002).

The potential for wider effects on ecological carrying capacity as a result of SPM depletion by shellfish cultures is invariably situation-specific and scale-dependent in terms of the size of the cultivation area to the system in question (Anderson et al., 2006). Carrying capacity is also expected to be temporally variable, as the amount of phytoplankton and other SPM in estuaries is likely to be influenced by factors operating from tidal time scales to longer term climatic events such as El Niño Southern Oscillation cycles (Dame and Prins, 1998; Prins et al., 1998; Zeldis et al., 2000). Evidence that SPM depletion

from elevated oyster culture has the potential to reach or exceed carrying capacity at bay-wide scales suggests that wider ecosystem effects are certainly possible. Such effects could conceivably arise not only as a function of direction depletion but also through alteration in SPM size spectra and phytoplankton species composition; thus the type and quality of food available to zooplankton and other consumers (Prins et al., 1998; Dupuy et al., 2000; Pietros and Rice, 2003; Leguerrier et al., 2004), with consequences for local populations of higher trophic level organisms such as fish. Food-web modelling for Marennes-Oléron Bay predicted a shift from pelagic to benthic consumers as a result of intertidal trestle cultivation of oysters, reflecting SPM depletion in the water column and enrichment of benthic meiofauna (Leguerrier et al., 2004). This prediction is supported by Lin et al. (2009), whose ECOPATH model simulations and field sampling both revealed a substantial increase in phytoplankton and zooplankton biomass and decrease in benthic infaunal biomass following the complete removal of oyster racks from a coastal lagoon where intensive oyster cultivation (up to 2932 racks km^{-2}) had been conducted previously.

4. Wider ecological effects

4.1. Habitat creation by farm structures

Marine farm structures and artificial structures in general, provide a three-dimensional reef habitat for colonisation by fouling organisms and associated biota (Costa-Pierce and Bridger, 2002). In a manner similar to that described above for the accumulation of oysters and debris, elevated shellfish aquaculture structures provide a novel habitat that can support a considerably greater biomass, richness and density of organisms than adjacent natural habitats (e.g. *Crassostrea virginica* cages, Dealeris et al., 2004; *Mytilus edulis* ropes, Murray et al., 2007; see also Fig. 2). It is also well-recognized that the biota fouling artificial structures can be quite different to that in adjacent rocky areas (Glasby, 1999; Connell, 2000), and can comprise a diverse assemblage of macroalgae and filter-feeding invertebrates (Hughes et al., 2005). Hence, there is considerable interest in the role played by artificial structures within the ecosystem, such as increasing local biodiversity, enhancing coastal productivity, and compensating for habitat loss from human activities (Ambrose, 1994; Costa-Pierce and Bridger, 2002; Hughes et al., 2005).

Many of the ecological roles of the habitat created by shellfish farming are well-recognized for on-ground oyster culture, as noted earlier in this paper. There is also evidence of a comparable role for suspended subtidal oyster culture structures (e.g. Lin et al., 2007), intertidal trestles (e.g. Hilgerloh et al., 2001) or other intertidal structures used for oyster cultivation (O'Beirn et al., 2004). From McKindsey et al. (2006), it is evident that the habitat complexity created by intertidal shellfish culture is likely to provide a range of ecosystem services including an enhanced food supply, a refuge from predation, a settlement surface, and protection from physical (e.g. water movement) and physiological (e.g. desiccation) stress. Dealeris et al. (2004) conclude that oyster cages used for the grow-out stage of *C. virginica* have a habitat value that is considerably greater than non-vegetated seabed and at least equal to seagrass. It is also evident that some elevated culture systems provide a habitat that can be extensively colonised by wild or naturalized oysters, as described for *C. gigas* in western France (Cognie et al., 2006). As we further discuss below, the creation of novel habitat and the presence of cultivation structures can affect the wider ecosystem in a number of ways.

4.2. Effects on fish

The aggregation of various fish species around suspended aquaculture operations and other artificial structures is well-recognized

(Relini et al., 2000; Gibbs, 2004; Einbinder et al., 2006; Morrissey et al., 2006), reflecting the role of such structures in offering shelter from predation, habitat complexity and a food source. There has also been discussion of the potential for direct negative effects of cultured oysters and mussels on fish populations, primarily due to the consumption of fish eggs and larvae (Gibbs, 2004; McKindsey et al., 2006; Keeley et al., 2009). The association of fish with on-ground oyster culture has been described in a number of studies (see references in Grabowski, 2004 and Dumbauld et al., 2009). Similarly, in the case of on-ground clam culture in the United States, Powers et al. (2007) found that the emergent habitat provided by fouling of mesh bags led to densities of mobile invertebrates and juvenile fish that were elevated by comparison with adjacent sand flats, and comparable to natural seagrass.

