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Assessing Marine Habitat Sensitivity: A case study with eelgrass (*Zostera marina* L.) and kelps (*Laminaria, Macrocystis*)

Évaluation de la sensibilité de l'habitat marin : une étude de cas sur la zostère marine (*Zostera marina* L.) et des laminaires (*Laminaria*, *Macrocystis*)

Herb Vandermeulen

Department of Fisheries and Oceans, Maritimes Region
Marine Environmental Sciences Division
Bedford Institute of Oceanography
PO Box 1006, Dartmouth, NS B2Y 4A2

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ABSTRACT

The definition of ‘habitat sensitivity’ used in this paper follows the ICES (2002) definition - “Habitat sensitivity can be defined in relation to the degree and duration of damage caused by a specified external factor. Sensitivity may refer to structural fragility of the entire habitat in relation to a physical impact, or to intolerance of individual species comprising the habitat to environmental factors, such as exposure, salinity fluctuations or temperature variation.” The objective of this working paper is to quantify the ‘sensitivity’ of selected marine macrophytes (eelgrass and kelps) against various chemical, biological and physical factors. Thresholds at which the plants begin to suffer are tabulated.

Both eelgrass and kelps are sensitive habitats, and eelgrass is more sensitive than kelp. More studies are required to help define kelp sensitivity accurately.

Present finfish cage aquaculture practices in Canada have the potential to negatively impact both eelgrass and kelps (eelgrass in particular). A ‘zone’ model is presented to help guide future research on this topic.

RÉSUMÉ

La définition de « sensibilité de l’habitat » utilisée ici est la même que le CIEM (2002). « La sensibilité de l’habitat peut être définie en terme du degré et de la durée des dommages causés par un facteur externe identifié. La sensibilité peut avoir trait à la fragilité structurelle de l’habitat entier en relation avec l’impact physique ou à l’intolérance des espèces individuelles constituant l’habitat à des facteurs environnementaux, comme l’exposition, les fluctuations de la salinité ou les variations de température (traduction libre). » L’objet de ce document de recherche est de quantifier la « sensibilité » de quelques macrophytes marins (zostère marine et laminaires) à divers facteurs chimiques, biologiques et physiques. Les seuils auxquels ces plantes marines commencent à montrer des signes de stress sont présentés sous forme de tableaux.

Les gisements de zostère marine et de laminaires sont des habitats sensibles, alors que la zostère marine est plus sensible que les laminaires. D’autres études doivent être menées pour aider à définir précisément la sensibilité des laminaires.

Les pratiques actuelles d’élevage de poissons en cage au Canada peuvent avoir des incidences nuisibles sur la zostère marine et les laminaires (la zostère en particulier). Un modèle « zonal » est présenté pour aider à orienter les recherches futures sur ce sujet.

INTRODUCTION

Sensitivity

Marine habitat can be defined as a set of physical, chemical and biological conditions which are conducive to the survival of a population of organisms. The organisms use that particular marine space for all or part of their life history for the purposes of feeding, migration, refuge, reproduction, etc[1].

The core question is 'What makes a particular marine habitat "sensitive"?' The author was unable to find a formal definition of sensitivity within Habitat Management or *Oceans Act* program documents[2]. However, a consensus was reached during the national finfish aquaculture peer review meeting (Institute of Ocean Sciences, Sidney, BC – February 22 to 25, 2005) to use the ICES definition for habitat sensitivity:

> "Habitat sensitivity can be defined in relation to the degree and duration of damage caused by a specified external factor. Sensitivity may refer to structural fragility of the entire habitat in relation to a physical impact, or to intolerance of individual species comprising the habitat to environmental factors, such as exposure, salinity fluctuations or temperature variation" (ICES 2002).

The ICES definition is consistent with the United Nations International Maritimes Organisation (IMO) 'Particularly Sensitive Sea Area' (PSSA) terminology. A PSSA is defined as:

> "an area that needs special protection through action by IMO because of its significance for recognized ecological, socio-economic or scientific reasons and because it may be vulnerable to damage by international shipping."[3]

The IMO views a sea area as sensitive if a physical (and sometimes chemical) factor, international shipping, may damage it.

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[1] The *Fisheries Act* is quite specific in its definition, S34.(1) - "fish habitat" means spawning grounds and nursery, rearing, food supply and migration areas on which fish depend directly or indirectly in order to carry out their life processes

[2] DFO documents do consider habitat sensitivity from time to time, but loosely. For example, Pacific Region's 'Guidebook: Environmentally Sustainable Log Handling Facilities in British Columbia.' classifies habitat as red, yellow or green in order of decreasing productivity and propensity for being "biologically sensitive to disturbance". Kelps and eelgrass are cited as examples of sensitive habitat, but the rational for this designation is not provided. See http://www-heb.pac.dfo-mpo.gc.ca/publications/pdf/274124.pdf

[3] Annex 2, Paragraph 1.2 of the IMO Assembly Resolution A.927(22) "Guidelines for the designation of special areas under MARPOL 73/78 and guidelines for the identification and designation of particularly sensitive sea areas"

The premise of this working paper is that sensitive habitats are those which are not very common and only exist within a relatively narrow range of physical, chemical and biological conditions (i.e. habitats which are vulnerable to changes in those conditions over time). For example, a hypothetical coastal marine habitat which can only be found on a cobble bottom in a salinity of 10 to 20‰ and a current regime of <20 cm s^{-1} might be considered 'sensitive.'

The terms 'rare and fragile' could be used to describe a very sensitive marine habitat. However, biogenic habitat like macrophyte beds or sponge and bivalve reefs may be rare in a region simply because the organisms are at the edge of their distribution range. Biogeography should not be used as a trump card to force a 'sensitive' designation.

"Critical habitat" should not be confused with the concept of "sensitive habitat". Critical habitat refers to habitat that is important to the survival of a population of organisms, as in Canada's *Species at Risk Act*:

> ''critical habitat'' means the habitat that is necessary for the survival or recovery of a listed wildlife species…..[4]

"Sensitive habitat" refers more to the chances of survival of the habitat itself, rather than the species dependent upon that habitat.

The objective of this working paper is to quantify the 'sensitivity' of selected marine macrophytes (eelgrass and kelps) against various chemical, biological and physical factors. Thresholds at which the plants begin to suffer will be tabulated.

Aquaculture activities may or may not influence these factors to the detriment of macrophyte growth and survival. The potential influences of aquaculture (or any other human activity) on marine macrophytes should be assessed on a case by case basis (Chambers et al. 1999).

Eelgrass

Eelgrass (*Zostera marina* L.) is a vascular marine macrophyte found rooted in sandy or muddy substrates on all three Canadian coastlines (den Hartog 1970, Figure 1)[5]. The plants can form extensive subtidal, perennial beds widely recognized as important nearshore habitat for juvenile (and adult) invertebrates

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[4] *Species at Risk Act* S2.(1)

[5] *Ruppia maritima* L. is the other broadly distributed seagrass in Canada (Short et al. 2001). The plants are rather small and occur in the upper intertidal or in salt marshes. The west coast also has *Zostera japonica* Ascherson & Graebner (an introduced species), *Phyllospadix scouleri* Hooker and *P. torreyi* S. Watson (Short et al. 2001). *Phyllospadix* is a relatively rare, highly specialized form of seagrass found attached to rocks on wave tossed shores. *Zostera japonica* are small, mainly intertidal plants frequently of annual habit - similar to an intertidal form of *Z. marina* on the east coast, and *Z. noltii* Hornemann in Europe.

and fish (Short and Wyllie-Echeverria 1996; Chambers et al. 1999). The beds provide cover from predation, reduce local current regimes (allowing for settlement of organisms) and increase secondary productivity by adding to local habitat complexity and surface area (Chambers et al. 1999; Boström et al. 2002; Duarte 2002; Laurel et al. 2003).

The presence or absence of eelgrass seems to follow a narrow range of conditions, however. If salinity or temperature is too high, the plants become susceptible to disease. If currents are too strong the plant's rooted rhizomes become exposed and the individual leaf bundles (turions) will be washed away. If water column nutrient concentrations are too high the plants will waste away due to shading by increased phytoplankton and epiphyte loads. If sediment bioturbation rates are too high seedlings (or even adult plants) will not establish in the area. *Zostera* appears to be both an important and a sensitive habitat (Short and Neckles 1999).

Kelps

Seaweeds are also important marine macrophytes for generating nearshore habitat for fauna. The algae, particularly larger forms such as kelps, provide cover and structure – as well as a food source for a variety of herbivores (Chambers et al. 1999). Dissolved and particulate organic material from kelp thalli can be an important source of carbon and nutrients for detrital food chains (Fredriksen 2003).

Seaweeds vary widely in their 'sensitivity' to environmental conditions. Some appear to thrive under degraded and extreme conditions (e.g. the green algae *Ulva* and *Enteromorpha*); while others appear to have far more specific requirements (e.g. many of the deeper water foliose red algae). Seaweeds are individually plastic and very ecologically diverse as a group. It is difficult to determine which environmental conditions lead to the presence or absence of an algal population at a particular site (Lobban and Harrison 1994).

The kelps, large members of the brown algae (Phaeophyta), do appear to consistently occur as monospecific stands or beds under a relatively predicable set of conditions (i.e. subtidal, rocky bottom, moderate temperature and presence of currents). Hence, it should be possible to explore environment / abundance issues with kelps, and provide some guidance on kelps as marine habitat.

In Canada, the kelps (Figure 2) include the genera *Laminaria, Nereocystis, Macrocystis, Agarum, Alaria, Hedophyllum, Costaria, Egregia, Eisenia, Pterygophora, Dictyoneurum, Dictyoneuropsis,* and *Postelsia.* About half of these genera are relatively patchy in distribution (i.e. not that common) and most are restricted to the west coast. These macrophytes are large (1 to over 10m) and relatively robust in form compared to seagrasses. The genera are distinguished morphologically primarily by differences in stipe and blade (or lamina) size and shape. Our discussion will focus on the most common genus, *Laminaria*[6], and the largest, *Macrocystis*[7].

PART 1 - EELGRASS

Chemical Factors

Nutrient loading

Eutrophication is defined elegantly by Nixon (1995) as an increase in the rate of supply of organic matter to an ecosystem. Concomitant with that supply of organic matter is nutrients. Marine eutrophication is a relatively new anthropogenic phenomenon which has been growing over time (Nixon 1995). Short and Wyllie-Echeverria (1996) conclude that anthropogenic nutrient inputs to coastal areas is the primary cause of the present world-wide decline in seagrasses. The decline will likely accelerate in the future (Duarte 2002).

