ECOSYSTEM LEVEL EFFECTS OF MARINE BIVALVE AQUACULTURE

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EXECUTIVE SUMMARY

This paper reviews the present state of knowledge on environmental issues related to bivalve aquaculture, with emphasis on suspended mussel culture. Material reviewed includes Canadian and international studies on the role of wild and cultured bivalve populations in controlling ecosystem-level dynamics. The focus is on identifying potential changes in ecosystem processes (material and energy fluxes, and nutrient cycling) at the coastal ecosystem scale. Potential mechanisms for ecosystem-level effects include the utilization of particulate food resources by cultured bivalves and associated fauna, the subsequent release of unutilized materials in dissolved (urine) and particulate (feces and pseudofeces) form, and the removal of minerals from the system in the bivalve harvest. The potential consequences to coastal ecosystems from intensive bivalve aquaculture are summarized in the following sections.

CONTROL OF SUSPENDED PARTICLE DYNAMICS

Dense bivalve populations may exert a strong influence on suspended particulate matter (including phytoplankton, detritus, and some auto- and heterotrophic picoplankton and micro-zooplankton) in some coastal systems through their huge capacity to clear particles from the surrounding water (Dame 1996). Grant (2000) studied 15 embayments in Prince Edward Island (PEI) and concluded that the mussel biomass under culture in 12 of these embayments was potentially capable of removing food particles much faster than tidal exchange could replace them. Similarly, Meeuwig et al. (1998) concluded that mussel culture operations in many PEI embayments significantly reduce phytoplankton biomass through grazing. Similar conclusions have been reached for numerous international coastal regions (reviewed by Dame 1996). These relatively simple calculations of the time required for bivalve populations to clear the water column of particles indicate that intensive bivalve aquaculture has the capacity to alter matter and energy flow at the coastal ecosystem scale. However, gaps in knowledge exist regarding a number of important processes that could potentially mitigate the suspected impact of bivalve feeding. These include the following: (1) the effects of physical processes such as water column stratification, mixing and flow velocity, and spatially dependent tidal flushing; (2) the replenishment of food particles through primary production within the embayment; (3) bivalve-mediated optimization of primary production (Prins et al. 1995);

and (4) the large flexibility of bivalve feeding responses to environmental variations (Cranford and Hill 1999).

A strong indication that bivalve filter-feeders are able to control suspended particulate matter in some coastal systems comes from documented ecosystem changes that occurred after large biomass variations in natural and cultured bivalve populations. Population explosions of introduced bivalve species in San Francisco Bay and dramatic reductions in oyster populations in Chesapeake Bay have been implicated as the cause of large changes in phytoplankton biomass and production experienced in these systems (Nichols 1985; Newell 1988; Nichols et al. 1990; Alpine and Cloern 1992; Ulanowicz and Tuttle 1992). Research on the whole-basin environmental effects of bivalve aquaculture in France and Japan indicate that intense bivalve culture in these regions led to changes in particulate food abundance and quality, resulting in large-scale growth reduction and high mortalities in the cultured bivalves (Héral et al. 1986; Aoyama 1989; Héral 1993). Speculation that intense bivalve culture can affect coastal ecosystems by reducing excess phytoplankton associated with eutrophication has been supported by some laboratory and field observations, but has not been rigorously proven.

DIVERSION OF MATERIALS TO BENTHIC FOOD WEBS

The feeding activity of bivalve filter-feeders results in the packaging of fine suspended material into larger feces and pseudofeces that rapidly settle to the seabed, especially under conditions with slow or poor water flushing and exchange. These activities divert primary production and energy flow from planktonic to benthic food webs. While the dynamics of bivalve feces deposition (settling velocity, disaggregation rate and resuspension) are poorly understood, enhanced sedimentation under shellfish culture is well documented. Mortality and fall-off of cultured bivalves, induced by seasonal colonization by fouling organisms, can result in additional acute benthic organic loading.

The spatial scale and degree of seabed organic enrichment effects caused by the increased vertical flux of naturally occurring particles are dependant on the biomass of cultured bivalves, local hydrographic conditions, and the presence of additional organic inputs from other natural and anthropogenic activities. The recycling of organic biodeposits under suspended mussel culture operations in PEI, and at several other international regions, has been shown to have local to inlet-wide benthic impacts (Dahlback and Gunnarsson 1981; Tenore et al. 1982; Mattsson and Linden 1983; Kaspar et al. 1985; Shaw 1998; Stenton-Dozey et al. 1999; Mirto et al. 2000; Chamberlain et al. 2001). The increased oxygen demand in sediments from mussel biodeposits can, under certain conditions, result in the generation of an anaerobic environment that promotes ammonification and sulfate reduction, increased sediment bacterial abundance, and changes in benthic community structure and biomass. Aquaculture is not solely responsible for such impacts in PEI, as many basins are also stressed by nutrient enrichment from agricultural run-off. Observations of seabed impacts under mussel lines in PEI are, therefore, not directly transferable to bivalve culture sites in many other regions of Canada. Biodeposition patterns and the dispersion *of bivalve biodeposits are also controlled by water depth and local water movement. Slight differences in these physical properties can result in marked differences in the degree of impact observed on seabed geochemistry and communities under different suspended mussel culture sites (Chamberlain et al. 2001). Further research is needed to assess the ability of different coastal regions to resist or assimilate the effects of increased organic enrichment through a variety of physical and biogeochemical processes.*

The increased coupling of planktonic and benthic food webs by cultured bivalves has the potential to change energy flow patterns in coastal ecosystems, including altering food availability to zooplankton and larval fish (Horsted et al. 1988; Newell 1988; Doering et al. 1989). Bivalve filter-feeders have a competitive advantage over zooplankton for food resources because they are able to respond immediately to increased food availability, while zooplankton must go through a complete life cycle before being able to fully exploit increased food resources. Direct ingestion of zooplankton by bivalves may also reduce zooplankton abundance (Horsted et al. 1988; Davenport et al. 2000). However, effects of bivalve culture on zooplankton communities are largely speculative owing to the limited research conducted.

ALTERED COASTAL NUTRIENT DYNAMICS

The consumption and deposition of suspended particulate matter by bivalves, as well as the excretion of dissolved nutrients, can play a significant role in controlling the amounts and forms of nitrogen in coastal systems and the rate of nitrogen cycling (reviewed by Dame 1996). This transformation and translocation of matter by bivalves appears to exert a controlling influence on nitrogen concentrations in some coastal regions (Dame et al. 1991) and can provide a means of retaining nutrients in coastal areas, where they are recycled within detrital food chains, rather than being more rapidly exported (Jordan and Valiela 1982). Benthic nutrient mineralization can increase at culture sites as a result of the increased organic matter sedimentation, greatly speeding up the rate of nitrogen cycling (Dahlback and Gunnarsson 1981; Kaspar et al. 1985; Feuillet-Girard et al. 1988; Barranguet et al. 1994; Grant et al. 1995). The high flux of ammonia excreted from dense bivalve populations may have a major effect on phytoplankton production (Maestrini et al. 1986; Dame 1996) and may potentially contribute to more frequent algal blooms, including those of the domoic-acid-producing diatom Pseudo-nitzschia multiseries (Bates 1998; Bates et al. 1998). Aquaculture-induced changes in the relative concentrations of silica, phosphorus and nitrogen (e.g. Hatcher 1994) may also favor the growth of other harmful phytoplankton classes (Smayda 1990), but this has yet to be observed in nature. Bivalve aquaculture may also play a significant role in nutrient cycling in coastal systems, as nutrients stored in the cultured biomass are removed by farmers and the nutrients are no longer available to the marine food web. Kaspar et al. (1985) suggested that the harvesting of cultured mussels may lead to nitrogen depletion and increased nutrient limitation of primary production, but there is little direct evidence of environmental effects. The retention and remineralization of limiting nutrients in coastal systems is necessary to sustain system productivity, but the potential impacts of bivalve cultures on coastal nutrient dynamics is poorly understood.

CUMULATIVE ENVIRONMENTAL EFFECTS

Any attempt to assess ecosystem-level effects of bivalve aquaculture must consider the complexity of natural and human actions in estuarine and coastal systems. Infectious diseases associated with intense bivalve culture, as well as exposure of cultured organisms to 'exotic' pathogens introduced with seed or broodstock, can have a significant and perhaps more permanent impact on ecosystems than the direct impact of the bivalves themselves (Banning 1982; ICES 1995; Bower and McGladdery 1996; Hine 1996; Renault 1996; Minchin 1999; Miyazaki et al. 1999). The presence of additional ecosystem stressors can also influence the capacity of bivalves to impact the ecosystem. The effects of chemical contaminants and habitat degradation are complex, but are well documented as having the potential to adversely affect bivalve health. Bivalve neoplasias show strong correlations to heavily contaminated environments (Elston et al. 1992), and the severity of infection is related to sub-optimal growing conditions (Elston 1989). Dissolved contaminants are frequently scavenged onto particulate matter, a mechanism which increases their availability for wild and cultured filter-feeders to ingest. Weakened bivalves with impeded feeding activity, along with spawning failure or poor quality spawn, can all contribute to morbidity, mortality and fall-off.

Land-use practices that transport sediments into estuaries can impact coastal water quality. Cultured bivalves and their support structures could alter sedimentation patterns within embayments, resulting in accelerated deposition of fine-grained sediment. Presently, there is no consensus on whether dense bivalve populations cause a net increase or decrease in sedimentation rates in coastal regions. However, if bivalve cultures influence the natural equilibrium among the major factors controlling sediment aggregation rate, sedimentary conditions within coastal regions may be altered.

INTEGRATION OF ECOSYSTEM EFFECTS

The available literature has shown that extensive bivalve culture has the potential, under certain conditions, to cause cascading effects through estuarine and coastal foodwebs, altering habitat structure, species composition at various trophic levels, energy flow and nutrient cycling. Simulation modelling has been one of the more focused approaches to assessing the net ecosystem impact of bivalve interactions with ecosystem components. Modelling can quantitatively and objectively integrate the potential negative ecosystem effects of the impact of mussel grazing on phytoplankton, zooplankton and the benthos, with the potentially positive effects of increased recycling of primary production and retention of nutrients in coastal systems (Fréchette and Bacher 1998). For example, such an integrative approach can help to assess whether or not the severity of ecosystem effects in different coastal areas are regulated by water motion and mixing. Numerical models can also be directed toward assessment of system productive capacity, fish/land-use interactions, farm management and ecosystem health. Past work has provided an excellent means of identifying gaps in knowledge.

A variety of methods has been applied to assessing the environmental interactions of bivalve aquaculture operations (Grant et al. 1993; Dowd 1997; Grant and Bacher 1998;

Smaal et al. 1998; Meeuwig 1999), but there is no standard assessment approach. Fully coupled biological-physical models may be envisioned (e.g. Prandle et al. 1996; Dowd 1997) that predict ecosystem changes in chlorophyll, nutrients and other variables of interest as a function of culture density and location. To do this, shellfish ecosystem models must be integrated with information on water circulation, mixing and exchange to account for transport and spatial redistribution of particulate and dissolved matter. Box models (Raillard and Menesguen 1994; Dowd 1997; Chapelle et al. 2000) offer a practical means to couple coastal ecosystem models with physical oceanographic processes. The bulk parameterizations of mixing required for these box models can be derived directly from complex hydrodynamic models (Dowd et al. 2002). Another promising avenue for improving ecosystem models is the use of inverse, or data assimilation, methods (Vallino 2000). These systematically integrate available observations and models, thereby combining empirical and simulation approaches, and improve predictive skill. Simulation models that focus on estimating mussel carrying capacity and related ecosystem impacts provide powerful tools for quantitative descriptions of how food is captured and utilized by mussels, as well as site-specific information on ecosystem variables and processes (Carver and Mallet 1990; Brylinsky and Sephton 1991; Grant 1996).