Conceivably, therefore, the ecological role of elevated oyster farm structures, combined with habitat alterations from the deposition of oysters and associated debris, may affect fish populations in a number of ways. However, a body of published information from primary literature comparable to that describing the effects of oyster reef or on-ground culture systems is unavailable for elevated culture systems, and the limited information available describes changes that are often viewed as neutral or positive (rather than adverse) effects (McKindsey et al., 2006). For example, Dealeris et al. (2004) describe a greater association with submerged aquaculture gear by some fish species but not others. Similarly, Dumbauld et al. (2009) cite a thesis that revealed no overall increase in fish richness or abundance adjacent to oyster racks, but a greater prevalence of structure-oriented species. Trophic modelling in Marennes-Oléron Bay represents one of few attempts to understand the wider ecosystem role of elevated intertidal oyster (*C. gigas*) culture (Leguerrier et al., 2004). These authors suggested that oyster cultivation could increase the food supply to fish, which was predicted to occur as a result of increased meiofaunal production. Similarly, increased turbidity (e.g. induced by erosion around oyster farm structures) may provide a refuge from predation for small or juvenile life-stages of fish (Chesney et al., 2000; Leguerrier et al., 2004). A field mesocosm study of Pacific oyster cultivation effects in western France showed that the microhabitat created beneath trestles was more frequented by flatfish than adjacent homogenous habitat (Laffargue et al., 2006). More recently, an experimental scale deployment of oyster cages suggested that aquaculture gear could benefit populations of ecologically and economically important fish and epibenthic macrofauna in a way comparable to oyster reef habitat (Erbland and Ozbay, 2008). Similarly, the Lin et al. (2009) study of the system-wide effects of oyster rack removal described an unexpectedly large decline in the biomasses of zooplanktivorous and piscivorous reef fish post-removal. These authors suggested that the oyster racks might have previously attracted and benefited reef fish by reducing predation or enhancing their food sources.

4.3. Effects on seabirds

Effects on seabirds from elevated oyster culture conceivably arise due to the alteration of food sources, displacement of foraging habitat, and as a result of disturbance (e.g. noise) related to farm activities (Kaiser et al., 1998; Connolly and Colwell, 2005). The additional issue of entanglement has been widely discussed in relation to other forms of aquaculture or fishing practice (Butler, 2003; Bull, 2007), but is unlikely to be an important consideration for intertidal oyster culture where primarily rigid structures are used. Similarly, the effects of plastic and other marine debris on seabirds have received attention internationally (Lloyd, 2003). For example, ingestion of plastic debris by albatross chicks is reported to have caused mortality through dehydration, gut blockage and/or toxic effects during digestion (Auman et al., 1998). Such issues are likely to be minimal at well-operated oyster farms.

Adverse effects on seabirds from elevated oyster culture could, however, arise due to the displacement of food sources, although such

effects have not been observed in the case of oyster culture or in naturalized populations of introduced Pacific oysters. A study of the ecological role of naturalized Pacific oysters 20 years after their introduction in Argentina study revealed higher densities of local and migratory birds, and higher foraging rates, inside oyster beds compared with reference areas, which were attributed to greater prey availability (Escapa et al., 2004). In the case of elevated intertidal culture, trophic modelling by Leguerrier et al. (2004) similarly suggested that birds could benefit from an enhanced food supply.

Clearly, the consequences for birds and other higher trophic level animals that arise as a result of intertidal oyster farm effects on their food supply (nature, quantity and availability) will depend on their dietary preferences and ability to adapt to changes induced by cultivation. Overall, the few studies of oyster culture effects provide information consistent with other forms of aquaculture, suggesting an attraction of many seabird species to culture areas for foraging on fish and fouling epibiota, and even the cultured crop itself (Ross et al., 2001; Roycroft et al., 2004; Kirk et al., 2007). There has been related discussion of whether the aggregation of bivalve-feeding birds at culture sites may act as a pathway for disease transmission to the culture species and to human consumers (see McKindsey et al., 2006 and references therein); however to our knowledge associated ecological risks have not been identified.

Despite their potential to provide food sources and other habitat (e.g. roosting structures), the large areas of estuarine habitat that may be occupied by intertidal shellfish farms means that they also have the potential to displace seabirds from foraging sites. For example, any bird species that avoid structured habitats may be susceptible to displacement effects. The evidence for such effects is equivocal and indicates that influences will be species and situation-specific (see Dumbauld et al., 2009 and references therein). For some bird species there is evidence of avoidance or a decreased association with oyster structures compared with open tidal flats (e.g. wintering shorebirds in California; Kelly, 2001). In contrast, the few other published studies directly investigating interactions between elevated oyster culture and birds provide little evidence for significant adverse effects. A study of intertidal cultivation in California concluded that off-bottom oyster long-lines did not negatively affect the foraging behaviour of most bird species, but rather enhanced it. In that study there was a greater diversity of birds, and a greater density of some species of shorebird and wading bird, in long-line plots compared with controls (Connolly and Colwell, 2005). In relation to trestle culture in Ireland, Hilgerloh et al. (2001) found that oyster structures did not affect the feeding behaviour of birds. For most species, bird densities were lower in the farm area than a reference area; however, the authors recognized that this pattern may have reflected natural environmental differences. In addition to modifications to benthos, Hilgerloh et al. (2001) also noted that macroalgae fouling of oyster trestles and associated small mobile gastropods provided a food source for some species.