Point sources of nutrient loading are not routinely permitted within sensitive marine habitats. It would be unusual to site a Canadian aquaculture facility in an eelgrass bed, for example. However, point and non-point sources of nutrients can cause elevated nutrient concentrations within a defined water mass (bay, estuary, eddy, etc.), and that water mass may be large enough to encompass a number of sensitive habitats.

a) Direct effects

Elevated nutrient concentrations can have *direct* physiological effects on marine plants (e.g. elevated tissue residue concentrations, growth of thallus and development of reproductive tissues). Eelgrass is very effective in removing nitrogen from sediment and the water column for thallus growth (Pedersen and Borum 1992). *Zostera* growth can be reduced by naturally occurring nutrient limitation (Boström et al. 2004).

Lee et al. (2004) report that area normalized leaf mass (mg dry weight cm^{-2}) may be the best index of *Zostera marina* response to estuarine eutrophication. This index was found to be superior to more classically used morphometrics such as number of leaves per shoot, blade width and leaf length.

Burkholder et al. (1992) found that eelgrass may be affected by direct toxicity at even ‘low’ nitrate loading rates of 3.5 μM NO_3^--N day^{-1}. The nitrate appeared to damage the plants’ meristems and led to leaf loss. Water column nitrate toxicity was also reported by Touchette et al. (2003). Burkholder et al. (1994) conclude

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[6] *Laminaria* occurs on all three of Canada’s coasts. Many different species exist, and the taxonomy of this group changes over time. *Laminaria groenlandica (bongardiana)* Rosenvinge (west coast and Arctic), *L. saccharina* (L.) Lamouroux (all three coasts), *L. digitata* (Huds.) Lamour. (east coast), *L. longicruris* Bach.Pyl. (east coast and Arctic), and *L. solidungula* Agardh (arctic and east coast) are among the more commonly recognized species.

[7] *Macrocystis* is restricted to the west coast. *Macrocystis integrifolia* Bory is in British Columbia.

that elevated nitrate levels in nearshore waters due to eutrophication (c.a. 5 to 10 µM NO_3^- -N day^{-1}) will have a direct adverse effect on *Zostera marina.*

Interestingly, the $\delta^{15}N$ tissue residues in *Z. capricorni* reflected the source of nitrogen loading in Moreton Bay, Australia (Udy and Dennison 1997). It was possible to discriminate between prawn-farm aquaculture and sewage effluent nitrogen sources from the stable isotope tissue residues in the plants.

b) Indirect effects

The *indirect* effects of elevated nutrient concentrations in a water column (i.e. eutrophication) include the following:

i) elevated turbidity due to stimulation of phytoplankton growth

The eutrophication of coastal waters can lead to the stimulation of phytoplankton growth and a subsequent increase in water column turbidity. The turbidity effect of eutrophication can result in reduced water column light levels which negatively impact eelgrass and macrophyte growth (Pedersen 1995; Kemp et al. 2004, see ‘Light levels’ in Physical Factors section below).

ii) increased algal epiphyte load

Under normal conditions, grazers remove epiphytic algae from seagrass leaves and improve growing conditions for those macrophytes (Hily et al. 2004). However, under eutrophic conditions, epiphytes and macroalgae can seasonally outgrow grazing pressure (Burkholder et al. 1992), or selective grazing pressure can allow certain epiphytes to bloom (Duffy and Harvilicz 2001). The presence of epiphytes is detrimental to *Zostera*. For example, Williams and Ruckelshaus (1993) report that increasing epiphyte load from 50 to ~200 mg per eelgrass shoot reduced shoot growth rates from ~ 1 cm $shoot^{-1}$ d^{-1} to 0.2 cm $shoot^{-1}$ d^{-1}.

The inhibitory effect of epiphytes comes about by shading (Burkholder et al. 1992; Short et al. 1995; Hauxwell et al. 2001; Brush and Nixon 2002; Kemp et al. 2004), interference with nutrient uptake (Hauxwell et al. 2001), interference with carbon uptake (Sand-Jensen 1977) and loss of the biomechanical integrity of the host plant (Cancemi et al. 2003). The issue of shading and low light effects is taken up in more detail in the Physical Factors section below.

iii) alterations in geochemistry

As noted above, eelgrass rhizomes are effective in removing nutrients from sediment. If *Zostera* dies back in an area due to eutrophication of the water column, sediment nutrient concentrations are likely to increase.

Eelgrass can reduce sediment pore water hydrogen sulphide concentrations in the daytime (Hebert and Morse 2003). *Zostera* can also buffer broader aspects of sediment geochemistry in the face of moderate eutrophication, but the plants’ capacity to moderate can be overrun (de Wit et al. 2001).

Eutrophication can cause elevated carbon content in sediment, lowered oxygen concentrations, elevated hydrogen sulphide concentrations, negative redox potential, mobilization of metals, mobilization of nutrients, etc. (Rozan et al. 2002). These changes may result in negative effects for rooted marine plants like seagrass (e.g. Cancemi et al. 2003), or even seaweeds (via additional nutrient release into the water column).

Eelgrass rhizomes are protected from damage by hydrogen sulphide in sediment pore water via a supply of oxygen from the leaves to the rhizomes along hollow channels called lacunae. At water column oxygen levels of below 20% of air saturation, the lacunal system cannot provide enough oxygen for sulphide re-oxidation, and the tissue concentration of hydrogen sulphide in the rhizomes rises rapidly (Pedersen et al. 2004).

Terrados et al. (1999) experimentally altered sediment geochemistry with the addition of sucrose. The subsequent increase in pore water sulphide levels (over 70 μM H_2S) and reduction in sediment redox potential caused reduced leaf growth in *Z. marina* over time*.*

Goodman et al. (1995) demonstrated that the eutrophication effects of elevated sediment sulphide and reduced light availability were additive in their inhibitory effect on *Z. marina.* A combination of high sediment sulphide concentration (800 – 1000 μM) and low light (15% of solar irradiance) reduced photosynthetic rates to about one tenth that observed under high light (50% of solar irradiance) plus low sulphide (below 400 μM) conditions. Elevated sediment sulphide had the potential to reduce photosynthetic rates at any light level.

Williams and Ruckelshaus (1993) found a positive relationship between *Zostera marina* shoot growth rates and pore water ammonium concentration. The half saturation constant was 96 μmol L^{-1}, and no inhibitory effects were seen even at pore water ammonium concentrations ~2000 μmol L^{-1}. However, Kaldy et al. (2004) report that high sediment ammonium concentrations can be toxic to some vascular marine macrophytes.

Peralta et al. (2003) found that high porewater nitrate concentrations (20 mM) inhibited *Z. marina* growth*.* This corroborates the findings of Burkholder et al. (1992) and Touchette et al. (2003) on water column based nitrate toxicity. Under degraded conditions with excess nutrient loading, eelgrass may be replaced by algal mats / canopies (Hauxwell et al. 2001). Sfriso and Marcomini (1999) found that the sediment nutrient (nitrogen and phosphorus) recycling capability of *Ulva* algal mats was at least an order of magnitude lower than the capacity of *Zostera* dominated areas*.*

iv) shifts in macrophyte species composition

Shifts in species composition can occur along the eutrophication gradient. As nutrient loading increases, slow growing seagrasses and macroalgae are replaced by fast growing algae, with phytoplankton dominating at the highest loading rates (Duarte 1995).

Karez et al. (2004) exposed a series of six flow through mesocosms to enrichment from 1 to 32 μM dissolved inorganic nitrogen (with 0.06 to 2.0 μM dissolved inorganic phosphorus). Along this gradient, corticated filamentous algae tended to be highest at low nutrient levels with foliose algae predominating at increasing nutrient level. This effect was partially mediated by an increase in herbivore numbers at higher nutrient levels, preventing ephemeral algae from developing high biomass at high nutrient levels. *Ulva* (a foliose alga) dominated at the higher nutrient levels. Nitrate based eutrophication may especially favour the growth of green algae (*Ulva* or *Enteromorpha*) over eelgrass (Harlin and Thorne-Miller 1981).

Patricio et al. (2004) describe a eutrophication gradient in the Mondego estuary in Portugal. The non-eutrophic section had *Zostera noltii* meadows, *Z. noltii* was absent in the intermediate eutrophic section with periodic abundance of macroalgae and *Enteromorpha* blooms occurred regularly in the strongly eutrophic section. Cummins et al. (2004) used a field cage plot experiment in Australia to demonstrate that typical *Enteromorpha* bloom biomass (c.a. 4.5 kg wet wt m^{-2}) led to >50% reductions in seagrass (*Halophila ovalis, Z. capricorni, Ruppia megacarpa*) biomass in a meadow affected by the bloom.

Deegan et al. (2002) report that as nitrogen load increased in a series of estuarine ponds (16 to 1679 kg N y^{-1}) so did macroalgal biomass, along with decreased eelgrass shoot density and biomass, decreased fish and decapod abundance and biomass, and decreased fish diversity. Moreover, $\delta^{15}N$ values indicated that fish were not linked to a food web based on macroalgae, and fish grew better and had greater survivorship in eelgrass compared to macroalgal habitats. Over time, eelgrass meadows produce more plant biomass than macroalgal areas driven by eutrophication (Dolbeth et al. 2003).

Short and Burdick (1996) record a steady decline in *Zostera marina* in Waquoit Bay, Massachusetts over a five year period. The decline was related to housing development and subsequent groundwater nitrogen loading. The resulting eutrophication stimulated algae (epiphytes, macrophytes, and phytoplankton) which shaded the eelgrass.

Hauxwell et al. (2001) compared two estuaries in Waquoit Bay, one with a loading of 5 kg N ha^{-1} yr^{-1} and the other with 30 kg N ha^{-1} yr^{-1}. At the higher loading rate, a macroalgal canopy grew along the bottom which interfered with eelgrass growth. They identify a 9 – 12cm critical macroalgal canopy height at which eelgrass declines. Most of this effect was due to light limitation of eelgrass by macroalgal canopy shading, but unfavourable biogeochemical conditions were also generated.

Hauxwell et al. (2001) also present data from three estuaries which demonstrate that *Z. marina* will not be present when nitrogen loading rates are 300 kg N ha^{-1} yr^{-1} or higher. In general, nutrient loading rates of approximately 30 kg N ha^{-1} yr^{-1} will lead to substantial eelgrass loss (80 to 96% of bed area) and ≥ 60 kg N ha^{-1} yr^{-1} will cause total disappearance (Short and Burdick 1996; van Katwijk et al. 1999; Hauxwell et al. 2003). Both direct and indirect effects are probably the cause for this absence. Deep-water eelgrass populations appear to respond to the negative effects of eutrophication more predictably than shallow water populations (Frederiksen et al. 2004).