RESEARCH NEEDS

Few studies have assessed the potential environmental interactions of the bivalve aquaculture industry, and few quantitative measures presently exist to measure the ecosystem-level effects of this industry. Research on the ecosystem-level impacts of bivalve aquaculture is currently at a relatively early stage of development compared with finfish culture and for many other anthropogenic activities. As a result, ecologically relevant studies are needed on many topics, particularly the long-term responses of major ecosystem components (phytoplankton, zooplankton, fish, benthos, as well as the cultured bivalves) to bivalve-induced changes in system energy flow and nutrient cycling. The following general research areas have been identified to address gaps in knowledge:

- Ecological role of bivalve filter-feeders: *accurately quantify the density-dependant role of bivalves in controlling phytoplankton and seston concentrations, including studies of hydrodynamics, bivalve ecophysiology, and phytoplankton community and productivity responses to grazing pressure.*

- Organic loading: *identify important processes controlling the severity of seabed organic enrichment impacts caused by bivalve biodeposits and determine the capacity of different coastal ecosystems to assimilate or recover from the effects of aquaculture-related organic loading.*

- Nutrient dynamics: *develop a predictive understanding of the potential effects of bivalve aquaculture on nutrient concentrations, elemental ratios and rate of cycling in coastal systems, and study the consequences of altered nutrient dynamics to phytoplankton communities and blooms, including harmful algal blooms.*

- Ecosystem structure: *investigate the effects of bivalve culture on ecosystem structure resulting from direct competition between bivalves, zooplankton and epibionts for trophic resources, and the transfer of energy and nutrients to benthic food webs.*

- Numerical modelling: *integrate knowledge obtained on the consequences of bivalve culture on ecosystem structure and function through the use of ecosystem modelling to assess the net impact of aquaculture activities on major system components and to address issues of aquaculture productive capacity and sustainability.*

- Ecosystem status: *develop a scheme for classifying and assessing the state of ecosystem functioning for regions supporting bivalve aquaculture. Integrate multiple ecosystem stressors from anthropogenic land- and marine-use in ecosystem studies of culture systems.*

EFFETS ÉCOSYSTÉMIQUES DE L'ÉLEVAGE DE BIVALVES MARINS

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RÉSUMÉ

Dans cet article, nous passons en revue l'état actuel des connaissances sur les enjeux environnementaux de l'élevage de bivalves, en mettant l'accent sur la culture de moules en suspension. Nous abordons des études menées au Canada et à l'étranger sur le rôle des populations de bivalves sauvages ou de culture dans la dynamique des écosystèmes. Nous visons surtout à déterminer les modifications possibles des processus écologiques (flux de matière et d'énergie et cycles des éléments nutritifs) à l'échelle de l'écosystème côtier. Les mécanismes possibles des effets écosystémiques comprennent l'utilisation de particules de nourriture par les bivalves d'élevage et la faune connexe, l'excrétion subséquente de matières non utilisées sous formes dissoute (urine) ou particulaire (fèces et pseudofèces) et l'enlèvement de minéraux de l'écosystème par la récolte des bivalves. Les répercussions possibles de l'élevage intensif de bivalves sur les écosystèmes côtiers sont résumées dans les sections suivantes.

DYNAMIQUE DES PARTICULES EN SUSPENSION

Dans certains écosystèmes côtiers, les populations denses de bivalves, en raison de leur énorme capacité de filtrer les particules dans l'eau (Dame 1996), peuvent fortement influer sur les particules en suspension (qui comprennent le phytoplancton, le détritus, le picoplancton autotrophe ou hétérotrophe et le microzooplancton). Dans une étude de 15 baies à l'Île-du-Prince-Édouard, Grant (2000) a conclu que la biomasse des moules élevées dans 12 de ces baies pouvait consommer les particules de nourriture beaucoup plus rapidement que ces dernières pouvaient être remplacées par les apports des marées. Dans le même ordre d'idées, Meeuwig et al. (1998) ont montré que l'élevage des moules dans de nombreuses baies de l'Î.-P.-É. réduit considérablement la biomasse du phytoplancton. Des conclusions semblables ont été tirées pour de nombreuses régions côtières du monde (études passées en revue par Dame [1996]). Les calculs relativement simples du temps requis pour que des populations de bivalves filtrent toutes les particules de la colonne d'eau indiquent que l'élevage intensif de bivalves peut modifier les flux de matière et d'énergie à l'échelle de l'écosystème côtier. Toutefois, nos connaissances présentent des lacunes en ce qui a trait à un certain nombre de processus importants qui pourraient atténuer l'impact de l'alimentation des bivalves, notamment : 1) les effets de processus physiques comme la stratification et le mélange de la colonne d'eau, la vitesse

des courants et le renouvellement de l'eau par les marées; 2) le renouvellement des particules de nourriture par la production primaire; (3) l'optimisation de la production primaire par l'intermédiaire des bivalves (Prins et al., 1995); 4) la grande souplesse de la réaction alimentaire des bivalves aux variations environnementales (Cranford et Hill, 1999).

L'observation de modifications de l'écosystème qui ont suivi d'importantes variations de populations naturelles ou cultivées de bivalves indique clairement que les bivalves filtreurs peuvent réguler les particules en suspension dans certains écosystèmes côtiers. On a attribué à des flambées de populations de bivalves introduits dans la baie de San Francisco et à des chutes des populations d'huîtres dans la baie Chesapeake les grandes variations dans la biomasse et la production de phytoplancton observées dans ces écosystèmes (Nichols, 1985; Newell, 1988; Nichols et al., 1990; Alpine et Cloern, 1992; Ulanowicz et Tuttle, 1992). Des recherches concernant les effets environnementaux de l'élevage de bivalves sur des bassins entiers en France et au Japon ont montré que la conchyliculture intensive dans ces régions a modifié l'abondance et la qualité des particules de nourriture, ce qui a entraîné une réduction de la croissance et de fortes mortalités chez les bivalves d'élevage (Héral et al., 1986; Aoyama, 1989; Héral, 1993). Certaines observations faites en laboratoire et sur le terrain appuient l'hypothèse selon laquelle l'élevage intensif de bivalves peut influer sur les écosystèmes côtiers en réduisant le phytoplancton excédentaire associé à l'eutrophisation, mais l'hypothèse n'a pas été rigoureusement vérifiée.

DÉTOURNEMENT DE MATIÈRES VERS LES RÉSEAUX TROPHIQUES BENTHIQUES

L'alimentation des bivalves filtreurs a pour effet d'agglutiner de la matière fine en suspension en des fèces et pseudofèces de plus grande taille qui se déposent rapidement sur le fond marin, surtout dans des conditions de faible renouvellement ou échange d'eau. Cette activité trophique détourne de la production primaire et des flux d'énergie des réseaux trophiques planctoniques vers les réseaux benthiques. La dynamique de sédimentation des fèces de bivalves (vitesse de sédimentation, taux de désagrégation et remise en suspension) est méconnue, mais il est bien établi que la sédimentation est accrue sous les installations conchylicoles. La mortalité et la tombée de bivalves d'élevage, attribuables à la colonisation saisonnière par des salissures, peuvent occasionner d'importants apports supplémentaires de matière organique au milieu benthique.

L'étendue spatiale et le niveau de l'enrichissement du fond marin en matière organique causé par la sédimentation accrue dépendent de la biomasse des bivalves d'élevage, des conditions hydrographiques locales et de la présence d'autres apports organiques naturels ou anthropiques. Il a été montré que le recyclage des dépôts organiques sous des élevages de moules en suspension à l'Î.-P.-É. et ailleurs au monde a des incidences sur le milieu benthique à une échelle spatiale variant de petite à moyenne (Dahlback et Gunnarsson, 1981; Tenore et al., 1982; Mattsson et Linden, 1983; Kaspar et al., 1985; Shaw, 1998; Stenton-Dozey et al., 1999; Mirto et al., 2000; Chamberlain et al., 2001).

Dans certaines conditions, la demande accrue en oxygène des sédiments recevant de la matière organique provenant de mytilicultures peut donner un milieu anaérobie qui favorise l'ammonification, la réduction des sulfates, un accroissement de l'abondance des bactéries dans le sédiment et des modifications de la structure et de la biomasse de la communauté benthique. À l'Î.-P.-É., ces impacts ne sont pas exclusivement attribuables à l'aquaculture, car de nombreux bassins sont également stressés par l'enrichissement en éléments nutritifs provenant du lessivage des terres cultivées. Par conséquent, les observations d'impacts sur le fond marin sous les cordes à moules à l'Î.-P.-É ne sont pas directement applicables aux sites d'élevage de bivalves dans de nombreuses autres régions du Canada. La profondeur de l'eau et les mouvements d'eau à l'échelle locale déterminent aussi le régime de sédimentation organique et la dispersion des dépôts provenant des bivalves. De légères différences dans ces propriétés physiques peuvent produire des différences marquées dans le niveau d'impact observé sur la géochimie et les communautés du fond marin sous des élevages de moules en suspension (Chamberlain et al., 2001). Des études approfondies sont nécessaires pour évaluer la capacité de différentes régions côtières à résister aux effets de l'enrichissement accru en matière organique, ou à assimiler ces apports, par divers processus physiques ou biogéochimiques.

Le couplage accru des réseaux trophiques planctonique et benthique attribuable aux bivalves d'élevage peut modifier le régime de flux d'énergie dans les écosystèmes côtiers, notamment la disponibilité de nourriture pour le zooplancton et les larves de poisson (Horsted et al., 1988; Newell, 1988; Doering et al., 1989). Les bivalve filtreurs possèdent un avantage concurrentiel sur le zooplankton pour l'obtention de ressources alimentaires parce qu'ils peuvent réagir immédiatement à une disponibilité de nourriture accrue, tandis que le zooplancton doit passer un cycle vital entier avant d'être en mesure d'exploiter pleinement les ressources alimentaires accrues. En outre, l'ingestion de zooplancton par les bivalves peut réduire l'abondance du zooplancton (Horsted et al., 1988; Davenport et al., 2000). Toutefois, nos connaissances des effets de l'élevage de bivalves sur les communautés zooplanctoniques reposent largement sur des hypothèses puisque peu de recherche a été effectuée à cet égard.