Bird disturbance from noise and traffic does not appear to have been investigated in relation to elevated culture in estuaries, nonetheless it is generally recognized that some seabird species are sensitive to human activities (Goss-Custard and Verboven, 1993; Kelly, 2001; Butler, 2003; Roycroft et al., 2004). For example, Goss-Custard and Verboven (1993) found that oystercatchers were disturbed by the presence of humans in foraging areas, but were also surprisingly flexible in their ability to redistribute their foraging activities. In New Zealand, Butler (2003) found that nesting king shags were highly susceptible to disturbance by boats, leading to part or complete abandonment of nests and chicks.

4.4. Interactions with marine mammals

There are a number of publications concerning interactions between marine mammals and aquaculture (e.g. Würsig and Gailey,

2002; Kemper et al., 2003), but few address intertidal culture of oysters or other bivalves. For aquaculture generally, potential effects on marine mammals include displacement, entanglement, in-water noise, alteration of trophic pathways, and disruption of migration pathways in the case of large cetaceans (Watson-Capps and Mann, 2005). In relation to intertidal cultivation specifically, issues of entanglement or attraction (e.g. to external food inputs) sometimes associated with other forms of aquaculture or fishing do not appear to be regarded as particularly significant (Würsig and Gailey, 2002); marine mammal entanglement appears a greater issue in industries where loose or thin line is used (e.g. Suisted and Neale, 2004).

Watson-Capps and Mann (2005) suggest that small cetaceans may avoid shellfish farms because of human activities, exclusion by structures, or as a result of effects on water clarity or prey availability. These authors report exclusion of bottlenose dolphins (*Tursiops aduncus*) by pearl oyster farms in Western Australia, in a bay where racks were suspended or fixed to the seabed in relatively shallow water (~2–4 m deep). Tracks of individual dolphins showed that adult females tended to stay on the periphery of the farm boundary rather than travel through it. Field and captive studies have found that smaller dolphin species appear reluctant to swim through wooden structures or those with ropes (Kastelein et al., 1995; Watson-Capps and Mann, 2005; Heinrich, 2006). Overall, the nature of habitat exclusion will greatly depend on the type of culture method and the particular species of marine mammal present in the cultivation area. As such, site-specific knowledge is required in order to undertake a robust assessment of risks.

Würsig and Gailey (2002) raise the general issue of potential effects from vessel traffic on acoustic communication, although there appear to be no studies that have specifically addressed such possibilities. In-water noise, especially vessel noise, is regarded as the primary issue of concern because of sound travel in the water column. The potential significance of in-water noise from oyster culture will depend primarily on the vessel traffic generated as a result of oyster farming relative to other activities. As oyster farmers undertake most work during lower tidal conditions when elevated structures are out of the water, in-water noise generation from non-vessel farming activities is likely to be minor. Presumably, any effects on trophic interactions from intensive oyster cultivation (see above) could also have consequences for marine mammal food sources. Again, however, the significance of such interactions is unknown.

4.5. Non-indigenous species and pest organisms

The historic role of the oyster industry in the global spread of non-indigenous species, biofouling pests, toxic or noxious microalgae, and disease is well-recognized. This is especially true in the case of macroscopic biofouling (Boudouresque et al., 1985; Minchin, 2007; Mineur et al., 2007; McKindsey et al., 2007), and associated organisms (e.g. Duggan, 1979; Utting and Spencer, 1992). A number of studies have also documented survival of toxic and nuisance microalgal species (e.g. those associated with biotoxin production and shellfish poisoning) as a result of aquaculture transfers, and oyster transfers in particular (McKindsey et al., 2007). In fact, the introduction of Pacific oysters for aquaculture, and other oyster species to a lesser extent, is regarded as one of the most important historical pathways for the global spread of non-indigenous species (Verlaque, 2001; Wallentinus, 2002; McKindsey et al., 2007). Ruesink et al. (2005), for example, estimated that more than 40% of non-indigenous marine species in Europe, the western United States, and North Sea may have been introduced by oyster aquaculture.

The development and implementation of risk-based guidelines for aquaculture transfers (e.g. ICES, 2005b) are likely to have minimized the present day risk of inadvertent transfers of unwanted species with movements of oysters and seed-stock, especially at international scales (McKindsey et al., 2007). However, at smaller spatial scales

there remains the risk that oyster aquaculture activities will lead to the secondary transfer of unwanted organisms, either from previously established populations or from new introductions that have been mediated by other pathways (e.g. global vessel movements). Hence, below we discuss risks to natural ecosystems as a result of oyster cultivation and transfer, considering the transfer of fouling species and diseases separately. The focus of our discussion is on non-indigenous and pest species, but it is worth noting that regional scale shellfish transfers have the potential to extend the range of indigenous species beyond natural barriers to their dispersal, which is arguably an important but overlooked effect (Forrest et al., 2009). Literature on the role of shellfish aquaculture in the introduction of toxic and nuisance phytoplankton tends to focus on species that pose risks to aquaculture operations and human health (e.g. Crawford, 2003). A review of this issue can be found in McKindsey et al. (2007), and is not further discussed here.