Low oxygen levels

A reduction in dissolved oxygen concentration in the water column can come about from eutrophication (due to a greater biomass of respiring organisms in the water), poor flushing or mixing of a water mass, elevated water temperature, high concentrations of dissolved salts in the water, the addition of organic material or other ‘oxygen demanding’ chemicals from a point or non-point source, and other factors.

Eelgrass rhizomes can frequently be found growing in sediment with low oxygen concentrations. The plants accomplish this by supplying oxygen to the rhizomes via a well developed system of air spaces (lacunae) connecting leaves to below sediment tissues. The lacunal system is more developed in plants growing in more anaerobic sediments (Penhale and Wetzel 1983).

Although seeds of eelgrass are capable of germinating under anoxic conditions (Churchill 1992), the seedlings will have unusual morphology. Holmer and Bondgaard (2001) also demonstrated that photosynthetic and growth rates of *Z. marina* thalli are inhibited under low oxygen conditions in the water column (<63 µM). Both photosynthesis and growth stopped if low oxygen conditions were combined with high sulphide concentrations in the water (100 – 1000 µM).

The meristematic region of eelgrass leaves will quickly go anoxic if the water column is anoxic. This may be a key factor in seagrass die-off under low oxygen conditions (Greve et al. 2003).

A four day long bout of aquaculture related bottom water anoxia in a lagoon in south France caused the complete disappearance of local *Zostera marina* meadows (Plus et al. 2003). Recovery was relatively rapid (9 months) due to a replete seed bank and high seedling survival rate.

Biological Factors

Herbivory

The type and number of herbivores that are present in a system can also be altered by eutrophication. Karez et al. (2004) reported that the abundance of the common periwinkle (*Littorina littorea* L.) increased significantly with nutrient enrichment in mesocosm studies.

Healthy, growing eelgrass blades and rhizomes are not typically eaten directly by invertebrates or fish in Canada[8]. The only Canadian herbivores which consume significant quantities of *Zostera* tissue are Canada Geese and other brandts. If eelgrass availability declines, geese numbers can drop (Seymour et al. 2002). Other herbivores grazing on the surface of eelgrass blades can cause damage, however.

The Rissoidae are a group of taxonomically difficult tiny snails. They occur on both temperate coasts. Fredriksen et al. (2004) report that an unusually high density (over 30 individuals per shoot) of *Rissoa membranacea,* a European species, caused leaf breakage and eelgrass bed decline in Skagerrak, southern Norway. The snails typically target epiphytic algae, but their high densities were causing epidermal damage in the *Z. marina* leaves*.*

Similarly, Zimmerman et al. (2001) discovered that the appearance of the commensal limpet *Tectura depicta* (not found in Canada) coincided with the decline of a large eelgrass bed in Monterey Bay, California. The limpets (at a density of 5 to 8 individuals per eelgrass shoot) were actively targeting the *Zostera* epidermis.

At unnaturally high densities in the laboratory, isopods will damage eelgrass (Williams and Ruckelshaus 1993). Different species of the isopod *Idotea* are known to scar and detach eelgrass blades via direct consumption. Duffy et al. (2001) report loss of aboveground biomass of eelgrass in mesocosms with *Idotea* densities of c.a. 100 individuals per square meter, similar to natural densities at the time of the experiment.

The presence of herbivores versus epiphytes may be mediated by current regimes. The density of the mud snail *Hydrobia ulvae* on eelgrass blades decreased rapidly as average current speed increased beyond about 10 cm s^{-1} in experimental flumes in the Wadden Sea (Schanz et al. 2002). The effect was a higher epiphyte load on blades from plants growing in higher current regimes.

Eelgrass seeds and seedlings may face different pressure from herbivores than mature blades. A number of invertebrates have the capacity to consume seeds and seedlings under experimental conditions, including the eastern mud snail *Ilyanassa (=Nassarius) obsoleta* and the hermit crab *Pagurus longicarpus* (Wigand and Churchill 1988). The extent of predation on seeds and seedlings in nature is not known, however.

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[8] Bak and Nojima (1980) report on a tropical sea urchin eating *Z. marina* in south west Japan. There is limited video evidence of urchins apparently consuming eelgrass in British Columbia (Patty Menning, DFO Habitat Management Biologist, pers. comm.)

Bioturbation

Bioturbation is the reworking or movement of sediment by organisms. Environmental impacts can lead to changes in bioturbation rates. For example, once a rooted marine macrophyte bed disappears from an area due to eutrophication, invertebrates can colonize the newly 'cleared' sediments and increase bioturbation rates (Philippart 1994). A shift in bioturbation rates can affect the future presence of *Zostera* via changes in the sediment 'seed bank' (number of viable seeds), or damage to seedlings or rhizomes (e.g. Townsend and Fonseca 1998).

The burrowing activities of an Atlantic deposit-feeding polychaete, *Clymenella torquata*, can serve to enhance the capture of *Zostera* seeds. When the worms occur at densities of 192 worms m^{-2} and greater, the seeds are more effectively trapped in the sediment. Changes in sediment topographic relief due to bioturbation are thought to be responsible (Luckenbach and Orth 1999). In the absence of this bioturbation, the seeds could be washed away and potentially 'lost' for recruitment purposes.

Alternatively, bioturbation can constrain the development of eelgrass beds. Backman (1984) discovered that once sand dollars (*Dendraster excentricus*) are established in an area (approximately 20 individuals m^{-2}), they can prevent colonization by eelgrass. The mode of inhibition was uprooting and erosion of rhizomes by the burrowing activities of the sand dollars. *D. excentricus* occurs in Pacific waters in Canada.

Thalassinid shrimp are strong bioturbators in the nearshore of the Pacific and Atlantic coasts. Dumbauld and Wyllie-Echeverria (2003) experimentally removed ghost shrimp (*Neotrypaea californiensis*) from a site in Willapa Bay, Washington with an application of the carbamate insecticide carbaryl (Sevin®). The removal of the shrimp allowed colonization of both *Z. marina* and *Z. japonica*. Normal shrimp densities of 100 m^{-2} prevented the establishment of *Zostera* via an inhibition of seedling survival and growth. Harrison (1987) saw similar inhibition of *Zostera* by the same species of ghost shrimp at similar order of magnitude densities in British Columbia.

Arenicola marina, an Atlantic lugworm, also reworks sediment to the point that *Zostera* expansion can be inhibited (Philippart 1994). Transplanted *Z. noltii* thalli disappeared (were buried) within 6 weeks at lugworm densities of 68 worms m^{-2}. *Hediste [Nereis] diversicolor* (an east coast rag-worm, other species of this genus occur on the west coast), also appears to hinder the expansion of *Z. noltii* (Hughes et al. 2000). Rag-worm densities of approximately 400 – 700 individuals m^{-2} appear to be sufficient to exclude *Z. noltii.* The worms inhibit the plants by breaking or damaging leaves on the sediment surface, damaging roots, and eating or burying seeds and seedlings.

Introduced species

The introduced European green crab (*Carcinus maenas*) routinely cuts *Zostera* shoots and shreds the plants sheath bundles on Canada's Atlantic coast. Crab densities of four or more per square meter can devastate a stand of eelgrass, causing one third to over two thirds of viable shoots lost within one week (Davis et al. 1998; David Garbary[9] unpublished results).

Reusch and Williams (1998) noted that experimental additions of the introduced mussel, *Musculista senhousia*, to eelgrass beds and transplant sites inhibited eelgrass rhizome elongation rates. Eelgrass rhizomes grew 40% less than controls when exposed to 800 g dry mass m^{-2} of *M. senhousia* in San Diego Bay, California. The source of interference was hypothesized to be mechanical; the mussels form a dense mat of byssal threads, debris and shell material which appears to inhibit rhizome elongation. Fragmented eelgrass beds were more likely to be affected than well established beds (Reusch and Williams 1999). *Musculista senhousia* has been introduced to British Columbia (Anonymous 1998).

Garbary et al. (1997) report an introduced green alga, *Codium fragile* ssp. *tomentosoides,* associated with depressions (erosional patches called 'blowouts') in an eelgrass bed on Canada's east coast. *Codium* has a particularly plastic growth pattern, and it can be found with its holdfast enclosing lengths of exposed eelgrass rhizome. Presumably this creates stress on the rhizomes due to the drag imposed by the *Codium* thallus, but this has not been tested in the field.

Pathogens

High temperature and salinity conditions (e.g. a warm, dry summer) can cause a slime mould to infest *Zostera marina* beds and wipe them out. van Katwijk et al. (1999) cite a number of declines in eelgrass populations related to the incidence of this wasting disease and elevated salinity. The effect may be exacerbated under low light conditions (Giesen et al. 1990).

The slime mould wasting disease pathogen is called *Labyrinthula zosterae* (Muehlstein 1989). Ralph and Short (2002) consider *L. zosterae* a primary pathogen of eelgrass, attacking healthy tissue. Salinities of 20 to 25 ‰ appear to reduce activity and allow eelgrass recovery.

If *Labyrinthula zosterae* covers more than 50% of a leaf blade of eelgrass, production essentially stops. Plants with leaves with >50% wasting index often drop their most infected leaves (Ralph and Short 2002). Hily et al. (2002) studied three *Zostera marina* beds in a high salinity regime (≥30‰) and found that a incidence of *Labyrinthula zosterae* of 20-25% did not cause significant long term damage to the eelgrass beds.

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[9] St. Francis Xavier University, Department of Biology, Antigonish, Nova Scotia

Marine pollution (eutrophication and toxic discharge) can increase the number of pathogens in a system and their impact (e.g. Danovaro et al. 2003). Hypothetically, the incidence of *L. zosterae* could increase under degraded environmental conditions.

Physical Factors

Light levels

Reduced water column light levels are noted as one outcome of eutrophication in the beginning of this paper. Eutrophication is just one mechanism that reduces light availability in a water column. Point and non-point sources of turbidity or coloured chemicals can be found both nearshore and offshore – there are natural and anthropogenic sources. Rivers dark with natural loads of dissolved humic substances can discharge into estuaries, offshore dredging and nearshore construction (e.g. Lee 1997) can create plumes of turbid water, and industries can discharge both coloured chemicals and particulate material.

The ‘footprint’ of support structures for marine activity (docks, wharves, floats, vessels, etc.) includes local shading of the bottom. This effect is not trivial if the support structure is large and the water is shallow.

Reduced water column light (due to turbidity or colour) harms *Zostera* growth / survival (Moore et al. 1996; Cabello-Pasini et al. 2003). Bricelj and Lonsdale (1997) describe detrimental shading of eelgrass by water column light attenuation due to brown tides (*Aureococcus anophagefferens,* the blooms do not appear to be related to eutrophication).

