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A Review of the Pathways-of-Effects Associated with the Removal and Release of Organic Material from Shellfish Aquaculture

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

This document reviews the scientific knowledge related to the stressor category "Release and removal of nutrients, non-cultured organisms and other organic material" in relation to the Site and Stock Management of shellfish farming, as identified in the Aquaculture Pathways of Effects developed by DFO's Aquaculture Management Directorate. The issues discussed here relate to the nature, scale and scope of these influences and an understanding of the potential for predicting and modeling these processes, placed within a Pathways-of-Effects context. A simplified conceptual diagram of the potential connectivity between shellfish aquaculture pressures and the state of coastal ecosystems (structure and function) is provided. Shellfish aquaculture represents a net addition of habitat to an ecosystem and requires minimal additions to the environment. Their food is extracted from the environment and their wastes return some nutrients and minerals back to the ecosystem. Concerns have been raised about the possible effects of extensive shellfish culture operations on coastal marine ecosystem and the related risks to the ecological functioning and sustainability of these regions. Such as, alterations to nutrient pathways by three basic mechanisms: biodeposition, accumulation and remineralization of organic matter to benthic habitat; the removal of seston in a bay to support the growth of cultured shellfish can alter the water column habitat bio-diversity, particle size, and trophic structure; and the translocation of organic matter remineralization from pelagic to benthic food webs. Key areas of stressor-effects uncertainty include impacts to higher trophic levels, farfield consequences of net reduction in production due to shellfish harvest (i.e., nutrient removal).

Examen des séquences des effets associées au retrait et au rejet de matière organique dans le cadre de la conchyliculture

RÉSUMÉ

Ce document passe en revue les connaissances scientifiques sur la catégorie d'agents de stress « Retrait et rejet de nutriments, d'organismes non cultivés et d'autre matière organique » en lien avec la gestion des sites et des stocks de conchyliculture, conformément à la définition donnée dans les séquences des effets de l'aquaculture élaborées par la Direction générale de la gestion de l'aquaculture (DGGA) de Pêches et Océans Canada (MPO). Les enjeux qui y sont discutés concernent la nature, l'échelle et la portée de ces répercussions, ainsi que la compréhension du potentiel de prévision et de modélisation de ces processus, dans un contexte de séquences des effets. On présente un diagramme conceptuel simplifié du lien potentiel entre les pressions exercées par la conchyliculture et l'état des écosystèmes côtiers (structure et fonction). La conchyliculture constitue l'addition nette d'un habitat à un écosystème et nécessite un minimum d'ajouts à l'environnement. Les mollusques extraient leur nourriture de l'environnement, et leurs déchets contiennent quelques nutriments et minéraux qui sont rejetés dans l'écosystème. Des préoccupations ont été soulevées quant aux effets possibles des entreprises qui pratiquent la conchyliculture extensive sur l'écosystème marin côtier et aux risques connexes pour la durabilité et la fonction écologiques dans ces régions. Voici des exemples de modifications de la circulation des nutriments par trois mécanismes : la biodéposition, l'accumulation et la reminéralisation de la matière organique dans l'habitat benthique; le retrait du seston dans une baie pour soutenir la croissance des mollusques d'élevage peut modifier la biodiversité de l'habitat de la colonne d'eau, la taille des particules et la structure trophique; le transfert de la reminéralisation de la matière organique du réseau trophique pélagique au réseau benthique. Les principaux domaines d'incertitude entourant le lien entre les agents de stress et les effets comprennent les impacts sur les niveaux trophiques plus élevés et les conséquences lointaines d'une réduction nette de la production attribuable à la cueillette des mollusques (c.-à-d. retrait des nutriments).

INTRODUCTION

The Pathways of Effect initiative led by the Aquaculture Management Directorate of Fisheries and Oceans Canada has identified three major categories of aquaculture activity, seven categories of stressors and twenty specific stressors that lead to eleven categories of ecosystem effects.