4.5.1. Fouling pests

Elevated or suspended structures (and associated shellfish crops) appear to provide ideal environments for some fouling species to proliferate at high densities, which can become problematical in terms of shellfish aquaculture production (Carver et al., 2003; Lane and Willemsen, 2004; Ramsay et al., 2008). Infected structures can also act as reservoirs for the subsequent spread of fouling pests to natural habitats, which can in some instances lead to significant ecological effects. Pest species associated with oyster transfer that may be problematic to oyster cultivation and are also reported to adversely affect natural habitats include various bivalve species (Carlton, 1992), macroalgae such as *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum* and *Undaria pinnatifida* (Trowbridge, 1998, 1999; Verlaque, 2001; Forrest and Taylor, 2002; Britton-Simmons, 2004; Mineur et al., 2007), tunicates such as *Ciona intestinalis*, *Styela clava* and *Didemnum vexillum* (Coutts and Forrest, 2007; Ramsay et al., 2008), and gastropods such as the slipper limpet *Crepidula fornicata* (Gouletquer et al., 2002).

The spread of such species from infested farms at local scales (e.g. within bays) is likely to be primarily driven by natural mechanisms; in particular the dispersal of planktonic propagules in water currents (Forrest et al., 2009). In contrast, spread at inter-regional scales often occurs via inadvertent transport with human activities (Minchin, 2007). For example, infested equipment, seed-stock or crop may be transferred among growing regions as part of routine oyster culture operations (Taylor et al., 2005). There is a high likelihood that associated fouling organisms will survive if such transfers occur without the application of treatments to reduce biosecurity risks (Forrest and Blakemore, 2006; Mineur et al., 2007). In this way, oyster farming activities have the potential to spread marine pests into natural habitats far from the founding population of the pest organism, potentially leading to irreversible effects on natural ecosystems (Ruesink et al., 2005). Hence, there is increasing interest in the development of treatment methods to reduce the spread of fouling pests with regional scale oyster industry transfers. For equipment there are a range of simple options that are straightforward to apply, whereas seed-stock and crop transfers are more problematical in that some treatments effective against fouling may also be detrimental to the culture species (e.g. Forrest and Blakemore, 2006). However, we note that in the case of elevated intertidal culture the tidal height at which the crop is grown can prevent or reduce infection by many of the notorious pests described for subtidal floating systems (Ramsay et al., 2008). In New Zealand, for example, the clubbed tunicate *S. clava* can reach high densities on intertidal rack structures, but is often uncommon at the top of the racks where crop grow-out occurs (B. Forrest, pers. obs.).

In addition to the transfer of non-indigenous fouling organisms, it is important to recognize that oysters cultured in many countries (in particular Pacific oysters) are also a non-indigenous species (Ruesink

et al., 2005; McKindsey et al., 2007). Pacific oysters are invasive primarily in artificial structures and in rocky habitats (Ruesink, 2007), but can also invade soft-sediment estuarine habitats (Cognie et al., 2006; Smaal et al., 2009). Naturalized populations of Pacific oysters in their adventive range can reach high densities in the estuaries where they are farmed, as well as in ports and harbours generally. Cognie et al. (2006) found that as much as 70% of the oyster stock in a Pacific oyster growing area of the French Atlantic coast comprised naturalized rather than cultured oysters. Concerns regarding naturalized populations of non-indigenous oysters primarily relate to their ecological impact and effect on amenity values (e.g. Hayward, 1997; Ruesink et al., 2005; Cognie et al., 2006; Diederich, 2006). Based on the many studies cited in this paper highlighting the structural and functional role of oyster reefs in natural ecosystems, it can be expected that dense aggregations of naturalized oysters have the potential to lead to significant ecological changes (arguably both adverse and beneficial) in habitats where they establish (e.g. as described by Escapa et al., 2004 for Pacific oysters in Argentina). However, the ecological role of naturalized populations is likely to be species- and situation-specific. For example, McKindsey et al. (2007) note that non-indigenous *Crassostrea* species in their adventive range do not form high-relief reefs to the same extent as *C. virginica* in its native range, hence are unlikely to provide the same ecosystem services.

4.5.2. Disease

Disease outbreaks have been ascribed to oyster introductions or translocations, although these appear highly species-specific (see Carnegie, 2005 for a review of effects in culture). The Pacific oyster is by far the dominant farmed oyster, with production of the next most important species (*C. virginica*) being less by an order of magnitude (FAO, 2006b,c). Other minor species noted by Garibaldi (1996) are (in order of importance) *Crassostrea iredalei*, *Saccostrea commercialis*, *Ostrea edulis* and *C. rhizophorae*. In addition, *Crassostrea ariakensis* (Cochennec et al., 1998) and *C. sikamea* (Ruesink et al., 2005) are worthy of mention in the context of disease risk.