MODIFICATION DE LA DYNAMIQUE DES ÉLÉMENTS NUTRITIFS EN MILIEU CÔTIER

La consommation de particules en suspension par les bivalves, la sédimentation de la matière qu'ils produisent ainsi que leur excrétion d'éléments nutritifs dissous peuvent jouer un rôle important dans la régulation des quantités et des formes d'azote et du taux de recyclage de cet élément dans les écosystèmes côtiers (synthèse de Dame, 1996). Ces transformation et translocation de matière par les bivalves semblent exercer une influence déterminante sur les concentrations d'azote dans certaines régions côtières (Dame et al., 1991) et peuvent constituer un moyen de retenir des éléments nutritifs dans des zones côtières, où ceux-ci sont recyclés dans des chaînes alimentaires détritiques, plutôt que d'être rapidement exportés (Jordan et Valiela, 1982). La minéralisation benthique des substances nutritives peut augmenter aux sites d'élevage en raison de la sédimentation accrue de matière organique, qui accélère beaucoup la vitesse de *recyclage de l'azote (Dahlback et Gunnarsson, 1981; Kaspar et al., 1985; Feuillet-Girard et al., 1988; Barranguet et al., 1994; Grant et al., 1995). Le flux élevé d'ammoniac excrété par les denses populations de bivalves peut avoir un effet important sur la production phytoplanctonique (Maestrini et al., 1986; Dame, 1996) et pourrait même contribuer à accroître la fréquence des proliférations d'algues, y compris de Pseudo-nitzschia multiseries, une diatomée qui produit de l'acide domoïque (Bates, 1998; Bates et al., 1998). Des changements attribuables à l'aquaculture dans les concentrations relatives de silice, de phosphore et d'azote (p. ex. Hatcher, 1994) peuvent aussi favoriser la croissance d'autres classes de phytoplancton nuisible (Smayda, 1990), mais cela n'a pas encore été observé dans le milieu naturel. L'élevage de bivalves peut également jouer un rôle important dans le cycle des éléments nutritifs dans les écosystèmes côtiers puisque les éléments nutritifs stockés dans la biomasse des bivalves d'élevage récoltés par les aquaculteurs ne sont plus disponibles au réseau trophique marin. Selon Kaspar et al., (1985), la récolte de moules d'élevage peut entraîner l'épuisement de l'azote et accroître la mesure dans laquelle la production primaire est limitée par le manque d'éléments nutritifs, mais il existe peu de preuves directes d'effets sur le milieu. La rétention et la reminéralisation des éléments nutritifs limitants en milieu côtier sont nécessaires au maintien de la productivité de l'écosystème, mais les impacts possibles de l'élevage de bivalves sur la dynamique des éléments nutritifs en milieu côtier sont méconnus.*

EFFETS ENVIRONNEMENTAUX CUMULATIFS

Toute tentative d'évaluation des effets écosystémiques de l'élevage de bivalves doit tenir compte de la complexité des processus naturels et des activités humaines dans les écosystèmes estuariens ou côtiers. Les maladies infectieuses liées à l'élevage intensif de bivalves et l'exposition de ceux-ci à des agents pathogènes « exotiques » introduits avec du naissain ou des géniteurs peuvent avoir un impact important sur les écosystèmes, voire même un impact plus permanent que l'impact direct des bivalves eux-mêmes (Banning, 1982; ICES, 1995; Bower et McGladdery, 1996; Hine, 1996; Renault, 1996; Minchin, 1999; Miyazaki et al., 1999). La présence d'autres facteurs d'agression de l'écosystème peut influer sur la capacité des bivalves de nuire à l'écosystème. Les effets des contaminants chimiques et de la dégradation de l'habitat sont complexes, mais il est bien établi qu'ils peuvent nuire à la santé des bivalves. Les néoplasies chez les bivalves présentent de fortes corrélations avec les milieux très contaminés (Elston et al., 1992), et la gravité de l'infection est liée à des conditions de croissance sous-optimales (Elston, 1989). Les contaminants dissous se fixent fréquemment aux particules, ce qui accroît leur ingestion par les filtreurs sauvages ou d'élevage. Les bivalves affaiblis dont l'alimentation est entravée ainsi que l'échec de la reproduction ou la mauvaise qualité du frai peuvent contribuer à la morbidité, à la mortalité et à la tombée des bivalves.

Les utilisations des terres qui entraînent le transport de sédiments vers les estuaires peuvent nuire à la qualité des eaux côtières. Les bivalves d'élevage et les structures sur lesquelles ils croissent peuvent modifier les régimes de sédimentation dans les échancrures de la côte en accélérant le dépôt de sédiments fins. Il n'existe actuellement aucun consensus à savoir si les populations denses de bivalves produisent une hausse ou *une baisse nette des taux de sédimentation dans les régions côtières. Cependant, si l'élevage de bivalves influe sur l'équilibre naturel entre les principaux facteurs qui déterminent le taux d'agrégation des sédiments, les conditions de sédimentation pourraient être modifiées dans les régions côtières.*

INTÉGRATION DES EFFETS ÉCOSYSTÉMIQUES

La littérature existante montre que, dans certaines conditions, l'élevage intensif de bivalves peut avoir des effets en cascade sur les réseaux trophiques estuariens ou côtiers, en modifiant la structure des habitats, la composition spécifique de divers niveaux trophiques, les flux d'énergie et les cycles des éléments nutritifs. Les modèles de simulation constituent une des méthodes les plus ciblées pour évaluer l'impact net sur l'écosystème des interactions des bivalves avec les composantes de l'écosystème. La modélisation peut intégrer de façon quantitative et objective les effets écosystémiques potentiellement négatifs de l'alimentation des moules sur le phytoplancton, le zooplancton et le benthos et les effets potentiellement positifs de l'accroissement du recyclage de la production primaire et de la rétention des éléments nutritifs dans les écosystèmes côtiers (Fréchette et Bacher, 1998). Par exemple, une démarche intégrative de ce type peut permettre d'évaluer si les mouvements et le mélange de l'eau déterminent ou non la gravité des effets écosystémiques dans différentes régions côtières. Des modèles numériques peuvent aussi servir à évaluer la capacité de production de l'écosystème, les interactions entre l'utilisation des terres et le poisson, la gestion des exploitations aquacoles et la santé de l'écosystème. Les travaux réalisés par le passé constituent un excellent moyen de relever les lacunes dans nos connaissances.

Diverses méthodes ont été utilisées pour évaluer les interactions environnementales des élevages de bivalves (Grant et al., 1993; Dowd 1997; Grant et Bacher, 1998; Smaal et al., 1998; Meeuwig, 1999), mais il n'existe aucune méthode d'évaluation normalisée. On peut envisager des modèles biologiques et physiques entièrement intégrés (p. ex. Prandle et al., 1996; Dowd, 1997) qui permettent de prédire les modifications des concentrations de chlorophylle et d'éléments nutritifs ainsi que d'autres variables d'intérêt en fonction de l'intensité et de l'emplacement des élevages. À cette fin, des données sur la circulation, le mélange et l'échange d'eau doivent être intégrées aux modèles des effets écosystémiques des mollusques pour tenir compte du transport et de la redistribution spatiale des matières particulaires et dissoutes. Des modèles à compartiments (Raillard et Menesguen 1994; Dowd 1997; Chapelle et al., 2000) offrent un moyen pratique de coupler les modèles de l'écosystème côtier avec les processus océaniques physiques. Les paramétrisations globales du mélange requises pour ces modèles à compartiments peuvent être calculées directement à partir de modèles hydrodynamiques complexes (Dowd et al., 2002). L'utilisation de méthodes inverses, ou d'assimilation de données, constitue une autre démarche prometteuse pour améliorer les modèles de l'écosystème (Vallino, 2000). En intégrant systématiquement les observations et modèles disponibles, ces méthodes combinent des démarches empiriques et de simulation et améliorent la capacité de prévision. Les modèles de simulation axés sur l'estimation de la capacité du milieu à soutenir des moules et des impacts écosystémiques connexes constituent des outils puissants pour décrire quantitativement l'obtention et l'utilisation de nourriture *par les moules et fournir de l'information propre à chaque site sur les variables et processus écosystémiques (Carver et Mallet, 1990; Brylinsky et Sephton, 1991; Grant, 1996).*

BESOINS EN RECHERCHES

Peu d'études ont été réalisées pour évaluer les interactions environnementales possibles de l'élevage des bivalves, et il existe peu de mesures quantitatives des effets écosystémiques de cette industrie. La recherche sur les impacts écosystémiques de l'élevage de bivalves est actuellement à un stade de développement peu avancé par rapport à la recherche sur les effets de la pisciculture et de nombreuses autres activités humaines. Il faut donc effectuer des études écologiques pertinentes sur de nombreux sujets, en particulier sur les réactions à long terme des principales composantes de l'écosystème (phytoplancton, zooplancton, poisson et benthos, en plus des bivalves d'élevage) aux modifications, attribuables aux bivalves, des flux d'énergie et des cycles des éléments nutritifs. Les domaines de recherche généraux suivants ont été relevés en vue de combler les lacunes dans nos connaissances :

- Rôle écologique des bivalves filtreurs : *quantifier avec exactitude le rôle de la densité des bivalves dans la régulation des concentrations de phytoplancton et de seston, notamment par des études sur l'hydrodynamique, l'écophysiologie des bivalves et les effets de la pression de broutage sur la composition et la productivité du phytoplancton.*

- Apports organiques : *cerner les processus importants qui déterminent la gravité des impacts d'enrichissement organique du fond marin causés par la sédimentation de matières produites par les bivalves, et déterminer la capacité de différents écosystèmes côtiers à assimiler les apports organiques provenant de l'aquaculture ou à se rétablir des effets de ces apports.*

- Dynamique des éléments nutritifs : *comprendre les effets possibles de l'élevage de bivalves sur les concentrations, les rapports et les taux de recyclage des éléments nutritifs dans les écosystèmes côtiers de façon à pouvoir prédire ces effets, et étudier les répercussions de la modification de la dynamique des éléments nutritifs sur les communautés phytoplanctoniques, notamment en ce qui a trait aux proliférations d'algues nuisibles ou non.*

- Structure de l'écosystème : *étudier les effets de l'élevage de bivalves sur le transfert d'énergie et d'éléments nutritifs aux réseaux trophiques benthiques et sur la structure de l'écosystème qui découle de la compétition alimentaire directe entre les bivalves, le zooplancton et les épibiontes.*

- Modélisation numérique : *intégrer par modélisation de l'écosystème les connaissances acquises concernant les répercussions de l'élevage de bivalves sur la structure et la fonction de l'écosystème pour évaluer l'impact net des activités* *aquacoles sur les principales composantes de l'écosystème et aborder les enjeux de la capacité de production et de la durabilité de l'aquaculture.*

- État de l'écosystème : *élaborer un système de classification et d'évaluation de l'état de fonctionnement de l'écosystème pour les régions où l'on pratique l'élevage de bivalves; intégrer aux études écosystémiques des systèmes aquacoles les multiples agents d'agression de l'écosystème qui découlent des activités humaines sur terre et en mer.*

INTRODUCTION

The bivalve aquaculture industry has expanded rapidly in Canada over the last two decades. Although highly diverse in structure, capital and material infrastructure, the most rapid development has occurred with mussel culture: an industry which, until recently, developed at an exceptional pace throughout Atlantic Canada. Ease of mussel spat collection and deployment throughout the water column, with comparatively inexpensive capital investment, have fueled the development of mussel aquaculture. In contrast, oyster, clam and scallop culture systems generally involve relatively small area operations, intertidal or bottom-culture. While significant suspended longline culture of oysters and scallops occurs in British Columbia (BC), the areas leased for these activities generally, with a few exceptions, occupy a small fraction of coastal embayments. Estuarine and coastal systems in Prince Edward Island (PEI) support 80% of bivalve culture in Canada and 98% of the total value of mussel landings in the Maritimes and Gulf Regions (www.gfc.dfo.ca), and a high proportion of suitable embayments is leased for mussel culture. The implications of such rapid and extensive water body transformation into mussel production have been recognized as having the potential for significant impact on ecological and oceanographic processes in Prince Edward Island (Shaw 1998).