Shaded eelgrass growing in low-organic sediments appears to be incapable of assisting in the reoxidation of sulphides, leading to anoxic and sulphide laden pore water conditions which may further reduce growth and survival (Holmer and Laursen 2002).

The water column itself does not have to be ‘dark’ to shade marine macrophytes. Eelgrass and seaweeds can become directly shaded at their surfaces by a cover of epiphytes (see Biological Factors section above). Hauxwell et al. (2001) report that approximately 2 mg cm^{-2} of epiphytic material on *Z. marina* leaves can reduce leaf surface light levels by 31%. About 8 mg cm^{-2} of epiphytic material reduced surface light by 63%. Drake et al. (2003) found an epiphyte biomass of ~110 µg C cm^{-2} on eelgrass leaves could reduce photosynthetic rates by 49%. At that biomass, the epiphytes were absorbing about 40% of the light available to the eelgrass leaves at photosynthetically active wavelengths. Kemp et al. (2004) have developed a model to accommodate both water column light attenuation and epiphyte based light attenuation for calculating maximal depth limits for seagrasses.

If *Z. noltii* is shaded to 15% of ambient light levels, leaf loss rate increases dramatically and the leaf net growth rate becomes negative. 30% shading still allows for some growth (Philippart 1995). 12% of I_o (irradiation at surface) is considered 'marginally sufficient' for the growth of *Z. marina* (Moore et al. 1996). Short et al. (1995) consider 10 to 20% of surface light as the minimum light limit for eelgrass survival. The estimated daily compensation point of young *Z. marina* was calculated as 5.7% of sea surface light by Abe et al. (2003).

In a study calculating standard photosynthesis versus irradiance curves (P-I curves) for eelgrass, Marsh et al. (1986) found that the photosynthetic compensation point (oxygen production = oxygen consumption) occurred at about 3 µmol photons m^{-2} s^{-1} at 10ºC and about 17 µmol photons m^{-2} s^{-1} at 20ºC. Saturating light levels were at 36 and 78 µmol photons m^{-2} s^{-1}, respectively.

Peralta et al. (2003) consider 55 µmol photons m^{-2} s^{-1} to be 'subsaturating light' for *Z. marina*. Holmer and Laursen (2002) recorded reduced shoot density and leaves per shoot in spring collected eelgrass plants exposed to 20 – 25 µmol photons m^{-2} s^{-1} light levels. Fall collected plants were less sensitive to these reduced light levels.

Storm induced water column turbidity reduced light levels to near zero for more than three weeks over a coastal eelgrass bed in Baja California. The plants died after sugar and starch content in the leaves decreased by ~85% over that time span (Cabello-Pasini et al. 2002).

Salinity and temperature

Zostera marina is typically found under estuarine conditions. van Katwijk et al. (1999) discovered that plants from estuaries were negatively affected by 26‰ water and higher. Plants acclimated to higher salinities still showed negative effects if exposed to 30‰. Moreover, lower salinities appeared to protect estuarine acclimated plants from the negative effects of high nutrient loads. *Zostera noltii* also suffers mortality at higher salinities (Vermaat et al. 2000). Kerr and Strother (1985) demonstrated that *Z. muelleri* will continue to photosynthesise in low salinity waters, but photosynthesis does stop in fresh water.

Herman et al. (1996) discovered a correlation between a decline in eelgrass and reduced concentrations of silica in *Zostera* leaves (dissolved silica concentrations typically decline under eutrophic conditions due to algal uptake). However, a subsequent study determined that the eelgrass decline in this instance was not due to silica, but an increase in salinity in the area over time (Kamermans et al. 1999).

Elevated temperatures can weaken eelgrass and make it more susceptible to disease (Burkholder et al. 1992, see 'fungal and bacterial pathogens' section above). Greve et al. (2003) found that the meristematic region of eelgrass (near the base of the leaves) will go anoxic due to respiration demands at water temperatures above 30ºC. At elevated temperatures (ca. 28 - 30ºC), *Z. marina* will lose shoot weight, have smaller and fewer leaves, and shorter roots (Touchette et al. 2003).

The photosynthetic rate of eelgrass goes up with temperature, but rapidly drops off at about 30ºC (Marsh et al. 1986). Eelgrass leaf carbon budgets (respiration versus photosynthesis) are also likely to become negative at temperatures >25ºC and eelgrass grown at ≥25ºC dies off rapidly (Zimmerman et al. 1989).

Currents and scour

Zostera grows on soft bottoms that can be scoured out by currents. Even non-scouring current regimes may have a negative effect on plant growth, and the species in this genus prefer quiet waters. Increasing current velocity from 5 to c.a. 12.5 cm s^{-1} led to a linear reduction in shoot number in *Z. noltii* from over 3500 to less than 2500 m^{-2}, along with reductions in leaf length (Schanz and Asmus 2003).

Increasing current speed from 2 to 35-40 cm s^{-1} *increased* leaf production in *Z. marina* (Fonseca and Kenworthy 1987), and it appears that eelgrass needs about ≥16 cm s^{-1} of current for optimal conditions for photosynthesis (Koch 2001). Minimal current regimes may improve porewater geochemistry for seagrass growth (Koch 1999), or enhance nutrient uptake (Thomas and Cornelisen 2003).

Eelgrass is quite sensitive to wave action in shallow waters (van Katwijk and Hermus 2000; Koch 2001; van Katwijk and Wijgergangs 2004). Krause-Jensen et al. (2003) provide data which indicate that the upper limit of eelgrass on shore may be determined by wave exposure, with stronger exposure limiting the beds to deeper waters. Shallow beds exposed to wave action will exhibit variable shape and position over time (Frederiksen et al. 2004b).

As average current speeds increase, eelgrass beds tend to have a lower proportion of seedlings, distinct ridges may form at the outer (current side) edges of the bed while wave scoured depression (blowouts) may occur inside the bed and migrate through it, and the bed will tend to exhibit more vertical relief. Under high energy, erosional conditions eelgrass beds can take on a ‘leopard skin’ or even donut or U shape due to increasing size and number of blowouts. At near maximal current conditions for eelgrass, the beds will often turn into small, raised elliptical patches formed parallel to the current. The maximum current velocity regime for *Z. marina* is between 120 to 180 cm s^{-1}, although currents as low as ≤50 cm s^{-1} may have negative effects (Fonseca et al. 1983; Fonseca and Kenworthy 1987; Koch 2001).

An abrupt transition point appears to exist for *Z. marina* at that current speed leading to 50% plant cover, ~25 cm s^{-1}. Above that current speed, eelgrass is unlikely to occur as contiguous beds (Fonseca and Bell 1998).

In Nova Scotia, eelgrass can be frozen into the underside of ice which ultimately breaks up into large pieces and floats away. In an experiment to mimic this ice scouring and rafting, Schneider and Mann (1991) created bare patches in an eelgrass bed in spring which did not completely 'heal' even 14 months later. Recovery of the experimental patches was entirely based upon regrowth from the edges, no seedlings were observed. The ice effect has caused an annual form of eelgrass to develop in some Nova Scotian shallow water areas subject to ice scour (<25cm depth at low tide). These annual plants do not survive the winter, do not develop much below sediment biomass, have high reproductive effort and overwinter as seeds (Robertson and Mann 1984).

Sedimentation

Seagrass leaves add structure to the near bottom water column. The leaves act as a baffle, slowing down currents on a localized micro scale which allows for sediment trapping and stabilization (Heiss et al. 2000; Abdelrhman 2003). This physical alteration causes changes in local sediment composition and geochemistry. Dense eelgrass (*Z. marina*) growing in low or moderate current locations in temperate waters exhibits this influence quite strongly, while tropical seagrasses with a less aggregated habit may not (Mellors et al. 2002; van Keulen and Borowitzka 2002). Flow reduction increases with the density of eelgrass beds (Peterson et al. 2004).

If eelgrass is overwhelmed by a rapid sedimentation event, it does not survive burial particularly well. Mills and Fonseca (2003) demonstrate that *Z. marina* can only tolerate burial covering less that half of photosynthetic surfaces, and even burial to 25% of plant height leads to >50% mortality after 24 days.

Even if eelgrass is not buried by sedimentation, excessive amounts of particulate material settling on leaves can lead to mortality. The mechanism for damage appears to be reduced photosynthesis due to shading of leaves by the deposition of particulate material (Tamaki et al. 2002).

Effects of Aquaculture on Seagrasses

The report of Plus et al. (2003) has already been mentioned. They found that bottom water anoxia in the Thau Lagoon (South France) caused complete disappearance of local *Zostera* meadows after four days. The anoxia came from aquaculture activity, and "The triggering factor was the degradation of green algae and probably organic matter coming from aquaculture…" De Casabianca et al. (1997) determined that shellfish farming was the major source of eutrophication in the lagoon, providing nitrogen loading rates about 15 times the terrestrial inputs to the system. Loading came in the form of biodeposition and ammonia excretion.

Zostera (*Z. marina* and *Z. noltii*) were likely the original plant community in Thau Lagoon. With increasing eutrophication from shellfish aquaculture, *Zostera* was replaced by “opportunistic and nitrophilous species” *Ulva* and *Gracilaria.* In effect, the *Zostera* was “pushed” into less nutrient laden portions of the lagoon by aquaculture activities (De Casabianca et al. 1997b; De Casabianca et al. 2003). The Thau Lagoon work demonstrates that far field effects of aquaculture can harm eelgrass[10].

Posidonia oceanica (L.) Delile is an important Mediterranean and Adriatic seagrass. In the late 1990s, a number of publications appeared documenting fish farm impacts on *P. oceanica* (Delgado et al. 1997; Delgado et al. 1999; Katavic and Antolic 1999; Pergent et al. 1999). The impacts included the following:

- decreases in shoot density, shoot size, underground biomass and photosynthetic rate;
- total seagrass demise under cages and beyond (bay wide declines in meadow cover, most impacts <500m from cages);
- increased epiphyte load on the seagrass, attracting herbivores which cause further leaf damage;
- persistent seagrass decline even several years after the cessation of fish farming activities (due to excess of organic matter remaining in sediment).

Ruiz et al. (2001) describe similar detrimental fish farm effects on *P. oceanica.* They map the complete collapse of over 50% of a 40 ha meadow over a decade after the onset of fish farming. The area under the fish farm (7ha) was destroyed first (i.e. an example of strong near field effects of aquaculture on a seagrass).