Diggles et al. (2002) reports several diseases and parasites associated with Pacific oysters, most of which are globally ubiquitous and appear to pose a threat to oyster production (especially in hatcheries) or product value rather than natural ecosystems. These include various species of planocercid flatworm and mud-worm (Handley and Bergquist, 1997; Handley, 2002) and the ostreid herpes virus (OsHV-1) (Hine et al., 1992). Summer mortalities of Pacific oyster seed have been linked, but so far inconclusively, to this virus in California (Friedman et al., 2005). Other pathogens implicated in summer mortality include *Vibrio* spp. (Bower, 2002) and *Nocardia crassostreae* (Bower, 2006a). A variety of other diseases have been reported in Pacific oyster culture, including oyster velar virus disease which resulted in mortalities approaching 100% (Bower, 2001a), ciliate infections associated with mortalities exceeding 50% in oyster seed (Bower, 2001b), and *Marteilioides chungmuensis*, which degrades the appearance of Pacific oysters and thereby reduces marketability (Bower et al., 2006).

In New Zealand, pathogens of Pacific oysters have been extensively investigated and no organisms listed by the World Organisation for Animal Health (OIE, 2001) or other significant pathogens have been reported (Hine, 1997; Diggles et al., 2002; Hine, 2002). Culture of Pacific oysters in New Zealand is considered unlikely to pose a threat to naturalized conspecifics or other species. Elsewhere, however, Pacific oysters have carried pathogens following human transportation. For example, nocardiosis, reported from Pacific oysters and *O. edulis* (Bower, 2006b) is caused by the bacterium *Nocardia crassostreae* which is thought to have originated in Japan and then spread to the west coast of North America with Pacific oysters (Straus et al., 2008).

The Pacific oyster appears to be more resilient to the significant diseases (Elston, 1993; FAO, 2006a) suffered by other oysters. For instance, it is partially resistant to *Perkinsus marinus* (Bower, 2006b) which ravages *C. virginica*. Similarly, in comparative challenges with *Mikrocytos mackini* (Bower, 2007a), Pacific oysters appear more resistant than other oysters, and *Haplosporidium nelsoni* appears to have greater pathological impact on *C. virginica* than *C. gigas* (Bower, 2007b). The decline of *C. virginica* in the eastern United States due to over-harvesting (Mackenzie, 1996) has also been in part attributed to *H. nelsoni* and *P. marinus* that may have been introduced with Pacific oysters (Carnegie, 2005). The protozoan parasite *Marteilia refringens*, although thought to have occurred in Pacific oysters, has been confirmed in oysters such as *C. virginica*, *O. edulis*, *O. chilensis*, and non-ostreid bivalves (Bower, 2007c).

The apparent advantage to aquaculture of Pacific oysters being relatively disease-resistant also presents a liability in that this species potentially provides an asymptomatic reservoir of pathogens that could be more damaging to other oysters and bivalves. Thus, its higher resistance might offer advantage or disadvantage depending on context. It is apparent that even where disease in oysters is reasonably well known, the likelihood and consequences (e.g. enhanced spread or virulence) of disease transmission from cultured stock to natural ecosystems is incompletely understood to the extent that a precautionary approach is warranted. Although Pacific oysters appear relatively disease-resistant, this species potentially carries a number of virulent pathogens that should be screened out before stock is moved. Safeguards are also justified for minor oyster species. *C. ariakensis*, for example, can show resistance to *P. marinus* (Powers, 2006), while *C. ariakensis* from its home range (East Asia) has harboured other *Perkinsus* species as well as three strains of herpes virus and several other pathogens (Moss et al., 2007) that should be excluded from any population intended for translocation. Given evidence that *C. gigas* may hybridize with other *Crassostrea* species (e.g. Huvet et al., 2004; Powers, 2006), consideration of changed disease susceptibility through hybridization is warranted. Depressed performance of *M. edulis* × *M. galloprovincialis* hybrids is documented by Beaumont et al. (2004), and Fuentes et al. (2002) report their lower hybrid viability when challenged by infection with *M. refringens*.

5. Synthesis of ecological effects and evaluation of relative risks

5.1. Rationale and approach

To inform further research and management, it is useful to consider the relative importance of the different ecological effects of elevated oyster aquaculture. The benthic impacts of elevated culture are well documented by comparison with many of the other interactions between cultivation and the environment. Nonetheless, from the information presented in this paper it is evident that the broad range of key ecological effects is sufficiently recognized that the potential for adverse consequences can be evaluated in a relative context. The qualitative risk ranking method that is widely used in risk assessment (Burgman, 2005), and which has previously been used to assess aquaculture effects (Crawford, 2003), provides a useful screening tool for understanding relative risk. The method involves applying subjective scores to both the relative likelihood that a particular effect will occur, and the magnitude of its consequences.

The judgement of consequences in ecological risk assessment often includes notions of the severity, extent and reversibility of effects (e.g. Suter, 1990; Crawford, 2003; Serveiss et al., 2004). These three criteria were made explicit by Emmett (2002) in relation to shellfish aquaculture, and are adopted in the present paper (Table 1). Hence, for each of the issues identified for elevated oyster culture (i.e. reflected in the section sub-headings throughout the paper), we evaluated relative ecological risk as low, medium or high in relation to: (i) the severity of adverse effects, without consideration of their

Table 1

Categories and scores used to assess the relative ecological significance of effects from elevated oyster culture, and level of knowledge on which the assessment is made.