Unlike finfish aquaculture, bivalve culture requires minimal additions to the environment, except for the animals themselves and the infrastructures used to grow them. Their food is supplied by the environment and their wastes return nutrients and minerals to the ecosystem. However, dense populations of bivalve filter-feeders are characterized as 'ecosystem engineers' (Jones et al. 1994; Lawton 1994), owing to their ability to modify, maintain and create entire habitats through their effects on suspended particles and the formation of structurally complex shell habitat. Suspended and bottom culture of bivalves increases the surface area available for attachment and grazing by other species, and spaces between shells provide refugia from physical stress (currents and waves) and predation (Ragnarsson and Raffaelli 1999). Potential mechanisms for ecosystem-level effects include the utilization of particulate food resources (primarily phytoplankton and detritus, but including some auto- and heterotrophic picoplankton and micro-zooplankton) by the bivalves and associated epifauna, the subsequent release of unutilized materials in dissolved (urine) and particulate (feces and pseudofeces) form, and the removal of minerals from the system in the bivalve harvest.

This paper reviews the present state of knowledge on environmental issues related to bivalve aquaculture, with particular attention given to the potential effects (both positive and negative) of suspended mussel culture. Our focus is on identifying potential changes in ecological processes (material and energy fluxes as well as nutrient cycling) at the coastal ecosystem scale (e.g. estuary or embayment) and on identifying gaps in knowledge that need to be addressed through continued research. The temporal scale addressed is primarily long-term to include ecosystem changes over seasonal, life-cycle and aquaculture site development time-scales. However, shorter time-scales are considered when important physical, chemical and biological processes have longer-term implications.

POTENTIAL ECOLOGICAL EFFECTS OF FILTER-FEEDING

Bivalve filter-feeders have a large capacity to filter water, directly altering concentrations of the seston in the surrounding water (Bayne et al. 1989; Dame 1993, 1996; Jørgenson 1996; Smaal et al. 1997). It has often been suggested that dense bivalve populations exert a strong long-term influence on energy flow at the scale of whole estuaries, bays and coastal systems by controlling phytoplankton and seston concentrations through their filter-feeding activity (Cloern 1982; Officer et al. 1982; Nichols 1985; Hily 1991; Smaal and Prins 1993; Dame 1996; Dame and Prins 1998; Prins et al. 1998). This speculation stems primarily from measurements of water clearance (filtration) rate made on individual animals that are scaled-up to predict population or community grazing capacity. Several authors have compared estimates of the time required for resident bivalve populations or communities to clear all of the water volume in their coastal system (clearance time) with the time required for the water mass to be replaced by tidal exchange (residence time) and concluded that the bivalves can exert a significant and controlling influence on particulate matter in many shallow coastal systems (reviewed by Dame 1996; Dame and Prins 1998). A similar comparison, based on estimates by Grant (2000) of mussel culture area, feeding rate and tidal flushing in PEI embayments, is presented in Figure 1. This analysis suggests that for 12 of the 15 embayments studied, the mussel biomass presently under culture is potentially capable of removing food particles much faster than tidal exchange is capable of replacing them, and therefore appears to control phytoplankton and seston at the coastal ecosystem scale through overgrazing. Meeuwig et al. (1998) used a different mass balance approach to model phytoplankton biomass in 15 PEI embayments and estimated that the mussel farms in six of these systems reduced phytoplankton biomass by 45% to 88%. These order of magnitude calculations are strongly suggestive that intensive mussel culture has the capacity to alter matter and energy cycling for long periods in some coastal systems.

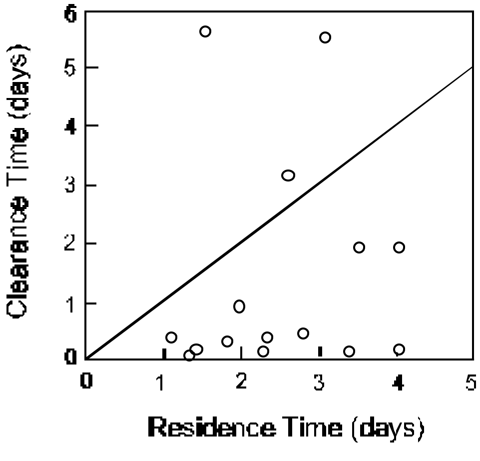

Figure 1. Comparison of predicted water mass residence time (tidal) and clearance time by mussel culture operations for 15 embayments in PEI. Mussel aquaculture potentially controls suspended particle concentrations (phytoplankton and detritus) where clearance time is less than residence time (point falls below unity line).

While simple scaling exercises, such as the one illustrated in Figure 1, are intuitive ecosystem indicators of carrying capacity and the potential impacts of existing and proposed aquaculture operations (includes biotic and abiotic factors controlling bivalve food supplies), these approaches neglect potentially important physical processes, such as water column stratification, mixing, and flow velocity, that could influence the effects of mussel culture operations on suspended particles. These approaches also use single flushing estimates for estuaries, when flushing is spatially dependent. Several biotic factors also need to be considered before placing too much emphasis on these results. First, comparison of water clearance and residence times does not consider replenishment of food particles within the estuary through internal primary production. Estimates of the time required for primary production within the system to replace the standing crop of phytoplankton (phytoplankton doubling time) are required before more definitive conclusions of the impact of bivalve filtration in these and other embayments can be reached (Dame 1996). Dame and Prins (1998) examined 11 coastal ecosystems and suggested that most of the systems produce sufficient phytoplankton internally to prevent overgrazing by resident bivalve populations. However, several of the systems studied, and particularly those under intense bivalve culture, require the import of food resources from outside the system to prevent particle depletion. Dowd (2000) examined a simple biophysical model that quantifies the relative roles of flushing, internal production and bivalve grazing on seston levels.

Another important consideration, when assessing the potential impact of bivalves on their and other filter-feeders' (e.g. zooplankton) trophic resources, is that bivalve grazing may directly stimulate system primary production such that algal cell removal may be compensated by an increase in algae growth rate. Factors that may contribute to this bivalve-mediated optimization of primary production are (1) increased light through reduced turbidity (assumes algae are light limited); (2) greater growth of algae through continuous grazing of older cells; (3) a shift to faster growing algae species; (4) increased rate of nutrient cycling; and (5) increased nutrient availability (Prins et al. 1995). Mesocosm studies examining the role of the clam *Mercenaria mercenaria* in controlling seston concentration indicated that a relatively low abundance of clams doubled primary production and altered the community structure of the plankton (Doering and Oviatt 1986; Doering et al. 1989). Grazing by mussels was also shown to result in increased picoplankton abundance (Olsson et al. 1992) and a shift to faster growing diatoms (Prins et al. 1995). While bivalve filter-feeders apparently contribute to optimizing primary production at relatively small temporal and spatial scales, the larger-scale significance of this interaction in natural ecosystems remains speculative.

An understanding of bivalve feeding rate is fundamental to accurately predict the role of bivalves in controlling seston availability and primary production. Mussels have been one of the most extensively studied marine organisms, but uncertainties and controversies regarding their physiology still exist that affect our capacity to accurately predict growth and the consequences of environmental variables on mussel bioenergetics (reviewed by Bayne 1998; Jϕrgenson 1996). Theories and models of bivalve functional responses to ambient food supplies vary widely in concept, resulting in considerable uncertainty on the actual ecological influence of dense bivalve populations (Cranford and Hill 1999;

Riisgård 2001). Controversy has been generated by the continued use of feeding rate measurements obtained in the laboratory using pure algal diets that are extrapolated to field conditions where cell types and concentrations and the presence of detritus may alter bivalve filtration and ingestion rates (Cranford 2001). Continued research is particularly needed on how the large seasonally variable energy/nutrient demands of mussels influence the uptake and utilization of naturally available food supplies (Cranford and Hill 1999). Further, genotype- and phenotype-dependent differences in marine bivalves also contribute to the large variance in feeding rate (reviewed by Hawkins and Bayne 1992), and this has yet to be considered in estimates of population clearance time.

The accuracy of some scaled-up estimates of bivalve population clearance time has been questioned based on the results of mesocosm studies (Doering and Oviatt 1986) and the use of new methodologies that permit bivalve feeding rates to be measured continuously under more natural environmental conditions than has been employed previously in the laboratory (Cranford and Hargrave 1994; Iglesias et al. 1998). Cranford and Hill (1999) used an *in situ* method to monitor seasonal functional responses of sea scallops (*Placopecten magellanicus*) and mussels (*Mytilus edulis*) and suggested that the coupling of coastal seston dynamics with bivalve filter-feeding activity may be less substantial than previously envisaged. That study confirmed previous results indicating that bivalves in nature do not always fully exploit their filtration capacity, but generally feed at much lower rates (Doering and Oviatt 1986). Prins et al. (1996) and Cranford and Hill (1999) showed that *in situ* and field measured clearance rates that use natural diets are similar and provide accurate predictions of bivalve growth. While it is, therefore, possible to scale up from individual measurements to bivalve populations, feeding behavior has also been shown to vary greatly over short- to long-time scales owing to external (variable food supply) and internal (variable energy demands of reproduction) forcing (Cranford and Hargrave 1994; Bayne 1998; Cranford and Hill 1999). The common practice of using average clearance rates for calculating population influences on phytoplankton may give equivocal results for much of the year.

Perhaps the best indication of the potential for bivalve filter-feeders to control suspended particulate matter at the ecosystem scale comes from observations of ecosystem changes that occurred after large biomass variations in natural bivalve populations, as well as the observed density-dependent effects of intensive cultivation practices. Population explosions of introduced bivalve species in San Francisco Bay and dramatic reductions in oyster populations in Chesapeake Bay have been implicated as the cause of the large changes in phytoplankton biomass and production experienced in these systems (Nichols 1985; Newell 1988; Nichols et al. 1990; Alpine and Cloern 1992; Ulanowicz and Tuttle 1992). Numerous similar examples can be drawn from the limnology literature with respect to the introduction, rapid growth and effect of zebra and quagga mussels (*Dreissena spp.*) on the water column in the Laurentian Great Lakes. Research on the whole-basin environmental effects of intense mussel and oyster aquaculture in the Bay of Marennes-Oléron, the most intensive growing region of the Atlantic coast of France, has focused on the impact of bivalve overstocking on growth and survival (Héral et al. 1986; Héral 1993). Intensive bivalve culture operations led to large-scale growth reduction and high mortalities in the Bay on two occasions. The large biomass of scallops under culture in Mutsu Bay, Japan also resulted in growth reduction and high mortality (Aoyama 1989). These impacts of intensive aquaculture appear to result in a feedback on bivalve growth from bivalve-induced changes in particulate food abundance and quality.

POTENTIAL ECOLOGICAL EFFECTS OF BIODEPOSITION

An important issue related to particle consumption by bivalve filter-feeders is the resulting repackaging of fine suspended material into larger feces and pseudofeces. Bivalves effectively remove natural suspended matter with particle sizes greater than 1 to 7 µm diameter, depending on species, and void them as large fecal pellets (500-3000 µm) that rapidly settle to the seabed, especially under conditions with slow or poor water flushing and exchange. This particle repackaging diverts primary production and energy flow from planktonic to benthic food webs (Cloern 1982; Noren et al. 1999). While the dynamics of bivalve feces deposition (settling velocity, disaggregation rate and resuspension) are poorly understood, enhanced sedimentation under shellfish culture is well documented (Dahlback and Gunnarsson 1981; Tenore et al. 1982; Jaramillo et al. 1992; Hatcher et al. 1994). Furthermore, mortality and fall-off of cultured bivalves, induced by seasonal colonization by fouling organisms that use suspended bivalves and their lines as substrate, can result in additional acute benthic organic loading.