In their assessment of the impact of finfish aquaculture on *Posidonia oceanica*, Holmer et al. (2003) mention the following:

- Many Mediterranean fish farms have been established over *P. oceanica* meadows.
- *P. oceanica* is severely impacted right below the cages due to reduced light levels and deterioration in sediment conditions; carbohydrate pools within the plants’ rhizomes become reduced. The density / biomass of *P. oceanica* under fish cages is reduced by 30 to over 90%. Rhizome growth is reduced, preventing further expansion of the bed.
- Epiphytes and macroalgae invade the seagrass near cages (the negative effects of aquaculture induced epiphyte load on *P. oceanica* is described by Cancemi et al. 2003).
- Elevated tissue nutrient concentrations in plants under cages can attract herbivores to the seagrass bed, greatly increasing herbivory pressure.

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[10] Mojica and Nelson (1993) document near field reductions in the seagrasses *Halodule wrightii* Ascherson and *Syringodium filiforme* Kützing by a clam grow out facility in Florida. USA, Simenstad and Fresh (1995) describe similar negative effects of benthic shellfish culture on *Zostera marina.*

- Impacts were recorded up to 200m away from the fish farm operations (but see Dimech et al. 2002, where reference level conditions may require 300m or more distance from cages).
- Impacts occur very soon (months) after the onset of farming operations.
- Recovery times of *P. oceanica* are very long (in the order of centuries).

Lotze et al. (2003) surveyed a number of eelgrass beds along the southern shore of the Northumberland Strait (New Brunswick). They determined that bays with nutrient loading (including from aquaculture) coincided with negative impacts on eelgrass beds.

Based upon the information at hand, it is possible to hypothesise on potential effects of finfish cage aquaculture on *Zostera marina* in Canada. Figure 3 depicts a cage and eelgrass in four different 'impact zones' around the cage. Zone A is the area immediately under the cage and some meters around it. Zone A will be characterized by maximal shading, sedimentation, nutrient loading, alteration in sediment chemistry and low oxygen effects. In Zone A, eelgrass will likely be dead or dying and covered in epiphytes and bacterial / fungal mats. In Zone B (more moderate effects of finfish aquaculture) the plants will be somewhat stunted with heavy to moderate epiphyte cover, primarily on the older (distal) portions of the blades. Benthic algal mats may predominate in Zone B, interfering with eelgrass growth. A positive growth effect may be seen at a greater distance from the cage due to moderate nutrient loading (Zone C; shading, sedimentation, geochemical and oxygen effects expected to be minimal at this distance from the cage). At the reference location (Zone D), more natural water column and sediment conditions will be found. Plants in Zone D will have normal growth rates and epiphyte loads. Due to a lack of site specific studies in Canada, it is not possible to provide width estimates for each of these zones.

Summary

Quantifiable factors affecting eelgrass are listed in Table 1. The plants can be toxified directly by high nutrient and pore water sulphide concentrations, and are impacted indirectly by the secondary effects of eutrophication including phytoplankton and macrophyte growth causing shading of thalli. Low oxygen levels harm the plants as well.

Zostera is sensitive to bioturbation, some herbivores and the negative influences of a number of introduced species. If weakened, eelgrass beds are susceptible to the fungal pathogen, *Labyrinthula zosterae.*

Eelgrass had relatively high light requirements, and is quite sensitive to the combination of high temperature and high salinity. Even moderate current regimes can cause beds to become eroded or lost altogether, and burial is not well tolerated.

The relatively constrained range of physical, biological and chemical factors favourable for eelgrass growth stresses its designation as a sensitive habitat.

PART 2 - KELPS

Chemical Factors

Nutrient loading

a) Direct effects

Under natural conditions, many kelps will take advantage of elevated winter water column nitrogen levels (mainly in the form of nitrate) by accumulating and storing nitrogen reserves at that season for a later pulse of growth in spring and early summer when water temperatures and light levels are more favourable for growth (Chapman and Craigie 1977). These internal nitrogen reserves can only last for a few months, however, and naturally low water column nitrogen levels in the late summer in temperate seas will eventually restrict growth (Korb and Gerard 2000).

The Arctic kelp, *L. solidungula*, is unusual in its ability to continue to grow under nitrogen limitation for many months at a time at low temperatures (Korb and Gerard 2000). Nitrogen levels of $\leq 1\ \mu M\ l^{-1}$ appear to limit the growth of juvenile *Macrocystis pyrifera* (L.) Agardh (Dean and Jacobsen 1986).

The artificially enhanced upwelling of nutrients driven by a power plant discharge increased tissue nitrogen content in *M. pyrifera* in California (Jahn et al. 1998). *Laminaria* appears to be stimulated by moderate amounts of eutrophication, but excessive amounts may be inhibitory (Conolly and Drew 1985). More detailed studies are required to determine what level of nutrient loading is harmful to kelps.

Nitrogen replete *Laminaria saccharina* (L.) Lamour is more tolerant of high temperatures than when nutrient limited (Gerard 1997).

b) Indirect effects

The *indirect* effects of elevated nutrient concentrations in a water column (i.e. eutrophication) include the following:

i) elevated turbidity due to stimulation of phytoplankton growth

The author could not find any publications describing kelp loss due to water column turbidity from phytoplankton. This may not be an issue for kelps in any case, given their ability to grow at extraordinarily low light levels (see ‘Light levels’ in Physical Factors section below).

ii) increased algal epiphyte load

The author could not find any publications describing harmful effects of algal epiphytes on kelps.

iii) shifts in macrophyte species composition
Eutrophication will cause shifts in the species composition of seaweeds, promoting the growth of annual forms over perennial (Worm et al. 1999). However, kelps form tall canopies of 1m or more in height which will shade out weedy understory algae.

Similarly, a dense *Macrocystis* canopy will shade out *Laminaria* thalli, which are much shorter (Dayton et al. 1999). La Niña events on the west coast of the United States support *Macrocystis pyrifera* canopy growth, enhancing the shading effect on *Laminaria farlowii,* especially in shallow waters. The driving factor for this effect appears to be elevated water column nutrient concentrations brought on by the colder waters of La Niña years (Dayton et al. 1999). El Niño / La Niña regime shifts certainly can affect waters as far north as the offshore of Vancouver Island, but the author is not aware of any literature describing *Macrocystis / Laminaria* fluctuations due to this driver in Canada. The effects of light levels are discussed in more detail below under Physical Factors.

Low oxygen levels

The author could not find any information on the effects of low oxygen tension on kelps.

Biological Factors

Herbivory

Sea urchins are dominant herbivores in kelp beds (Steneck et al. 2002). Given the opportunity, urchins will graze back kelps to the point of local extinction, leaving only coralline algal dominated areas called “barrens” (Scheibling et al. 1999). Densities of urchins are much higher (10 fold or more) in the barrens than in kelp beds, but the fitness of the urchins in the barrens is lower (e.g. lower gonadal biomass in the barrens, Konar and Estes 2003). Recolonization of barrens by *Laminaria* is unlikely if urchin biomass exceeds roughly 200 g m^{-2}, or about 20 urchins m^{-2} (Chapman 1981). The data of Johnson and Mann (1993) also support a ‘break point’ of about 20 to 30 urchins m^{-2}, algae can recolonize below that urchin density. If the urchins are removed (via disease or wave action), the kelps can return to the area (Miller 1985; Steneck et al. 2002).

The ‘kelp / urchin barren’ cycle represents two alternate community states in the rocky subtidal of Atlantic Canada. In this environment, *L. longicruris* will dominate over other seaweeds and will rapidly recolonize even after storm removal (Johnson and Mann 1988).

The ‘kelp / urchin barren’ cycle is the outcome of a temporal escape from herbivory by algae. Other seaweeds palatable to urchins escape grazing via spatial escape, by growing in shallow water where the effectiveness of urchin grazing is reduced via currents and wave action (Himmelman and Nedelec 1990; Siddon and Whitman 2003).

Urchins are not restricted to consuming adult kelp tissues. Sala and Graham (2002) report that, under normal field densities, *Strongylocentrotus purpuratus* is more effective than most snails in removing young microscopic sporophytes of *M. pyrifera.*

Lacuna vincta Montagu 1803, the common Atlantic chink shell, is found on both coasts and will feed on kelp and other algae (Fredriksen 2003). Even small amounts of tissue damage from this mollusc can cause kelp stipes to break when exposed to waves and currents (Duggins et al. 2001). The snail will graze on the blade margins of *L. longicruris* and promote the tearing away of the marginal tissue, causing a significant reduction in canopy area without elevating mortality rates overall (Johnson and Mann 1986). However, Fralick et al. (1974) report on the devastation of a *Laminaria* bed at *L. vincta* densities of up to 277 per plant.

Tegula pulligo Gmelin (dusky turban snail) is found on the open coast of British Columbia. It will feed on thalli of *M. integrifolia* (Durante and Chia 1991) and *M. pyrifera* (Watanabe 1984), and graze upon young microscopic sporophytes of *M. pyrifera* (Sala and Graham 2002).

Johnson and Mann (1986) report that both the limpet *Notoacmaea testudinalis* and the chiton *Tonicella rubra* have no significant effect upon the recruitment of *L. longicruris* in Nova Scotia. On the west coast, removal of the chiton *Katharina tunicata* increases the biomass of *Laminaria groenlandica* (Duggins and Dethier 1985).

Asterina (Patiria) miniata (Bat Star) will also eat young sporophytes of *M. pyrifera*, but even relatively high densities of this starfish are unlikely to impact *M. pyrifera* recruitment (Leonard 1994). The Bat Star can be found on the outer coast of Vancouver Island.

Chess (1993) reports that the amphipod *Peramphithoe stypotrupetes* will burrow into the stipe of *L. setchellii* in the north-eastern Pacific, almost always killing the plant and sometimes entire beds. The extent of damage from this interaction is not known for British Columbia.

Fouling organisms

Many types of sessile invertebrates can settle upon and subsequently grow over kelp thalli. These organisms do not necessarily impede kelp growth (Hurd et al. 1994; Hurd et al. 2000), and may even be beneficial in some cases (Durante and Chia 1991). The introduced species *Membranipora membranacea* appears to be an exception, see below.

Introduced species

Codium fragile ssp. *tomentosoides* (mentioned in the eelgrass section) has been implicated in the decline of some east coast kelp beds by invading gaps within a bed and preventing kelp recruitment. The invasion phenomenon appears to be facilitated by an organism introduced from Europe on Canada's east coast, *Membranipora membranacea,* an encrusting bryozoan which causes the kelp thalli to become susceptible to storm damage and loss (Chapman 1999; Levin et al. 2002). An *M. membranacea* cover rate of over 50% of blade surface has been implicated in the defoliation of a *Laminaria* bed on the east coast (Lambert et al. 1992).

The central longitudinal axis of a *Laminaria* blade is the typical location of spore producing tissue, the sorus. Saier and Chapman (2004) found a direct relationship between the proportion of *L. longicruris* sorus covered in *M. membranacea* and spore release, with complete coverage corresponding to an almost 100 fold reduction in spore liberation.