Consequence category	Consequence score		
	Low	Medium	High
Severity of effect ^a	Minor	Moderate	Major
Spatial extent of effect	Local scale (<100 m from culture structures)	Bay-wide (100 m–1 km from culture structures)	Regional (>1 km from culture structures)
Duration of effect	Short-term (abates within <1 year)	Medium term (continues for 1–5 years)	Long term (continues for >5 years and may be irreversible)
Knowledge base	Based on perception or inference from related studies	Based on limited information on effects of elevated culture	Specific effects of elevated culture well known

^a Severity was assessed according to criteria previously used for shellfish aquaculture, and by discussion and consensus among the assessors (see text).

spatial extent or duration; (ii) the spatial extent of effects from site-specific to regional scales; and (iii) the duration of impact, in terms of the length of time effects would persist if farming operations were ceased and structures removed (Table 1). Issues were scored independently even though they may be inter-related; for example the effects of habitat creation were scored separately from (and did not include) the effects of fouling pests. Severity was assessed in relation to qualitative criteria used elsewhere for shellfish aquaculture (Emmett, 2002; Crawford, 2003) and considered the potential for adverse ecological changes to populations, communities and ecosystems in terms of structure (e.g. abundance, diversity, dominance) or function. The likelihood of adverse effects was scored in five categories (highly unlikely, unlikely, possible, probable, almost certain). The potential for the greatest adverse effect in a relative sense arises where there is a very high likelihood of a major ecological change that is irreversible and widespread. Note that as the focus of the assessment was on adverse effects, any effects that were regarded as positive or beneficial were scored as low risk (i.e. low likelihood and consequences of an adverse impact).

Scores against the consequence and likelihood criteria were made by three of the paper authors (Forrest, Keeley, Hopkins) based on the information herein and their individual experience. Although some correlation in assessor views was expected, for the purpose of providing guidance on relative risk we did not consider that canvassing a broader expert group was necessary. Obviously, actual levels of risk for most of the issues described in this paper will be context and scale-dependent, for example relating to site-specific factors such as the intensity of oyster farming in a given area, the sensitivity of the receiving environment, the presence of pre-existing stressors, and the extent to which mitigation of any adverse effects is undertaken. Hence, we provide risk intervals as a measure of the variability or uncertainty regarding effects (Burgman, 2005), rather than point estimates of risk as previously undertaken for shellfish aquaculture (e.g. Crawford, 2003). We recognize that it is desirable to have measurable endpoint criteria for the narrative categories of severity in Table 1 (Suter, 1990); however, we note that no clear and unambiguous standards for ecological change exist. Hence, to reduce discrepancies in scoring due to linguistic uncertainty and ambiguity with respect to the categories used (Regan et al., 2002), the three assessors independently assigned their range of scores, discussed reasons for differences, and reached a final range by consensus.

The five categorical scores of likelihood were converted to values from 1 to 5 (highly unlikely to almost certain), while severity, spatial extent and duration were scored as 1 (low), 2 (medium) or 3 (high). The calculation of consequences was treated as additive across these three categories (*severity + extent + duration*), and risk calculated as *likelihood × consequences*, with a maximum possible score of 45. For each issue, interval arithmetic was used to calculate the risk interval as the range from minimum to maximum values scored by the three assessors. We make no attempt to rank risks for each issue in terms of their acceptability, as this is inherently a value judgement that will differ from person to person and among different cultures. Furthermore, we emphasise that our purpose

here is to provide a screening tool for ascertaining the risk of adverse effects for the different issues *relative* to each other, and to identify areas of potential concern for which greater understanding or quantification may be desirable.

5.2. Key findings

Perhaps the most interesting point that arises from the risk assessment (Fig. 3A) is that the role of elevated oyster culture in the spread of pest organisms emerges as being particularly significant. This finding is consistent with an aquaculture risk assessment described by Crawford (2003) for Tasmania, and also with the general view that inadvertent pest introduction is one of the more significant issues associated with aquaculture in estuaries (DeFur and Rader, 1995). The reason is that, by comparison with all other issues, the spread of pest organisms by oyster farming can occur at regional scales (e.g. as a result on seed-stock transfer) potentially leading to ecologically significant and irreversible changes to coastal ecosystems (Elliot, 2003). Although, management approaches may be developed to minimize any pest risks that are considered unacceptable (e.g. treatment of seed-stock before regional transfer), there are few examples where such strategies have been completely effective (Piola et al., 2009). Furthermore, the non-target effects of control methods may also need to be considered (e.g. Dumbauld et al., 2006; Mallet et al., 2006; Locke et al., 2009). By comparison with pest organisms, the lower score but relatively wide risk interval for disease reflects the fact that this is not generally a significant issue for natural populations or ecosystems in the case of the dominant culture species (Pacific oysters), but may be important for other cultivation species (Fig. 3A).