Sediment organic enrichment effects are generally believed to be less dramatic with bivalve culture than with finfish culture where uneaten and partially digested food is deposited on the seabed (Kaspar et al. 1985; Baudinet et al. 1990; Hatcher et al. 1994; Grant et al. 1995). However, the zone of influence may be larger with bivalve aquaculture, if a large fraction of the total volume of coastal embayments is under culture and if hydrographic conditions permit the deposition and accumulation of biodeposits. Bivalve culture occupies a very significant portion of many embayments in PEI (mussel lease volume averaged 36% of total estuary volume for eight major PEI embayments) (Grant et al. 1995), but this is rare in other parts of Canada.

Organic enrichment of the seabed under suspended bivalve culture is due to the increased vertical flux of naturally occurring particles (Barranguet et al. 1994; Hatcher et al. 1994; Stewart et al. 1998). The seasonal biodeposition rate and organic content of fecal pellets was measured for scallops (*P. magellanicus*) and mussels (*M. edulis*) in two coastal regions in Nova Scotia (NS) (Cranford and Hill 1999), and organic matter biodeposition was observed to reach maxima in the spring and fall. That study showed that the daily biodeposition rate of a cohort of 25 mussels (80 mm shell length) increased natural sedimentation rates (g dry weight$\cdot$m$^{-2}\cdot$day^{-1}) by an average factor of 26 (mean of 160 daily biodeposition and sedimentation measurements). Fecal pellet organic content ranged from 20% to 70% with the highest values observed during the spring phytoplankton bloom. Feces generally had a similar organic content as other settled particles (Cranford and Hill 1999), despite containing partially digested organic matter.

If organic biodeposition by bivalves is sufficiently high, decomposition of organic biodeposits can increase the oxygen demand in sediments and generate an anaerobic environment that promotes ammonification and sulfate reduction. This is the classic response of sediments to eutrophication (Cloern 2001). An increase in benthic sulfate reduction has been observed under some intensive mussel culture sites (Dahlback and Gunnarsson 1981; Tenore et al. 1982) but not under others (Baudinet et al. 1990; Jaramillo et al. 1992; Grant et al. 1995; Chamberlain et al. 2001). Benthic responses to increased organic enrichment under suspended bivalve culture include increases in phytopigments, bacterial abundance and meiofauna community structure and biomass (Dahlback and Gunnarsson 1981; Mirto et al. 2000) and localized reductions in macrobenthic infaunal abundance and/or diversity (Tenore et al. 1982; Mattsson and Linden 1983; Kaspar et al. 1985; Stenton-Dozey et al. 1999; Chamberlain et al. 2001). These community impacts appear to be long-term, as little recovery of disturbed communities was observed 18 months after mussels were harvested (Mattsson and Linden 1983) and four years after an intensive mussel raft culture operation was removed (Stenton-Dozey et al. 1999). Although common in Europe and the northeastern United States, the raft culture technique is not utilized in Canada.

The pattern of enrichment effects can be observed in data from a survey of PEI inlets during 1997 (Shaw 1998). Redox potential (Eh), total $S^=$ and organic matter (OM) were measured in sediment collected at active lease sites, in adjacent reference areas away from mussel lines and in culture-free inlets where no mussel aquaculture occurred (Figure 2). The three geochemical variables have been shown to be indicators of benthic enrichment due to increased organic matter loading in areas of intensive finfish aquaculture (Hargrave et al. 1997). Significant ($p < 0.05$) differences in Eh, total $S^=$ and OM occurred between the three types of sampling sites. The most negative redox potentials (indicative of more anoxic conditions due to enhanced OM deposition) occurred in sediments under mussel lines. Concentrations of total $S^=$ and OM were not significantly different at lease and reference sites, but both of these variables were significantly higher than at culture-free sampling locations. The similarity in total $S^=$ and OM at lease and reference sites and differences in Eh between sampling locations implies that intensive mussel culture in PEI has had inlet-wide benthic impacts that are observable using sediment geochemical measurements.

The degree of benthic impact is expected to differ greatly between culture sites depending on the type and extent of culture activities and local environmental conditions. Observations of organic enrichment impacts from bivalve culture in PEI are not generally applicable to bivalve culture sites in other regions of Canada. The sedimentation patterns and dispersion of bivalve biodeposits are controlled by water depth and local water movement. Slight differences in these physical properties appear to explain the marked differences in the degree of impact observed on seabed geochemistry and communities under different suspended mussel culture sites (Chamberlain et al. 2001). Many embayments in PEI are also already stressed by similar eutrophication effects from land-use (see section on Aquaculture Interaction with Land-use), while culture activities in other regions tend to occur in areas with much lower agricultural nutrient inputs.

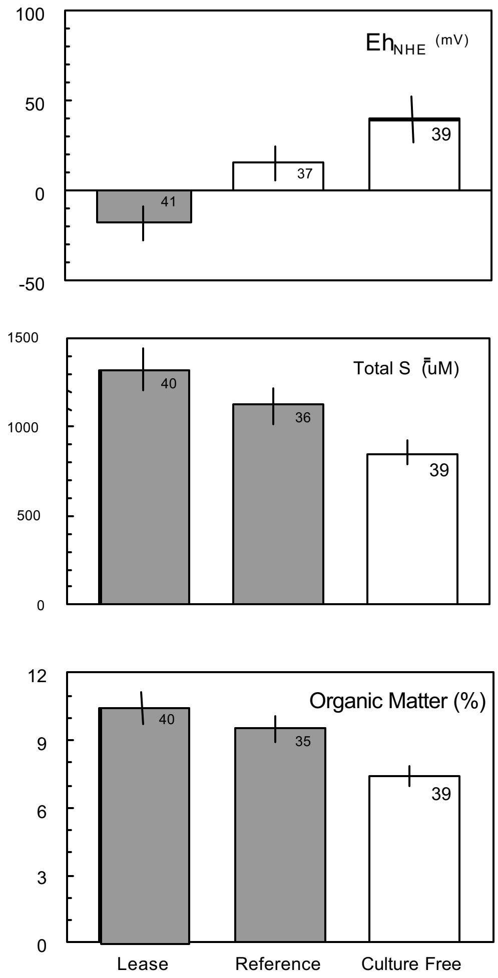

Figure 2. Data from Shaw (1998) summarizing mean (±SE) values for redox potentials (Eh), total $S^{=}$ and percent organic matter in surface sediment (2-4 cm depth layer) from 20 inlets in PEI. Samples were collected during late summer 1997 at stations under mussel lines on lease sites (Lease), at reference sites in the same inlet but >50 m away from mussel lines (Reference) and in inlets where mussel culture had not previously occurred (Culture Free). Numbers indicate pooled sample sizes. Differences in shading indicate significant differences (Mann Whitney U test, $p < 0.05$) between variables grouped by location.

Grant (2000) developed an approach for addressing the capacity of tidal action to redistribute materials deposited by mussel aquaculture operations in PEI estuaries. This modelling effort consists of estimating the balance between mussel egestion rate and the rate of tidal flushing. The aim was not to predict biodeposition effects, but to estimate the potential for whole coastal systems to resist organic loading through physical exchange processes. Estuaries identified as having the greatest risk of biodeposition effects had a relatively small tidal exchange and high percentage of the total estuarine volume under culture. There is little information available on the capacity of coastal ecosystems to assimilate organic loading and, subsequently, to resist biodegradation. Therefore, further research is needed.

The coupling of planktonic and benthic food webs, caused by the bivalves modifying, repackaging and increasing the sedimentation rate of fine suspended particles, changes the flow of energy in the ecosystem by altering the availability of food resources to other species. Crabs and demersal fish appear to benefit from culture activities as a result of the increased food availability from the fall-off of mussels and epibionts from lines (Lopez-Jamar et al. 1984; Freire et al. 1990). However, grazing competition with mussel culture can affect zooplankton and larval fish dependent on suspended seston as food. Bivalve filter-feeders have a huge competitive advantage over zooplankton, as they may significantly reduce the abundance of micro-zooplankton (<200 µm) (Horsted et al. 1988) and meso-zooplankton (up to 6 mm) (Davenport et al. 2000) through ingestion and are capable of immediately responding to increased food availability (e.g. phytoplankton bloom). The zooplankton must go through a complete life cycle before they can begin to fully exploit new resources. Mesocosm studies indicate that *Mercenaria* (infauna) and *Mytilus* (suspended culture) populations can alter pelagic food webs by suppressing the zooplankton (Horsted et al. 1988; Doering et al. 1989). Competitive pressure on zooplankton also comes from the periodic presence of large populations of cultured species larvae. The decline of oyster populations in Chesapeake Bay has been implicated in the observed increase in abundance of zooplankton and their major predators (Newell 1988). However, these potential effects on zooplankton communities are largely speculative, as they have never been documented in field studies.

CHANGES IN NUTRIENT DYNAMICS AND POTENTIAL CONSEQUENCES

The consumption and deposition of suspended particulate matter by farmed bivalves can play a significant role in controlling the amounts and forms of nitrogen in coastal systems and the rate of nitrogen cycling (reviewed by Dame 1996). This translocation of matter can provide a means of retaining nutrients, trace elements and contaminants in coastal areas where they are recycled within detrital food chains, rather than being more rapidly exported (Jordan and Valiela 1982). Benthic nutrient mineralization can increase at culture sites as a result of the increased organic matter sedimentation greatly increasing rates of nitrogen cycling (Dahlback and Gunnarsson 1981; Kaspar et al. 1985; Feuillet-Girard et al. 1988; Barranguet et al. 1994; Grant et al. 1995). Chlorophyll and nutrient mass-balance calculations for PEI estuaries show a tight correlation between phytoplankton biomass and nutrients, suggesting that nutrient availability in these intensively cultured systems primarily limits ecosystem productive capacity (Meeuwig et al. 1998). Nutrient cycling rates and availability may be increased at mussel farms through the mineralization of the large amounts of feces and pseudofeces trapped within the mussel socks. This permits nutrients to be released at shallower, more nutrient depleted depths than occurs if the nutrients are regenerated in the sediments. Decomposition of organic matter in aerobic surface sediments aids in recycling nutrients back to the water column for uptake by phytoplankton, while anaerobic decomposition in sediments under conditions of excessive organic enrichment (e.g. biodeposition) results in the production of nitrogen gas that may increase nitrogen limitation within the system. Conversely, phosphorus release from sediments is promoted under anaerobic conditions (Nixon et al. 1980).

An additional ecosystem consequence of bivalve aquaculture potentially stems from the transformation of much of the ingested particulate minerals into dissolved nutrients that are excreted as a necessary part of bivalve metabolic processes. The high flux of ammonia from dense bivalve populations appears to exert a controlling influence on nitrogen concentrations in some coastal regions (Dame et al. 1991; Strain 2002), and this aspect of bivalve culture may have a major positive effect on the phytoplankton (Maestrini et al. 1986; Dame 1996). There is little information available on the relative importance on ecosystem nutrient availability of the direct transformation of suspended particulate matter (excretion) into nutrients compared with nutrients supplied as a result of particulate matter translocation (biodeposition and remineralization) by bivalves. However, mineralization of biodeposits appears to be a more important nutrient source for phytoplankton production than direct excretion (Asmus and Asmus 1991; Prins and Smaal 1994).