Membranipora membranacea also occurs on the west coast, where it causes blade loss in *M. pyrifera.* The fouled blades are fragile and break off easily. Approximately one third of the blades will be lost with a 60 – 70% cover of *Membranipora* (Dixon et al. 1981).

Sargassum muticum (Yendo) Fensholt is a brown alga that was introduced to the west coast from Japan. In the subtidal, *Sargassum* can form a dense, tall canopy which inhibits the growth of native *L. bongardiana* (=*L. groenlandica*) (Britton-Simmons 2004).

Pathogens

Rogerson et al. (1998) demonstrated that the cosmopolitan marine amoeba *Trichosphaerium sieboldi* is capable of invading and digesting *Laminaria* tissues. They suggest that *T. sieboldi* could be a 'primary invader' of seaweeds in nature, but the extent of its influence is unknown.

Andrews (1977) describes a 'white rot disease' of the bladder kelp, *Nereocystis*, caused by a marine bacterium. Alginic acid decomposing bacteria, normally found as epiphytes on *Laminaria* thalli, can infect the kelps and cause a 'rot disease' under unfavourable conditions such as wounding, overcrowding (e.g. commercial cultivation) and high temperatures (Meili 1991). 'Black rot disease' of *Macrocystis* has been described by North (1979).

Laminaria (and other kelp) is commonly infected by endophytic brown algae which can distort stipes and blades, or cause dark spots (Peters and Schaffelke 1996; Ellertsdottir and Peters 1997). The brown algal endophyte, *Streblonema aecidioides* has been implicated in the exclusion of *L. saccharina* from shallow waters in the western Baltic (Schaffelke et al. 1996).

Physical Factors

Light levels

Kelps respond differently to different wavelengths of light depending upon the plants' developmental state and environment. Deep water *Laminaria*, and those living under ice cover, are more inhibited by UV light (as measured by inhibition of photosynthesis) than those not occurring under those conditions (Bischof et al. 2002). Adult *L. saccharina* are less sensitive to UV than young plants (Bischof et al. 2002).

Laminaria saccharina photosynthesis is inhibited by high irradiance (700 µmol photons m^{-2} s^{-1}) to the extent that damage to Photosystem II reaction centers is indicated (Bruhn and Gerard 1996).

Both *M. pyrifera* and *M. integrifolia* appear to be limited to depths greater than 3 or 4m due to high light intensity (or UV) inhibition of gametophytes and embryonic sporophytes in shallower waters. The depth limit corresponds to light intensities of c.a. 800 µmol photons m^{-2} s^{-1} (Graham 1996).

Laminaria saccharina becomes more sensitive to low light levels as temperatures increase (i.e. light compensation point increases with increasing temperature). The compensation point is about 5 µmol photons m^{-2} s^{-1} at 5ºC and 20 µmol photons m^{-2} s^{-1} at 25ºC (Davison et al. 1991).

Laminaria solidungula, an Arctic species, can survive seven months of darkness (Henley and Dunton 1997). It utilizes stored carbon reserves for a burst of spring blade growth at very low light levels (Dunton and Schell 1986). *Laminaria solidungula* is photosynthetically saturated at relatively low light levels, and has an estimated compensation point (photosynthesis=respiration) of about 3 µmol photons m^{-2} s^{-1} (Dunton and Jodwalis 1988). In Greenland, *L. saccharina* is adapted to a long dark winter as well, with a photosynthetic compensation point of only 2 µmol photons m^{-2} s^{-1} (Borum et al. 2002). *Laminaria digitata* is reported to have a compensation irradiance of 3 µmol photons m^{-2} s^{-1} at 15ºC (Rodrigues et al. 2000).

Macrocystis pyrifera gametophytes require ≥6 µmol photons m^{-2} s^{-1} to achieve maximum fertility (Deysher and Dean 1986).

Salinity and temperature

Working with *L. saccharina,* Gerard (1997) demonstrated that summertime nutrient limitation (a common situation for temperate kelps) tends to reduce photosynthetic output at elevated temperature. Reduced nutrient levels and elevated temperature work in concert during the late summer months to reduce *L. saccharina* productivity, but some population specific adaptation appears to be possible to reduce the effect (Gerard 1997). *Laminaria saccharina* populations near the southern limit of the species (New York) are capable of tolerating c.a.

20ºC, while more northerly populations (Maine) cannot (Gerard and DuBois 1988). High temperature preadapted *L. saccharina* will still photosynthesise quite well at 25ºC, but output is quickly curtailed at 30ºC (Davison 1987).

The photosynthetic rate of *L. saccharina* is reduced at lower temperatures, but photosynthesis will continue as long as light levels are adequate (Davison et al. 1991). Borum et al. (2002) report *L. saccharina* growing in Greenland at temperatures of <0ºC.

In laboratory culture experiments with *Laminaria saccharina, L. digitata* and *L. hyperborea,* Sjøtun and Schoschina (2002) demonstrated that *L. saccharina* was most proficient at developing gametophytes, and subsequently young sporophytes, at 0ºC. Both *L. saccharina* and *L. digitata* extend to the Arctic, while *L. hyperborea* does not.

Macrocystis integrifolia in British Columbia is generally found in moderately wave or current swept areas between 6 and 18ºC, and >23‰ (Druehl 1978).

The combination of elevated temperature and nutrient limitation are the main factors controlling the southern distribution limit of *M. pyrifera* (Hernandez-Carmona et al. 2001). *Macrocystis* tends to deteriorate as temperatures reach ≥20ºC (North 1979). Gametophytes of *M. pyrifera* are inhibited by 20ºC (Deysher and Dean 1986).

Laminaria digitata will continue to photosynthesise relatively well even at the low salinity of ~3 ‰ (Ohno 1976). However, low salinity reduces nitrogen uptake rates in *L. digitata* (Gordillo et al. 2002).

Currents and scour

Macrocystis integrifolia requires some water movement to break down diffusion boundary layers on the surface of its blades to enhance nutrient uptake. A seawater velocity of c.a. ≥4 cm s^{-1} appears to be sufficient (Hurd et al. 1996). Wave driven oscillatory flow can be just as effective for this purpose as the directional currents found in more exposed areas (Stevens et al. 2003).

Kelps are morphologically plastic plants, and they will change form depending upon environmental conditions. *Laminaria hyperborea* will allocate more of its growth to the stipe at more wave exposed localities (Sjøtun and Fredriksen 1995; Sjøtun et al. 1998). Kawamata (2001) coupled laboratory experiments with field observations to determine that *L. japonica* alters its morphology with increasing exposure to currents. 'Exposed' plants developed more massive holdfasts and narrow flat blades to reduce drag. Plants with the exposed morphology held fast even at 1.1 m s^{-1} in tank experiments.

Kelps are, however, prone to damage or complete removal by storm events. Mortalities tend to be high on wave impacted shores (Duggins et al. 2003).

Graham et al. (1997) found that a California field site with peak winter orbital velocities (calculated from wave height) of ~3 m s^{-1} had greater canopy loss of *M. pyrifera* after storms than more sheltered sites (<2 m s^{-1} peak winter orbital velocity). Moreover, sites with increased wave intensity had plants restricted to deeper waters, suggesting bulk removal of thalli in shallow waters by waves (Graham 1997).

Storm removal and subsequent recruitment patterns, coupled with predominating oceanographic conditions, can affect the structure of kelp beds for long periods of time (Tegner et al. 1997). In other words, the history of past catastrophic events often drives present day kelp bed structure.

Sedimentation

In a series of laboratory experiments, Devinny and Volse (1978) demonstrated that 10 mg cm^{-2} of sediment spread over a hard substrate was enough to prevent *M. pyrifera* spore attachment. Germlings were smothered at 108 mg sediment cm^{-2}. North (1979) reports that *Macrocystis* is variably sensitive to burial of stipe tissue and cannot tolerate burial of blades.

Effects of Aquaculture on Kelps

The author could not find any papers situating finfish cage cultures directly above kelp beds, or impacts of aquaculture on kelps. However, there is ROV video evidence of kelp die back under finfish cages in Newfoundland[11]. Bates (2002) concluded that algal communities close to finfish cages in New Brunswick had reduced red algal percent cover, blooms of ectocarpoid brown algae and “green tide” symptoms (blooms of benthic green algae). He did not describe significant changes in kelp community structure.

A few papers mention the potential use of *Laminaria* for absorbing excess nutrients from finfish aquaculture operations, and its potential value as a secondary crop (Petrell et al. 1993; Subandar et al. 1993; Ahn et al. 1998). Prof. Thierry Chopin (University of New Brunswick, Saint John) is presently involved in field trials of this concept in eastern Canada.

As for eelgrass, it is possible to hypothesise on potential effects of finfish cage aquaculture on kelps in Canada. Figure 4 depicts a cage and kelps in four different ‘impact zones’ around the cage. Zone A is the area immediately under the cage and some meters around it. Zone A will be characterized by maximal shading, sedimentation, nutrient loading and low oxygen effects. In Zone A, kelps will likely be dead or dying and covered in epiphytes and bacterial / fungal mats. In Zone B (more moderate effects of finfish aquaculture) the plants will be somewhat stunted with heavy to moderate epiphyte cover, primarily on the older (distal) portions of the blades. Benthic algal mats may predominate in Zone B, but these mats may not interfere with kelp growth. A positive growth effect may

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[11] Terry Fleet (DFO Senior Habitat Biologist), pers. comm.

be seen at a greater distance from the cage due to moderate nutrient loading (Zone C; shading, sedimentation and oxygen effects expected to be minimal at this distance from the cage). At the reference location (Zone D), more natural water column conditions will be found. Plants in Zone D will have normal growth rates and epiphyte loads. Due to a lack of site specific studies in Canada, it is not possible to provide width estimates for each of these zones.

Summary

Quantifiable factors affecting kelps are listed in Table 2. The list is much shorter than that for eelgrass, in part due to the depth of the literature on *Zostera,* but also because kelps appear to be far less sensitive than eelgrass. Kelps should survive in almost any cool, subtidal hard bottomed marine environment with adequate water circulation and light. Adult plants are perennial and adaptable to local conditions. Pending catastrophic events such as burial, storms or outbreaks of fouling organisms / disease / herbivory, kelp beds should persist over time.

Even the microscopic stages of kelps (gametophytes and the young sporophytes they produce) appear to be quite adaptable to stress (Gerard 1997b). However, the establishment of these microscopic stages may be the sensitive point in the life history of kelps (e.g. Tegner et al. 1995), acting as a bottle neck concerning the development of new kelp beds. Given the evidence at hand, kelp beds are not particularly sensitive, but their re-creation may be a sensitive event.