Despite the benthic effects of elevated oyster culture being relatively well-studied (Fig. 3B), the potential for adverse effects was judged as intermediate among the range of scores that were assigned across the different issues (Fig. 3A). While the effects of biodeposition and farm debris can be among the more obvious effects of oyster farms (where the latter is unmanaged), the ecological implications are relatively localized. Although some benthic effects (e.g. organic enrichment) may abate over time scales of several months to a few years, accumulated shell and debris could (unless removed) lead to long-term changes in estuarine habitat structure. The effects of contaminants, adverse effects on water quality and effects on marine mammals had the lowest risk scores (Fig. 3A), as the likelihood of adverse effects was considered very low even though the knowledge base was minimal (Fig. 3B). However, in the case of marine mammals we recognized that a very low likelihood interaction could have significant consequences if critical habitat or endangered species were adversely affected. Risks arising from inter-related issues of altered nutrient cycling and SPM received intermediate risk scores but relatively wide intervals, indicating that effects can be more pronounced where large scale intensive cultivation occurs (Fig. 3A,B). Crawford (2003) expressed the view that effects on other filter-feeders as a result of food depletion by oyster cultivation were unlikely, as oyster farmers had an economic incentive to keep stocking densities below carrying capacity.

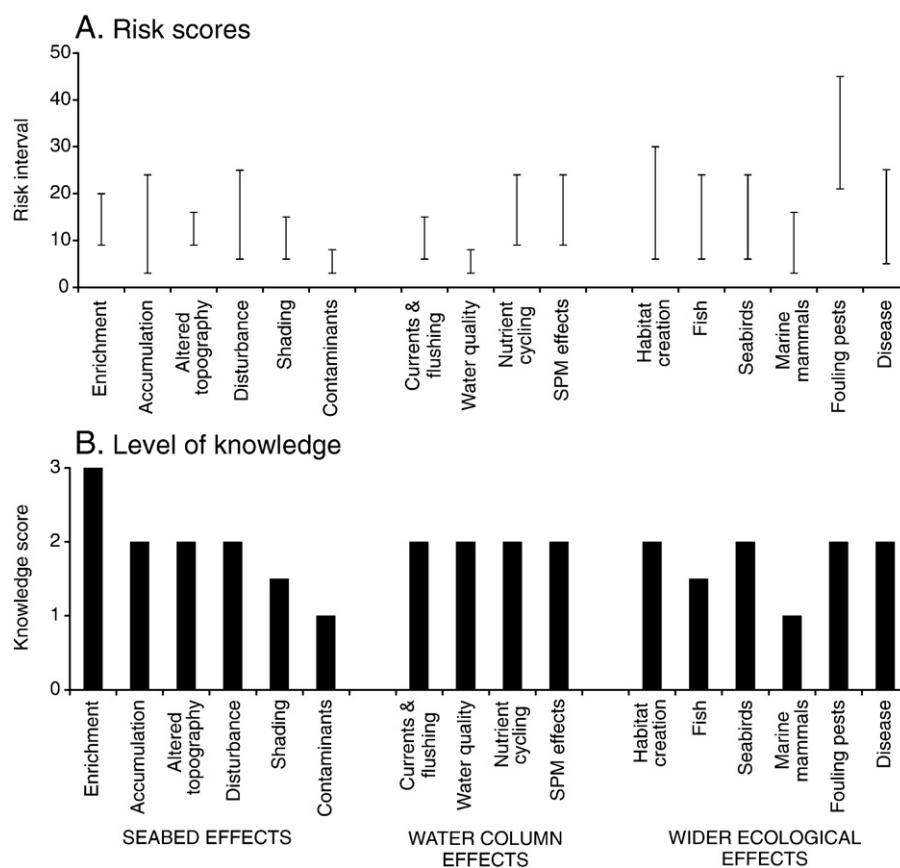


Fig. 3. Summary of: A. relative risk intervals; and B. knowledge scores, based on the consensus opinion of three assessors, for the range of ecological issues discussed in this paper.

The wide interval scored for habitat creation reflected the consensus that the well-recognized effects associated with aquaculture (e.g. local increase in biodiversity, provision of fish habitat) can be regarded as beneficial (reflected by the low end of the risk interval), yet the functional role of extensive areas of artificial habitat is poorly understood but has the potential to lead to adverse consequences (reflected as the high end of the risk interval). As an example of the latter, the assessors discussed a general scenario in which artificial habitat enhanced recruitment of an important predator with potential to cause cascading effects in adjacent natural ecosystems (e.g. described for floating piers in the case of the common jellyfish *Aurelia aurita*; Miyake et al., 2002). Where the effect of habitat creation on fish and seabirds has been specifically considered there is little evidence of significant adverse effects, but recognition that there is potential for such effects depending on species and context.