While the greater availability and faster cycling of nutrients in aquaculture systems can lead to enhanced production of phytoplankton and seagrass (Peterson and Heck 2001), these changes may also contribute to more frequent algal blooms, including those of the domoic-acid-producing diatom *Pseudo-nitzschia multiseries* (Bates 1998; Bates et al. 1998). Domoic acid production is enhanced 2- to 4-fold when *P. multiseries* is grown in the presence of high concentrations of ammonium (220-440 μM) relative to the same concentration of nitrogen in the form of nitrate (Bates et al. 1993). Observed aquaculture-induced changes in the relative concentrations of silica, nitrogen and phosphorus (e.g. Hatcher et al. 1994) may also favor the growth of harmful phytoplankton classes (Smayda 1990). Impacts of changing nutrient ratios on phytoplankton community composition, including the promotion of harmful algal blooms such as *Pseudo-nitzschia*, have been documented in relation to coastal eutrophication (e.g. Parsons et al. 2002), but a causative connection has yet to be proven rigorously (Cloern 2001). Similarly, no definitive conclusions can be drawn from the sparse literature on the scale of aquaculture impacts on microalgae community composition.

The retention and remineralization of limiting nutrients in coastal systems is necessary to sustain system productivity. Benthic filter-feeders promote the retention and recycling of nutrients within coastal ecosystems by storing assimilated minerals as tissue biomass that is released upon death and decomposition (Dame 1996). Kaspar et al. (1985) suggested that the harvesting of cultured mussels may lead to nitrogen depletion and increased nutrient limitation of primary production. However, ecosystem-level effects resulting from the removal of nutrients stored in the cultured biomass are largely speculative, and further studies are needed to examine the consequences to the marine food web of nutrient removal.

AQUACULTURE INTERACTIONS WITH LAND-USE

Any attempt to assess ecosystem-level effects of bivalve aquaculture must consider the complexity of natural and human actions in estuarine and coastal systems. Ecosystem responses to multiple stressors (contaminants, fishing activities, invasive species, habitat loss, climate change, coastal construction, etc.) are intimately connected (Cloern 2001).

The determination of the cumulative effect of all human activities on coastal ecosystems is difficult but essential for environmental assessments. The capacity of cultured mussels to alter and control food supplies, energy flow and nutrient cycling depends on how other stressors positively or negatively influence important bivalve physiological processes (clearance rate, digestive efficiency, biodeposition rate and ammonia excretion) and growth. For example, infectious diseases associated with intense bivalve culture, as well as exposure of cultured organisms to 'exotic' pathogens introduced with seed or broodstock, can have a significant and frequently acute and permanent impact on the organisms' physiological and nutritional status (Banning 1982; ICES 1995; Bower and McGladdery 1996; Hine 1996; Renault 1996; Minchin 1999; Miyazaki et al. 1999). As a mostly sessile component of an ecosystem, bivalves play a sentinel role, acting as a sponge for many of the components actively or passively added to its aquatic surroundings (Dewey 2000). Important biochemical, cellular, physiological and behavioral changes in bivalves occur with contaminant exposure, and these can affect populations and disrupt energy flow and the cycling of materials within coastal ecosystems (Capuzzo 1981).

Land-use practices that result in nutrients being transported into estuaries can be a major determinant of coastal water quality and eutrophication (Chapelle et al. 2000). Concentrations of nitrogen and phosphorus in PEI estuaries have increased substantially between the 1960s and 1990s, and 10 of the 20 embayments sampled in 1998 and 1999 exhibited nitrogen levels exceeding the threshold for eutrophic conditions (DFO 2000). The large influence of agricultural activities on PEI embayments was indicated by the close correlation between chlorophyll biomass and the area of the watershed over which agriculture extends (Meeuwig 1999). Speculations that intense mussel culture can affect coastal ecosystems in positive ways by reducing eutrophication have been supported by observed changes in estuarine ecosystems in which natural bivalve populations have either dramatically increased (e.g. San Francisco Bay: Cloern 1982; Officer et al. 1982) or decreased (e.g. Chesapeake Bay: Newell 1988). Both of these systems are highly eutrophic, owing to intense farming and industrial/residential development within their watersheds.

Bivalve filter-feeders in these and other estuaries are believed to mitigate eutrophic trends by ingesting large quantities of algae and suspended particulate matter. However, this suggestion has not been proven rigorously and is based primarily on scaled-up bivalve filtration rates that may have been overestimated (Cranford and Hill 1999) and on mass balance calculations (Meeuwig et al. 1998). Asmus and Asmus (1991) suggested that the ability of mussel beds and culture sites to reduce the standing stock of phytoplankton is unlikely to combat anthropogenic eutrophication because they also promote primary production and accelerate the turnover of phytoplankton through their effects on nutrient cycling. As noted above, intense shellfish farming also increases the retention of nutrients within coastal systems (see also review by Cloern 2001), further focusing the negative effects of nutrient loading on this region. While elevated phytoplankton levels have a clear benefit to aquaculture farm productivity, the accompanying increase in organic biodeposition rates (i.e. bivalves augment pelagic/benthic coupling) could stimulate benthic microbial metabolism, alter sediment chemistry and increase the probability that benthic communities, which are highly sensitive to eutrophication, will change. Eutrophic conditions can also depress bivalve physiological functions and growth through exposure to toxic algal blooms (Chauvaud et al. 2000), limiting their perceived grazing control on algae biomass. Conversely, the removal of nutrients from the system in the bivalve harvest may help to alleviate some of the eutrophication problem. Interactions in the coastal zone between farmed bivalves and the environmental consequences of nutrient loading are highly complex, and all aspects need to be addressed objectively and integrated quantitatively before any conclusions can be reached on whether or not bivalve farming has a net positive or negative result on ecosystem quality.

Sediment released into coastal waters during land-use has the potential to alter physical habitats and directly impact marine organisms, including cultured species. There are limited quantitative data available on the effect of agriculture run-off on substrate composition and suspended sediment concentrations in PEI waterways, but anecdotal observations indicate high suspended concentrations during rainfalls and an increasing proportion of bottom covered by fine sediments (DFO 2000). Cultured bivalves and their support structures could alter sedimentation patterns within embayments by altering flow dynamics with the net result being a tendency towards accelerated deposition of fine-grained sediment. With the exception of raft culture, little is presently known about how suspended culture alters water flow (Grant and Bacher 2001), but the impact on sedimentation patterns will likely be dependent on culture spacing and local hydrographic conditions. Sediment deposition, resuspension and transport are governed in the marine environment by particle aggregation processes, which effectively control the settling velocity of fine-grained sediment by orders of magnitude. If bivalve cultures influence the natural equilibrium among the major factors controlling aggregation rate (particle concentration, particle stickiness and turbulence) (Hill 1996), sedimentary conditions within a bay may be altered.

Pesticides have been detected in 75% of stream water samples collected in PEI between 1996 and 1999 (DFO 2000). While concentrations were well below acute lethal concentrations (rainbow trout LC_{50} values), there were 12 fish kills downstream from potato fields in 1994 to 1999 that were suspected, or shown, to be caused by pesticides (DFO 2000). There is also increasing concern over the endocrine disrupting potential of released pesticides, as well as possible links between exposure of bivalves to contaminants and the incidence and severity of bivalve diseases (Coles et al. 1994; Pipe and Coles 1995; Pipe et al. 1995, 1999; Anderson et al. 1996, 1998; DaRos et al. 1998; Kim et al. 1999). The principal mechanism by which dissolved contaminants are transported in the marine environment is by scavenging (uptake) onto particulate matter and particle settling. This particle-reactive nature of organic contaminants increases their availability for filter-feeders, including wild and cultured bivalves. Bivalves bioaccumulate many abiotic contaminants and, as a result, have been widely used since the 1970s as sentinel organisms for monitoring such contaminant levels. In fact, many 'Mussel Watch' experiments have used suspended mussels in cages or other infrastructures to monitor contaminant drift in plumes, a holding mechanism akin to suspension culture (e.g. Salazar and Salazar 1997). Mussels are also used to monitor changes in environmental quality by combining and linking measurements of chemical inputs and concentrations in tissues with a pollution stress response called 'scope for growth' (SFG). SFG integrates physiological responses that affect changes in growth rate and has successfully been used to detect, quantify and identify the causes and effects of pollution (e.g. Widdows et al. 1995). Bivalve clearance rate is a component of the SFG equation and is highly sensitive to contaminant stress (Donkin et al. 1989; Widdows and Donkin 1992; Cranford et al. 1999). Although largely speculative, reduced feeding rates associated with exposure to contaminants (e.g. simultaneous nutrient and contaminant loading from agriculture) could influence their perceived capacity to mitigate coastal eutrophication by reducing their influence on ecosystem energy flow and nutrient cycling.

Although the rapid breakdown of agricultural pesticides and herbicides in water may seem to negate their significance in impacting bivalves and other aquatic organisms, there is growing concern and evidence that even the transient passage of the chemicals themselves (acute exposure) or the chronic exposure to their breakdown products may play a role in long-term or sub-acute effects. This complicates correlation to point-source or wider influent effects and makes 'mystery mortalities' difficult to resolve. This conundrum has recently gained a higher profile as a knowledge gap, especially with respect to molluscs, due to growing evidence that bivalve neoplasias appear to show strong correlations to heavily contaminated environments. Elston et al. (1992) summarized a long list of numerous neoplasia triggers that have been and are associated with bivalve neoplasias. These include pesticides, herbicides, organochlorides (Farley et al. 1991; Craig et al. 1993; Gardner 1994; Harper et al. 1994; van Beneden 1994; Dopp et al. 1996; Strandberg et al. 1998), retroviruses (Appeldoorn and Oprandy 1980; Oprandy et al. 1981; Cooper and Chang 1982; Cooper et al. 1982; Farley et al. 1986; Sunila and Farley 1989; Sunila and Dungan 1991; House et al. 1998), senescence (Bower 1989; Bower and Figueras 1989) and natural environmental extremes, such as changes in water temperature (Brousseau 1987; Brousseau and Baglivo 1991a,b; McLaughlin et al. 1996). The species that are most susceptible to neoplastic diseases are mussels (*M. edulis* and *M. galloprovincialis*) and clams (*Mya arenaria* and *Mercenaria* spp.). Blue mussels have had acute outbreaks of haemic neoplasia (blood cell dysfunction and proliferation) along the northwest coast of the United States and southern BC (Bower 1989). A correlation to water quality was not apparent. However, severe outbreaks of haemic neoplasia have been found in soft-shell clams from Chesapeake Bay, New Bedford Basin (Massachusetts) and, more recently, along the north shore of PEI (McGladdery et al. 2001). All these areas are subject to high agricultural run-off or organochloride industrial waste (Craig et al. 1993; Dopp et al. 1996; Strandberg et al. 1998). In addition, samples of the same species, collected from the Sydney tar ponds, NS, also showed levels of the condition in significant excess of 'normal' levels (McGladdery et al. 2001).