In theory, established kelp beds should be immune to the effects of eutrophication, simply absorbing excess nutrients for growth and shading out weedy understory algae. It has even been suggested that large scale kelp cultivation could offset the effects of eutrophication (Fei 2004). There may be limits to the amount of eutrophication kelps can tolerate, however (Conolly and Drew 1985) and some field based studies on this topic are sorely needed.

The information gaps on kelp ecology and physiology are disconcerting. Further information may prove a greater degree of kelp sensitivity than concluded here. For example, low oxygen effects may exist and the etiology of bacterial and endophyte diseases may have population level impacts. Also, the large scale impact on kelp of introduced species such as *Codium* and *Sargassum* is not known at present, but could prove to be substantial.

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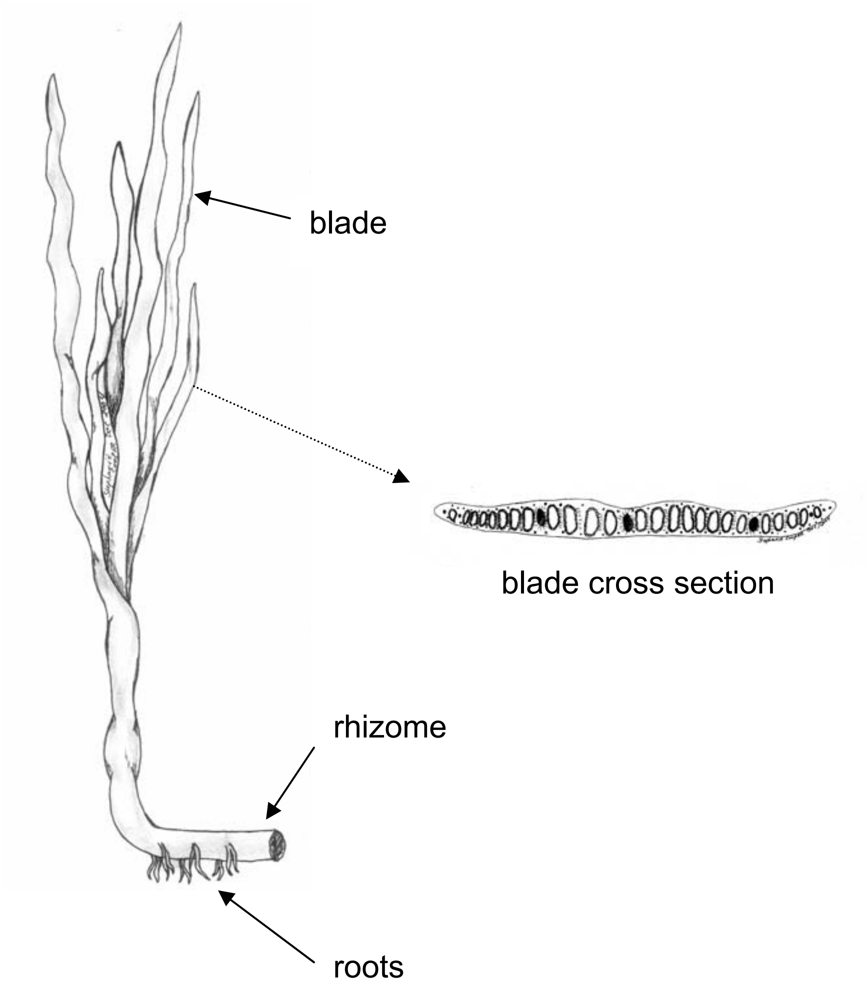

Fig. 1 Eelgrass – Blades 20 to 50 cm long or more with meristematic region at base of blade bundle. Blade cross section indicates vascular tissue (veins) as dark ovals, and air canals (lacunae) as clear ovals. Drawings by Stephanie Cooper.

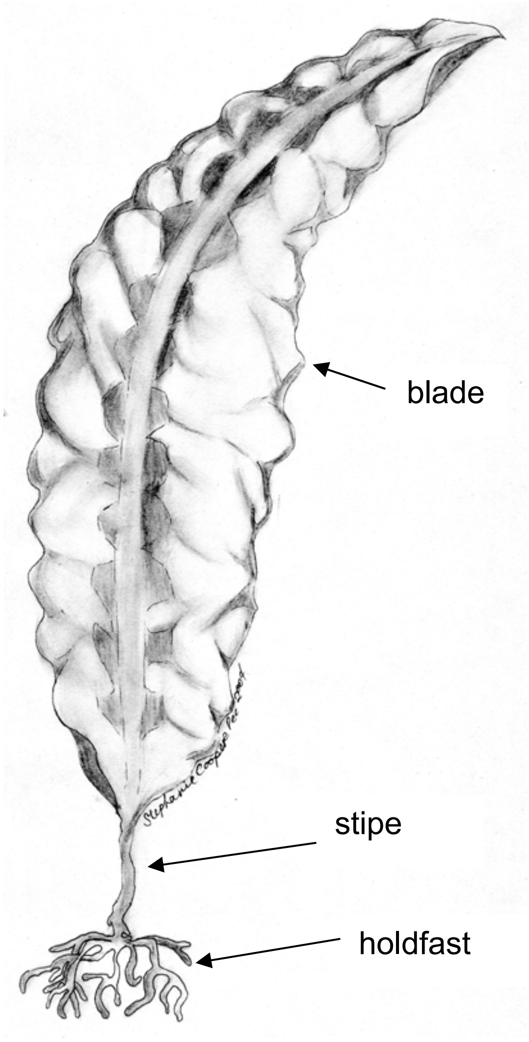

Fig. 2 ‘generic’ kelp morphology – Blades 50 to 100 cm long or more with meristematic region at base of blade. Drawing by Stephanie Cooper.

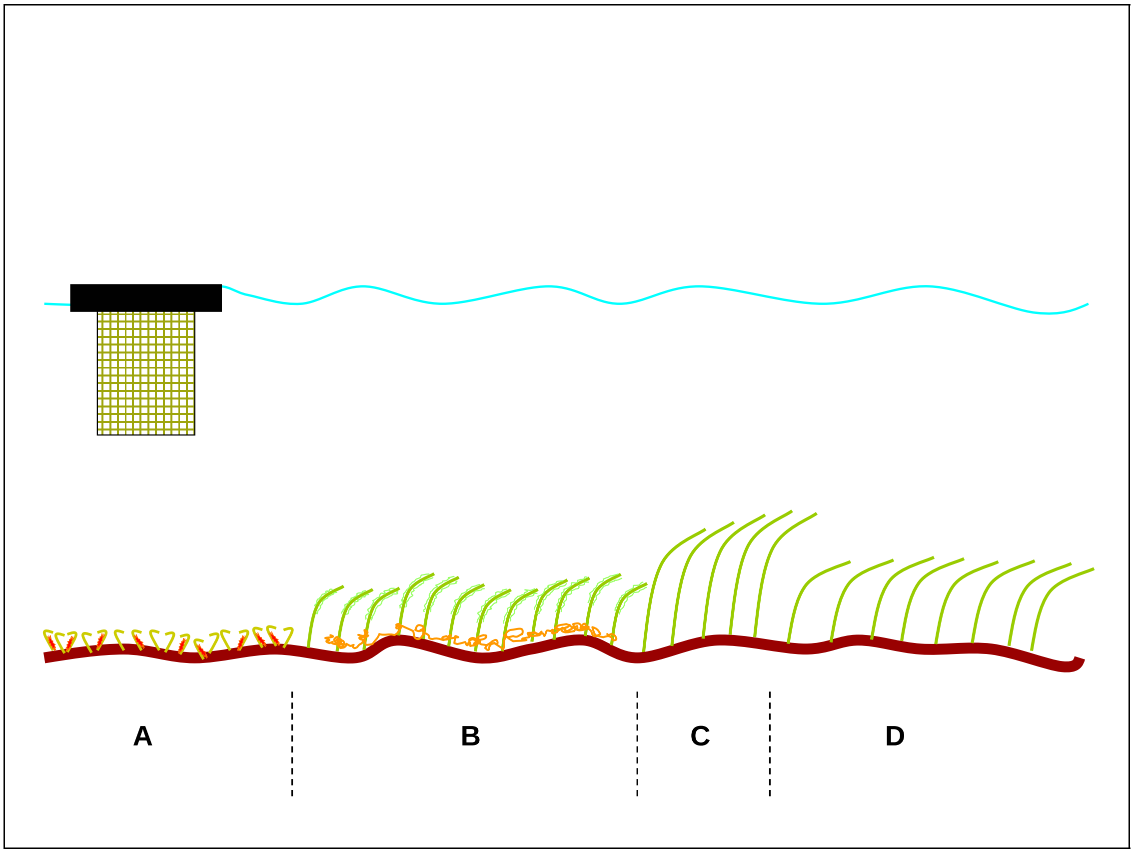

Fig. 3 Representation of finfish cage (mesh box on left) and potential effects on eelgrass at various distances away from the cage (zones A to D).