Overall, with the possible exception of pest species, the generally low to intermediate risk scores assigned across the issues largely concurs with the review of Dumbauld et al. (2009) who concluded that bivalve culture effects in US West Coast estuaries tended to be primarily localized and short-term, and not associated with larger scale ecosystem changes. In relation to shellfish aquaculture in New Zealand, Keeley et al. (2009) suggested that societal views on acceptability were likely to constrain development to a level that minimized the risk of significant ecosystem-wide effects. Nonetheless, it should be acknowledged that unrecognized estuary-wide or cumulative effects could have already occurred from some oyster farm developments, or could arise, for example: (i) in situations of high intensity oyster farming (e.g. in enclosed embayments dominated by oyster farms), or (ii) because of the occurrence of baseline ecological values of high importance. Without a comprehensive knowledge of baseline conditions and subsequent changes post-farm development, many of the wider or ecosystem-level impacts

described in this paper would be difficult to clearly determine retrospectively. Some uncertainty regarding effects is inherent in the wide risk intervals in Fig. 3A. For many of the issues the width of these risk intervals also reflects scale or context dependence. Wide intervals are inevitable when assessing the issues in a general context as in this paper, but may be reduced by evaluating specific culture sites and scenarios. Similarly, risk intervals may be reduced by disaggregating the issues (Burgman, 2005), for example by separately evaluating the positive and negative effects of habitat creation.

6. Conclusions and future directions

It is evident from recent reviews that the research focus and state of knowledge for elevated oyster culture described in this paper largely parallels that for other cultured bivalve species (and to some extent finfish) and other cultivation methods (e.g. McKindsey et al., 2006; Forrest et al., 2007b; Dumbauld et al., 2009; Keeley et al., 2009). Whereas the severity of some effects (e.g. biodeposition) may be quantitatively greater for other species or methods, there is considerable overlap in the ecological issues. As evident in this paper, although the general effects of elevated oyster culture are known and their relative ecological significance can be evaluated, there are still knowledge gaps and areas of uncertainty. The focus of previous research on assessment of benthic impacts (and phytoplankton depletion to a lesser extent) has resulted in other issues, which are arguably more important or less easy to manage, being overlooked. The association between oyster culture and the secondary spread of pest species, which could have significant non-local and irreversible consequences, is a case in point. Clearly, there is a need to redress the balance of effort in future studies. This could include, for example, site-specific risk profiling for actual and potential pests (e.g. assessment of the likelihood that high risk pest species will establish), estimation of

the significance of pest spread by oyster farming pathways relative to other sources of risk (e.g. vessels), and consideration of the feasibility of management (Taylor et al., 2005; Forrest et al., 2006).

Even though effects on the seabed are comparatively well understood and recognized for most types of aquaculture, there are nonetheless an overwhelming number of descriptive studies. There is still a need for greater application of model-based approaches to understand and predict the magnitude of effects as a function of key environmental (e.g. flushing characteristics) and farming-related (e.g. stocking levels, farm size and age, farming method) factors (e.g. DEPOMOD; Cromey et al., 2002; Weise et al., 2009). Similarly, there is scope for manipulative experimental approaches to elucidate for these same factors the relative importance of the key mechanisms that lead to benthic effects (e.g. sedimentation, enrichment, physical disturbance, shading, habitat creation). Acquisition of such knowledge would provide guidance for managers by identifying the types of environments or practices that allow oyster farming to be carried out with minimal impact, especially in relation to direct habitat change beneath cultures.

Research to address many of the complex issues where information gaps are evident (e.g. water column effects, functional changes, effects on higher trophic level animals) will require greater understanding of ecosystem processes, many of which occur beyond the immediate environment of the cultivation area (e.g. changes to food-web pathways). While modelling and related approaches have been undertaken to evaluate trophic effects from culturing oysters (Leguerrier et al., 2004; Lin et al., 2009) and other forms of bivalve aquaculture (e.g. Jiang and Gibbs, 2005; Anderson et al., 2006), the large amount of data required for reliable model estimates may limit their general utility outside specific case study areas. Hence, progress with understanding some of these complex issues will probably be slow, as it will require fundamental coastal ecosystem research in a range of environments. In the meantime, it is apparent that although there is some evidence of bay-wide ecological changes as a result of intensive intertidal shellfish cultivation, there appear to have been no catastrophic consequences.

Furthermore, primarily as a result of societal expectations, regulators and industry are increasingly managing or mitigating the potential for adverse effects from aquaculture in a comprehensive manner that addresses the range of ecological risks described in this paper, for example through the development of codes of practice and management plans (e.g. EPA, 2005; Taylor et al., 2005). Arguably, cultivation effects should be considered from an even broader perspective that recognizes the ecological changes resulting from cultivation collectively. When the range of effects is considered as a whole it could be argued that some nominally adverse effects may be compensated to some extent by more positive effects. For example, although natural seabed sediments and benthos may be altered beneath cultivation structures, benthic production may increase. Together with the creation of novel habitat, such changes may benefit some fish and bird species and provide a range of other beneficial ecosystem services such as local enhancement of biodiversity. More broadly, we suggest that management planning and responses to the development of oyster and other shellfish aquaculture in estuaries should be made in relation to other sources of environmental risk, and recognize the cumulative effects of anthropogenic activities in estuarine systems at a bay-wide or regional scale (e.g. Anderson et al., 2006), so that the effects of aquaculture are placed in context.

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