Another neoplasia condition that affects both hard- and soft-shell clams is gonadal neoplasia. The germinal cells proliferate without undergoing meiosis or differentiating into sperm or ova (Barber 1996; van Beneden et al. 1998). This condition shows a distinct geographic focus of infection, with rare outlying distribution spots. A hot spot in northern Maine shows a close correlation to forestry pest control programs, coinciding with spring warm up and gametogenesis, but there is no such correlation evident with another hot spot in southern New Brunswick (Gardner et al. 1991; Barber and Bacon 1999). Bivalve neoplasias, whether in cultured or wild populations, can be triggered by many different factors, including natural and anthropogenic causes.

Habitat degradation is well documented as having the potential to adversely affect bivalve health (Croonenberghs 2000; Dewey 2000; Moore 2000). For example, the ciliostatic properties of many *Vibrio* species (ubiquitous marine and estuarine Gram-positive bacteria) is well documented (DePaola 1981; Brown and Roland 1984; Nottage and Birbeck 1986; Nottage et al. 1989; DePaola et al. 1990). Although not demonstrated as being a factor in open-water (Tubiash 1974), the effects of these exotoxins on the ciliated larval stages of bivalves have been proven for numerous species under hatchery-rearing conditions (Tubiash et al. 1965, 1970; Elston et al. 1981, 1982, 2000; Elston 1989; Nicolas et al. 1992). Severity of infection is most commonly related to sub-optimal growing conditions (accumulation of dead or dying larvae, contaminated algal food, residual gametes, etc.) that enhance bacterial proliferation and compromise the immune responses of infected larvae (Elston 1989). Sensitivity to *Vibrio* spp. can vary considerably. Sindermann (1988) cites 10^2 *vibrio* cells·ml^{-1} as being potentially pathogenic to oyster larvae, while other bivalves can tolerate 10^5 cells·ml^{-1} (Perkins 1993). There is, therefore, a strong likelihood that chronic or acute blooms of these bacteria under open-water conditions could have a deleterious effect on bivalve larval recruitment, especially under conditions of warm water, rainfall and bivalve spawning (DeLuca-Abbott et al. 2000; Herwig et al. 2000). In addition, the effects of ciliostatic toxins on the ciliated digestive tracts of adult bivalves cannot be overlooked. At least two shell-deforming conditions in juvenile oysters and juvenile to adult clams have been linked to bacteria. 'Brown ring disease' of *Tapes* spp. in Europe is caused by a new *Vibrio* species, *V. tapetis* (Borrego et al. 1996; Castro et al. 1997; Novoa et al. 1998; Allam et al. 2000), and juvenile oyster disease of American oysters (*Crassostrea virginica*) is caused by a novel alpha-proteobacterium (Boettcher et al. 1999, 2000). Both these bacteria appear to proliferate in estuarine conditions and elicit energetically-costly defense mechanisms in the bivalves that are manifest in conchiolin deposition around the mantle margins. Histological profiles of the epithelial tissues of the mantle and digestive system have also shown extensive haemocyte infiltration, indicative of physiological stress (Plana and LePennec 1991; Allam et al. 1996). The linkage of these bacteria to overall habitat quality has yet to be determined.

Another set of recent studies has focused on immunosuppression induced in bivalves exposed to heavy metals and hydrocarbon-based chemical waste. The effect of these chemicals is complex, and initial results show a potential for hormesis (lower concentrations suppress haemocyte-mediated defence activities and greater concentrations show a neutral or increase in phagocytic activity), both ends of which have energetic costs to the bivalve (St-Jean 2002a,b). If these results are extrapolated for chronic, sub-lethal effects, some studies using scope for growth as a measure for carrying capacity may need to be revisited. This applies equally to the neoplasia conditions discussed above. Mortality and weakening due to infectious disease is relatively easy to quantify and correlate to environmental factors (epidemiology of the disease). However, immunosuppression and carcinogenic effects are more insidious and could readily be masked by or distort other more obvious environmental correlations. This is also important for assessment and interpretation of bivalve aquaculture impacts on environmental conditions. Weakening, impeded feeding and filtration activity, along with spawning failure or poor quality spawn can all contribute to morbidity, mortality and fall-off, with the environmental consequences discussed above.

There have been attempts to bring the effect of infection status on overall physiological performance of bivalves into bilateral correlations between physiological scope for growth and environmental carrying capacity as well as contamination, but such studies are rare and inconclusive (DaRos et al. 1998). Conceptual models of interactions between bivalve culture activities, eutrophication and ecosystem functioning are more rapidly evolving (Cloern 2001). But gaps in knowledge need to be addressed on how these and other stress components work together, if we are to broaden our understanding of cumulative environmental effects in the context of aquaculture.

INTEGRATION OF AQUACULTURE/ENVIRONMENT INTERACTIONS

A mechanistic understanding of coastal ecosystem functions is fundamental for formulating management strategies. The study of aquaculture ecosystems requires consideration of biological, physical, chemical and geological factors. Important biological processes include mussel feeding and egestion, as well as the dynamics of the supporting planktonic ecosystem and interactions with the benthic community. Physical processes governing water motion and mixing determine the transport and supply of dissolved and particulate matter. Nutrient dynamics and cycling depend on the transformations mediated by the various ecosystem components including bacteria. The sedimentation of particles is governed by the competing processes of flocculation and turbulence. These areas require research involving field measurements as well as comprehensive modelling studies that integrate available knowledge about natural- and human-driven parts of coastal ecosystems.

Coastal waters where aquaculture is practiced exhibit a variety of physical oceanographic processes (e.g. tidal and estuarine circulation). Dissolved and suspended matter in the water column are transported and mixed by water motion and eventually exchanged with the adjacent open ocean or deposited (utilized) locally. A basic understanding of particle dynamics requires tracking of the total particulate load (turbidity), food particles for shellfish (chlorophyll) and the water flux (mixing and exchange) (Grant and Bacher 2001). The effects of mussels on water column and sediment properties are influenced by circulation and mixing processes. It is hypothesized that the severity of these ecosystem effects in different coastal areas is regulated by water motion and mixing. Inclusion of oceanographic parameters is essential to a quantitative assessment of the validity of this hypothesis. Aquaculture effects are believed to be greatest in estuaries and inlets where water residence time is long and mussel biomass is high. In such areas, mussel feeding could dramatically reduce the concentration and alter the nature of suspended particulate matter, with the resultant potential to change pre-culture productivity within a defined area. In areas with greater flushing, water depleted of particles by mussels can be renewed by tidal exchange and culture-generated biodeposits may be flushed from the system.

A variety of models have been applied to assess the environmental interactions of bivalve aquaculture operations (Grant et al. 1993; Dowd 1997; Grant and Bacher 1998; Smaal et al. 1998; Meeuwig 1999). While all of the approaches include a comparison of physical water exchange to some sort of biological process like filtration, there are no standard methods for assessment of ecosystem effects. Bearing in mind the complexity of interacting factors, this is not surprising. Empirical studies, such as the calculation of budgets (e.g. carbon, nitrogen and energy) and simulation modelling, have been some of the more focused approaches to evaluating potential mussel aquaculture effects at an ecosystem level. As an example of the former, Carver and Mallet (1990) calculated the mussel carrying capacity of an inlet in eastern Canada by comparing estimated food demand to food supply based on organic seston concentrations delivered by a simple tidal prism model. The latter approach was used by Raillard and Menesguen (1994), who constructed a simulation model for a macrotidal estuary in France to describe relationships between oyster feeding, primary production and seston transport. Both approaches yield different, but complimentary, information.

Numerical models are powerful tools to help guide coastal ecosystem management because they integrate the important processes that represent this system complexity (Cloern 2001). The use of models also provides an excellent means to identify gaps in knowledge. Simulation models may be the most practical way to assess the potential net negative effect of mussel grazing on phytoplankton and zooplankton abundance and the potentially positive effect of increased remineralization on primary production (Fréchette and Bacher 1998). Similarly, ecosystem modelling can be used to quantitatively assess the contribution of cultured bivalves in combating eutrophication and of the ecological importance of nutrient losses in the mussel harvest. Fully coupled biological-physical models may be envisioned (e.g. Prandle et al. 1996; Dowd 1997) that predict ecosystem changes in chlorophyll, nutrients and other variables of interest as a function of culture density and location. To do this, shellfish ecosystem models, including carrying capacity models, must be integrated with information on water circulation, mixing and exchange to account for transport and spatial redistribution of particulate and dissolved matter. Box models (Raillard and Menesguen 1994; Dowd 1997; Chapelle et al. 2000) offer a practical means to couple coastal ecosystem models with physical oceanographic processes. The bulk parameterizations of mixing required for these box models can be derived directly from complex hydrodynamic models (Dowd et al. 2002). One interesting feature of the ecosystem model of Chapelle et al. (2000) is that the ecosystem effects of shellfish are incorporated by prescribing their biomass levels and, thereby, their effect of grazing and nutrient generation on the ecosystem, while avoiding the inclusion of mussel bioenergetic relations in detail. A promising avenue for improving ecosystem models is the use of inverse, or data assimilation, methods (Vallino 2000). These systematically integrate available observations and models, thereby combining empirical and simulation approaches, and improve predictive skill.

Simulation models that focus on estimating mussel carrying capacity and related ecosystem impacts provide effective tools for quantitative descriptions of how food is captured and utilized by mussels, as well as site-specific information on ecosystem variables and processes (Carver and Mallet 1990; Brylinsky and Sephton 1991; Grant 1996). An increased understanding of mussel feeding rates and efficiencies (ecophysiology) is fundamental to most model-based predictions of ecosystem effects, as the bivalve functional response is the basis for potential interactions between bivalves and the ecosystem. The ability to predict physiological responses of bivalves under culture conditions permits calculation of clearance, biodeposition and growth rates, and this ability presents tremendous opportunities to manage the sustainability of the industry (Carver and Mallet 1990; Labarta et al. 1998). From a mathematical perspective, the nonlinear functional relationships used to describe mussel bioenergetics have often led to poor model predictions due to their high sensitivity to inadequately known physiological parameters (Dowd 1997). Robust mathematical relations are being developed with the needs of simulation models in mind, such that bioenergetic models have been successful in predicting growth (Dowd 1997; Grant and Bacher 1998; Scholten and Smaal 1998).

Validation of models with field observations ('ground-truthing') is essential. *In situ* observations indicate where models are deficient and suggest how model structure should be altered. Model simulations can, in turn, provide a focus for field efforts. A variety of oceanographic instruments exists for monitoring biological and physical processes, and include tide gauges, current meters, fluorometers and transmissometers. Their deployment in mooring mode or as towed vehicles, in the case of particle sensors, is essential for monitoring the changing environmental conditions that occur at culture sites and the influence of mussels on these conditions. They also provide important ground-truthing information for other monitoring technologies such as remote sensing (Herut et al. 1999). Additionally, collection of data with this instrumentation is vital in the construction of models to predict the transport of water and particles at culture sites (Ouboter et al. 1998).