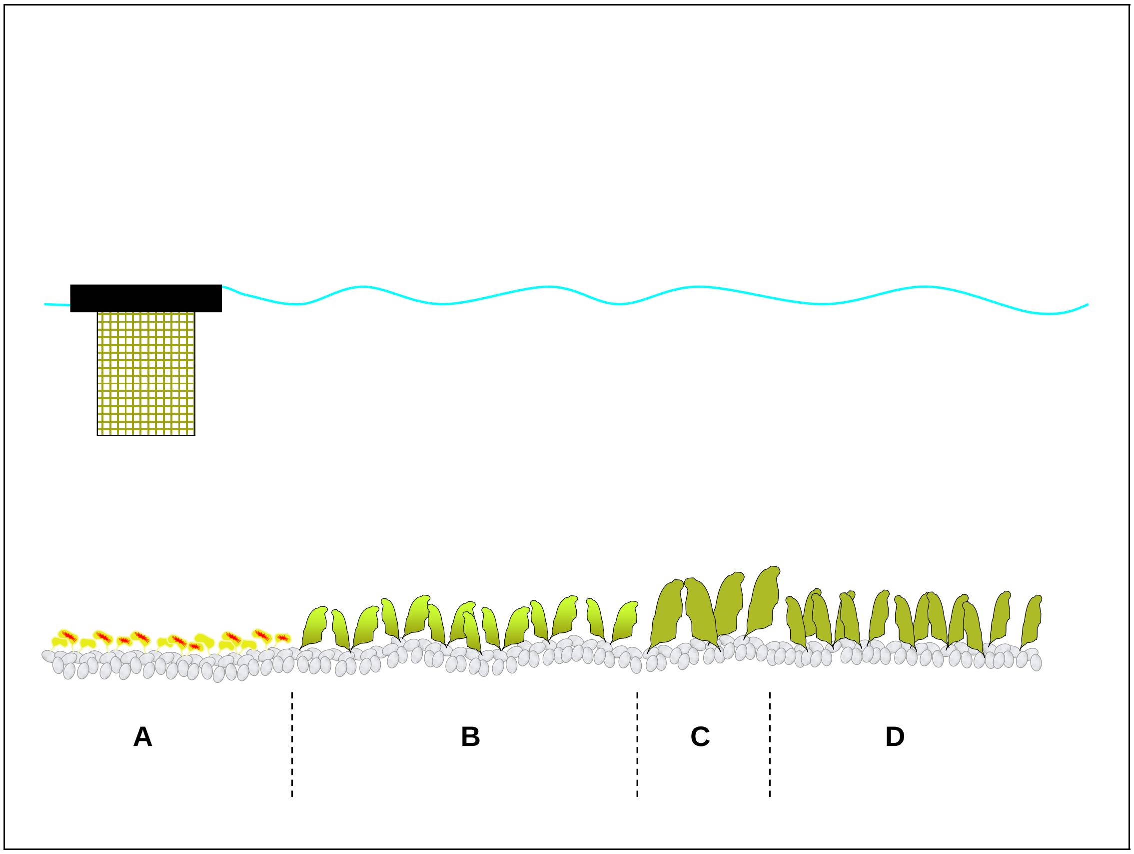

Fig. 4 Representation of finfish cage (mesh box on left) and potential effects on kelps attached on cobble at various distances away from the cage (zones A to D).

Table 1. Factors affecting eelgrass, with threshold levels

	item	threshold at which eelgrass beds may be damaged	reference
Chemical Factors			
Nutrient loading	Water column nitrate	5 to 10 µM NO_3^--N d^{-1} (*Zostera marina*)	Burkholder et al. 1994
	Pore water nitrate	20 mM (growth inhibition, *Z. marina*)	Peralta et al. 2003
	Pore water sulphide[12]	>70 µM H_2S (growth reduction, *Z. marina*)	Terrados et al. 1999
	Pore water sulphide[12]	>800 µM H_2S (photosynthesis reduced, *Z. marina*)	Goodman et al. 1995
	Nutrient loading[12]	30 kg N ha^{-1} yr^{-1} (loss of 80 to 96% of *Z. marina* bed area)	Hauxwell et al. 2003
	Nutrient loading[12]	≥60 kg N ha^{-1} y^{-1} (*Z. marina* beds gone)	Short and Burdick 1996; van Katwijk et al. 1999; Hauxwell et al. 2003
	Macroalgal canopy[12]	9 – 12 cm (decline in *Z. marina*)	Hauxwell et al. 2001
	Enteromorpha mat[12]	~4.5 kg wet wt m^{-2} (50% reduction in biomass, *Z. capricorni*)	Cummins et al. 2004

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[12] this item associated with effects of finfish aquaculture

Table 1. (Continued)

	item	threshold at which eelgrass beds may be damaged	reference
Low oxygen	Water column $[O_2]$[12]	<63 μM (*Z. marina* growth reduction)	Holmer and Bondgaard 2001
	Water column $[O_2]$ plus $[H_2S]$[12]	<63 μM O_2 plus ≥ 100 μM H_2S (*Z. marina* photosynthesis shut down)	Holmer and Bondgaard 2001
	Water column anoxia[12]	A few days (*Z. marina* beds gone)	Plus et al. 2003
Biological Factors			
herbivory	Rissoidae	>30 individuals per shoot (*Z. marina* bed decline)	Fredriksen et al. 2004
	Idotea	~100 individuals m^{-2} (*Z. marina* biomass loss)	Duffy et al. 2001
	seed and seedling predation by invertebrates	no threshold available at present	Wigand and Churchill 1988
bioturbation	*Dendraster excentricus*	~20 individuals m^{-2} (prevents colonization by *Z. marina*)	Backman 1984
	Neotrypaea californiensis	100 individuals m^{-2} (prevents colonization by *Z. marina* and *Z. japonica*)	Dumbauld and Wyllie-Echeverria 2003; Harrison 1987
	Arenicola marina	68 individuals m^{-2} (*Z. noltii* buried)	Philippart 1994
	Hediste [*Nereis*]	400 – 700 individuals m^{-2} (excludes *Z. noltii*)	Hughes et al. 2000

Table 1. (Continued)

	item	threshold at which eelgrass beds may be damaged	reference
Introduced species	*Carcinus maenas*	≥4 individuals m^{-2} (*Z. marina*)	Davis et al. 1998; David Garbary unpublished results
	Musculista senhousia	800 g dry mass m^{-2} (*Z. marina* rhizome inhibition)	Reusch and Williams 1998
	Codium fragile ssp. *tomentosoides*	no threshold available at present (*Z. marina*)	Garbary et al. 1997
pathogens	*Labyrinthula zosterae*	>50% of leaf blade (*Z. marina* leaf production stops)	Ralph and Short 2002
Physical Factors			
light[12,13,14]	% of surface light	<10% (*Z. marina*)	Short et al. 1995
	μmol photons m^{-2} s^{-1}	<10 to 20 (*Z. marina*)	Marsh et al. 1986; Peralta et al. 2003
	No light	Several weeks (*Z. marina* beds gone)	Cabello-Pasini et al. 2002
Salinity and temperature	Salinity	>26 to 30‰ (*Z. marina*)	van Katwijk et al. 1999
	Temperature	>25 to 30ºC (*Z. marina*)	Greve et al. 2003

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[13] light calculations should add shading effect of epiphytes (i.e. take light measurement at true blade surface)

[14] salinity, temperature and nutrient status will affect light compensation levels

Table 1. (Continued)

	item	threshold at which eelgrass beds may be damaged	reference
Currents and scour	cm s^{-1}	<16 (*Z. marina* inhibition)	Fonseca and Kenworthy 1987; Koch 2001
	cm s^{-1}	~ 25 (transition point for *Z. marina*)	Fonseca and Bell 1998
	cm s^{-1}	>50 (inhibition of *Z. marina*)	Fonseca et al. 1983; Fonseca and Kenworthy 1987; Koch 2001
	cm s^{-1}	>120 to 180 (max limit for *Z. marina*)	Fonseca et al. 1983; Fonseca and Kenworthy 1987; Koch 2001
Sedimentation[12]	depth of burial	≥25% of plant height (>50% mortality of *Z. marina*)	Mills and Fonseca 2003

Table 2. Factors affecting kelps, with threshold levels

	item	threshold at which *kelp* beds may be damaged	reference
Chemical Factors			
Nutrient limitation	water column nitrogen	≤1 μM l^{-1} (*M. pyrifera*)	Dean and Jacobsen 1986
Nutrient loading[15]	Nutrient loading	no threshold available at present	
	macroalgal canopy	no threshold available at present	
Low oxygen[15]		no threshold available at present	
Biological Factors			
herbivory	urchins	approximately 20 - 30 individuals m^{-2} ('barrens' situation, exclusion of *Laminaria*)[16]	Chapman 1981; Johnson and Mann 1993
	Lacuna vincta	~300 individuals per *Laminaria* thallus	Fralik et al. 1974
	Tegula pulligo	no threshold available at present (*M. pyrifera & integrifolia*)	Watanabe 1984; Durante and Chia 1991; Sala and Graham 2002
	Katharina tunicata	no threshold available at present (*L. groenlandica*)	Duggins and Dethier 1985
	Peramphithoe stypotrupetes	no threshold available at present (*L. setchellii*)	Chess 1993

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[15] this item associated with effects of finfish aquaculture

[16] 'barrens' are by nature patchy. Bay wide assessments may be required to determine if barren areas are extensive enough to cause large scale losses of kelp.

Table 2. (Continued)

	item	threshold at which *kelp* beds may be damaged	reference
fouling organisms / introduced species	*Membranipora membranacea*	60-70% cover (one third blade loss in *M. pyrifera*)	Dixon et al. 1981
	Membranipora membranacea	>50% cover (defoliation of *Laminaria* bed)	Lambert et al. 1992
	Membranipora membranacea	% cover of sorus proportional to spore output loss (*L. longicruris*)	Saier and Chapman 2004
	Codium fragile ssp. *tomentosoides*	no threshold available at present (*Laminaria*)	Chapman 1999; Levin et al. 2002
	Sargassum muticum	no threshold available at present (*L. groenlandica*)	Britton-Simmonds 2004
pathogens	*Trichosphaerium sieboldi*	no threshold available at present (*Laminaria*)	Rogerson et al. 1998
	‘rot disease’ bacteria	no threshold available at present (*Laminaria, Macrocystis*)	North 1979; Meili 1991
	Streblonema	no threshold available at present (*L. saccharina*)	Schaffelke et al. 1996

Table 2. (Continued)

	item	threshold at which *kelp* beds may be damaged	reference
Physical Factors			
light[15,17]	µmol photons m^{-2} s^{-1}	<5 at 5ºC <20 at 25ºC (*L. saccharina*)	Davison et al. 1991
	µmol photons m^{-2} s^{-1}	<3 at 15ºC (*L. digitata*)	Rodrigues et al. 2000
	µmol photons m^{-2} s^{-1}	<6 (*M. pyrifera* gametophytes)	Deysher and Dean 1986
	µmol photons m^{-2} s^{-1}	≥700 (*L. saccharina*)	Bruhn and Gerard 1996
	µmol photons m^{-2} s^{-1}	>800 (*M. integrifolia, M. pyrifera*)	Graham 1996
Salinity and temperature	Salinity	<23‰ (*M. integrifolia* range limit)	Druehl 1978
	Temperature	≥20ºC (*Macrocystis*)	North 1979; Druehl 1978; Deysher and Dean 1986
	Temperature	>25ºC (*L. saccharina*)	Gerard and DuBois 1988; Davison 1987
Currents and scour	cm s^{-1}	<4 (*M. integrifolia*)	Hurd et al. 1996
	cm s^{-1}	>300 (storm damage, *M. pyrifera*)	Graham et al. 1997

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[17] salinity, temperature and nutrient status will affect light compensation levels

Table 2. (Continued)

	item	threshold at which *kelp* beds may be damaged	reference
Sedimentation[15]	mg sediment cm^{-2}	≥10 (prevents spore attachment in *M. pyrifera*) ≥108 (smothers germlings of *M. pyrifera*)	Devinny and Volse 1978
	burial	stipe burial sometimes tolerated, blade burial not tolerated (*Macrocystis*)	North 1979