Decision-support systems have been developed that integrate available knowledge about natural- and human-driven parts of coastal ecosystems into computer-based models (Crooks and Turner 1999; deJonge 2000). While the prediction of future ecosystem changes is largely unfeasible as ecosystems do not exist in a stable state, computer models can be used to explore the main direction of effects on ecosystem functioning that result from various culture practices (deJonge 2000), and are useful for developing general ecological principles. It should also be emphasized that the study of culture impact using simulation models and field measurements can also be directed toward assessment of mussel growth and carrying capacity from the standpoint of farm management. For instance, bivalve studies based on physical transport of food particles to mussels and their bioenergetic use by the animals are part of a growth equation including biodeposition. The intake of food used to predict biodeposition is also part of a growth equation. Coupled with estimates of stocking density, these models produce farm yields, which may then be exported to economic models of profitability (e.g. Samonte-Tan and Davis 1998). An essential feature of the growth models is that they may be fully ground-truthed using mussel harvest/growth data from the farm sites. Ultimately, these models may be used to actively manage the location and extent of culture in coastal estuaries for multiple users. Such models will need to take into account culture dynamics, such as seed-stocking and fouling biomass, depth of activity and cumulative effects of neighboring human activities (e.g. agriculture run-off, construction sedimentation, boating and ballast activities, etc.).

Another new development that must be taken into consideration for ecological modelling is increasing interest in bivalve polyculture. Mussel culture, although predominant in Atlantic Canada, is rarely conducted in isolation from other bivalve culture. Some leases accommodate mussels, oysters, clams and, more recently, scallops. All have differing physiologies and production dynamics. Accurate modelling of single-species culture interactions with surrounding habitat ecology needs to take this into account in the future. Likewise, spat collection is frequently a 'hit and miss' operation, trying to maximize collection of the species of interest in amongst all the other bivalve species forming a continuum of production through the spring and summer spawning seasons. This further highlights the need to take the multi-species and interactive nature of bivalves into account, both within culture and pre-collection from the wild. As indicated at the start of this review, mollusc culture is much more intricately and inextricably linked to its environment than most finfish culture (even mariculture cages). Monospecific models of aquaculture interactions with habitat ecology cannot, therefore, be readily extrapolated to other bivalve species.

SYNOPSIS AND RESEARCH NEEDS

The culture of bivalve molluscs may involve a number of effects on the current state of coastal marine ecosystems. Extensive bivalve culture (suspended and benthic) has the potential for causing cascading effects through estuarine and coastal foodwebs, altering habitat structure, species composition at various trophic levels, energy flow and nutrient cycling. There have been few direct studies on the influence of mussels at the ecosystem level, but several studies have speculated on the potential for mussel cultivation to approach and even exceed the capacity of the ecosystem to maintain environmental quality (Deslous-Paoli et al. 1987; Rodhouse and Roden 1987; Asmus et al. 1990; Prins and Smaal 1990; Dame 1993, 1996). The rapid and extensive transformations of water bodies into mussel production could change the ecological function of some bays. Potential ecosystem-level effects (positive and negative) related to intensive bivalve aquaculture include the following:

- bivalve filter-feeder populations crop the resident phytoplankton so that they depend on the tidal input of offshore phytoplankton to sustain high density culture;
- large bivalve farming operations may help to reduce excess phytoplankton caused by eutrophication through grazing;
- the substitution of bivalves for zooplankton in estuaries and bays alters food webs;
- the increased sedimentation of organic matter through biodeposition acts to retain nutrients in the system;

- recycling of organic biodeposits increases the oxygen demand in sediments, generating an anaerobic environment that promotes ammonification and sulfate reduction;
- the rate of nitrogen cycling is increased through rapid deposition of organic matter, nutrient regeneration in sediments and the excretion of ammonia by mussels;
- a shortened cycle of nutrients between the benthos and phytoplankton may increase local nutrient availability as less material is exported; and
- the greater availability of nutrients leads to enhanced primary production, potentially contributing to more frequent algal blooms, including toxic species.

Few studies have been completed which adequately assess these potential environmental interactions of this newly developed industry, and few quantitative measures exist to measure ecosystem-level effects. A commonly employed means of addressing uncertainty resulting from gaps in knowledge is to establish rigorous environmental effects monitoring (EEM) programs that can provide early warning of adverse environmental effects and aid in identifying unforeseen effects (additional areas of concern). However, research is also needed to develop ecosystem-based EEM approaches and indicators that specifically address the close linkage that exists between cultured bivalves and numerous biotic (ecosystem structure and function) and abiotic ecosystem components. Development of effective EEM approaches would help to minimize the potential for exceeding system carrying capacity, while benefiting industry by optimizing farm yield.

The following research topics and associated research and development studies were identified by the authors for further study. While short-term laboratory and field studies at culture operations will be useful to address the identified gaps in knowledge, longer-term studies at new lease development sites (baseline to full development sampling) would be particularly insightful. While an immediate need for such research exists for heavily leased PEI embayments, the extensive development of the mussel industry in PEI largely precludes such studies, owing to the lack of many baseline data and difficulties in selecting the control sites needed for effective experimental designs. Such studies may be best conducted in regions where the industry is less well-developed. Intentional ecosystem manipulation experiments could also provide insights but would be both challenging and costly. Readers should note that the following separation of research topics is strictly an exercise to identify specific gaps in knowledge. The development of a mechanistic understanding of the temporal and spatial scales of ecosystem-level impacts from bivalve aquaculture requires a closely integrated multidisciplinary approach that includes major elements from each of the following research topics. Such an approach will permit even short time/small space observations to be fully utilized to address the long-term/large space issue that is the topic of this review.

1. *Ecological role of bivalve filter-feeders.* Studies are required to improve our understanding of the density-dependant role of bivalves in controlling phytoplankton and seston (including microbes) concentrations, and to determine if bivalves have a net negative (reduce standing stock) or positive (stimulate production) effect on suspended matter concentrations.

- Conduct seasonal studies of suspended particulate matter, phytoplankton biomass and primary production in estuarine and coastal systems under culture, and use the results to assess the potential for overgrazing of food resources by cultured bivalves.
- Determine the effect on suspended particulate matter, phytoplankton abundance, community structure and production of different levels of bivalve grazing pressure.
- Assess the capacity of available *in situ* and remote sensing technologies to visualize near- and far-field effects of mussel aquaculture on suspended particle fields (e.g. chlorophyll).

2. *Bivalve bioenergetics.* Given that bivalve physiological processes (feeding, respiration, biodeposition and excretion) are the primary mechanisms for potential interactions between bivalve aquaculture and the ecosystem, and therefore the sustainability of coastal operations, a more complete understanding of the physiological ecology of each species is needed to facilitate accurate prediction of ecosystem responses.
   - Identify interspecific differences in feeding and absorptive selectivity, particularly under field conditions, to quantify contributions from different food resources (e.g. retention of bacteria, differential ingestive and absorptive selection for algal species, and absorption efficiency of detritus sources) for use in carrying capacity predictions.
   - Develop robust predictive relations for the functional responses of culture species to environmentally relevant conditions.
   - Establish a clear genetic base to bivalve physiological performance.
   - Quantify the effect of the variable energy demands of gonad growth on bivalve feeding behavior.
   - Use mathematical relations for bivalve responses to internal and external forcing for continued improvement of bioenergetic models. Test growth predictions using site-specific harvest/growth data from aquaculture farms.

3. *Organic loading.* Studies are needed to determine the capacity of different coastal ecosystems to assimilate organic matter for use in predicting environmental impacts and ecosystem management.
   - Quantify organic biodeposition rates, benthic organic enrichment effects (e.g. anoxic conditions, sulfate reduction and reduced biodiversity) and recovery times at aquaculture and reference sites.
   - Study the settling and transformation of fecal wastes as a function of different physical environmental conditions.
   - Quantify the capacity of different environmental conditions to mediate organic enrichment impacts from aquaculture.
   - Develop and test surrogate measures of the total assimilative capacity of coastal systems.

4. *Nutrient dynamics*. Conduct detailed studies of nutrient dynamics in coastal systems, including those supporting and associated with bivalve aquaculture, to address the potential effects on nutrient availability and cycling.
    - Confirm nutrient limitation of phytoplankton production in coastal embayments, and identify biotic and abiotic processes contributing to nutrient limitation.
    - Document the import and export of nutrients in coastal aquaculture ecosystems, and determine the role of cultured bivalves in retaining and promoting the rapid recycling of nutrients within the system.
    - Assess the relative importance of bivalve excretion and particle biodeposition in the recycling of nutrients and the production of phytoplankton.
    - Conduct field studies to provide insights into potential interactions between nutrient dynamics and the onset of harmful algal blooms, especially those of the domoic-acid-producing diatom *Pseudo-nitzschia multiseries*.
    - Assess the potential consequences to ecosystem productivity of large nutrient losses to the bivalve harvest.

5. *Ecosystem structure*. Investigate the ecosystem-level effects of bivalve culture on ecosystem structure (abundance and biodiversity of pelagic and benthic communities) through direct competition for food resources by bivalves, zooplankton and epibionts, and the transfer of energy and nutrients to the benthic foodweb.
    - Assess the implications of reduced zooplankton abundance and composition on higher trophic levels including fish.
    - Determine the ecological role of fouling organisms (epibionts) associated with bivalve culture.
    - Investigate the ecological risk imposed by the introduction and transfer of exotic fouling and infectious agents with live shellfish transfers.
    - Investigate the ecological risk related to the potential increased incidence of infectious diseases associated with intensive culture operations.

6. *Cumulative effects.* Assess cumulative effects of anthropogenic land- and marine-use on coastal ecosystems.
    - Conduct research on the inputs and impacts of sediment, toxic chemicals, animal waste (including bacteria) and nutrients reaching embayments supporting bivalve aquaculture.
    - Assess the capacity of bivalve aquaculture to mitigate coastal eutrophication trends through their grazing on phytoplankton.
    - Investigate the effect of aquaculture on marine particle aggregation processes (particle dynamics) and the consequences to coastal sedimentation trends.
    - Conduct studies on the potential for culture activities to alter the transport and fate of particle-reactive contaminants originating from land-use.

7. *Ecosystem modelling.* Integrate knowledge obtained on the consequences of bivalve culture to ecosystem structure and function through the use and predictive power of ecosystem modelling.

- Test the ability of models to provide decision-support for the development of effective area-wide management strategies for promoting the environmental sustainability of the aquaculture industry.
- Conduct sensitivity analyses of modelled variables to assess the suitability of different ecosystem indicators for use in characterizing and monitoring ecosystem health and productive capacity.
- Develop and utilize new instrumentation and data collection strategies to obtain ecosystem data, including measurements of contaminants, for testing (ground-truthing) model predictions.
- Use models to test the hypothesis that the severity of aquaculture impacts in different estuaries is regulated primarily by water motion and mixing.

8. *Ecosystem status.* Develop indicators (methodologies and technologies) for use in aquaculture monitoring programs that provide information on ecosystem function. Test the effectiveness of selected indicators for detecting potential ecosystem-level effects of bivalve aquaculture. Identify indicator reference points that characterize ecosystem status.
    - Identify sensitive and cost-effective ecosystem health indices.
    - Establish baseline environmental conditions and the degree of natural variation in ecosystem health indices.
    - Develop a scheme for classifying the state of ecosystem functioning, including the identification of relative threshold levels.
        - Establish cause-effect relationships between culture practices (e.g. stocking density and husbandry practices) and identify candidate indicators.
        - Develop standard protocols for rapidly assessing mussel performance (growth rate, meat yield and yield per sock) at lease sites as an indicator of ecosystem impacts (i.e. impact on growth depends on impact of mussels on environment), and establish cause-effect relationships between environmental conditions and mussel performance.
        - Develop tools that incorporate information provided from ecosystem indicators that provide an integrated assessment of ecosystem status.

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