The specific categories of aquaculture activities are

1. Placement and Removal of Site Infrastructure;
2. Site and Stock management and
3. Use of Industrial equipment.

The seven categories of stressors are

1. Alteration of light
2. Release of chemicals and litter
3. Release of pathogens
4. Release and removal of fish
5. Release and removal of nutrients, non-cultured organisms and other organic material
6. Physical alteration of habitat structure, and
7. Alteration of Noise

The twenty potential (or possible) specific stressors are:

1. Photoperiod manipulation
2. Shading adjustments
3. Release of antifoulants
4. Release of therapeutants
5. Release of cleaners & disinfectants
6. Release of litter
7. Release of fuels & lubricants
8. Release of pathogens
9. Release of cultured organisms
10. Removal of predators
11. Crushing/ killing of benthic organisms
12. Release of fouling organisms
13. Removal of food and oxygen (as a result of increase in biomass of cultured organisms)
14. Release of harvest waste and mortalities
15. Release of excretory waste & excess feed

16. Release of human waste
17. Addition/removal of shoreline/bottom structure
18. Addition/removal of vertical site infrastructure
19. Resuspension/entrainment of sediments, and
20. Noise

The eleven categories of ecosystem effects are:

1. Wild /farmed fish health
2. Wild fish populations/communities
3. Habitat structure, cover and vegetation
4. Access to habitat /migration routes
5. Substrate composition
6. Food availability/ food supply
7. Primary productivity
8. Water flow
9. Oxygen (water column, benthos)
10. Contaminant concentration, and
11. Suspended sediment concentration

Which are grouped into four categories are:

1. fish health
2. fish communities
3. fish habitat, and
4. water quality

The primary purpose of this review is to place the existing scientific knowledge in the context of a pathways-of-effect as described by the Aquaculture Governance Renewal Committee lead by Fisheries and Oceans Canada. This document reviews the scientific knowledge related to the pathways of effects for the stressor category "Release and removal of nutrients, non-cultured organisms and other organic material" in relation to the Site and Stock Management of shellfish farming. A companion paper[1] reviews the knowledge in relation to this stressor category for finfish culture.

We rely heavily on the information compiled as part of the Cranford et al. (2003) state of knowledge review of the literature on Ecosystem Level Effects of Marine Bivalve Aquaculture

[1] CSAS Working Paper: Page, F., Chamberlain, J., Robinson, S., Reid, G., Chang, B. A Review of the Pathway of Effects associated with the releases of nutrients and organics from finfish netpen aquaculture.

and the DFO CSAS reviews produced for the 2006 National Science Workshop – Assessing Habitat Risks Associated with Bivalve Aquaculture in the Marine Environment (DFO, 2006). Additional information and text was provided by one of the reviewers (Cranford) that was pre-publication draft material which was subsequently published in Cranford, Ward and Shumway 2011 – Bivalve Filter Feeding: variability and limits of the aquaculture biofilter (Cranford et al., 2011). Although we refer to additional literature, much of this report is simply a reorganization of the above materials into a Pathways-of-Effect context. We do not claim to have conducted an independent extensive review of the scientific literature. The literature cited in the present document is therefore limited and readers are directed to refer to the above reviews for a more fulsome and extensive list of relevant references.

That shellfish aquaculture activities have an influence on their surrounding environment is clearly and definitively detailed within the scientific literature. The issues discussed here relate to the nature, scale and scope of these influences and an understanding of the potential for predicting and modeling these processes, placed within a Pathways-of-Effects context. A simplified conceptual diagram of the potential connectivity between shellfish aquaculture pressures and the state of coastal ecosystems (structure and function) is provided in Figure 1.

Unlike intensive finfish farms where a primary environmental concern is the consequence of increased organic matter loading, shellfish aquaculture represents a net addition of habitat to an ecosystem and requires minimal additions to the environment – except for the animals themselves and the infrastructure upon which they grow. Their food is extracted from the environment and their wastes return some nutrients and minerals back to the ecosystem.

Industry husbandry practices for rearing various shellfish species include a wide array of options including floating cages, bottom cages, bottom plots, suspended collectors, rafts, tables, longlines and poles. Potential marine shellfish culture sites are not nearly as limited by hydrodynamics and bathymetric conditions as is the case for finfish; suitable shellfish aquaculture sites span a wide spectrum of habitats from the intertidal zone to shallow and deep coastal embayments. This broad range of husbandry techniques and habitats translates into a greater complexity of potential environmental interactions and pathways-of-effects. Certain culture methodologies and practices have been identified as having a greater potential for environmental impact than others (ICES, 2004). This disparity among the effects of different industry practices is related primarily to variations in stocking densities per unit area and differences in environmental sensitivity or ability to absorb the impacts of bivalve culture. Of particular concern is the longline culture of mussels which is believed to have a relatively high potential for local and bay-wide impacts (ICES, 2004). This rearing technique involves the deployment of densely packed mussel cohorts throughout much of the water column, resulting in relatively high stocking densities per unit area and volume compared with other species currently cultured in Canada. At present long-line mussel culture constitutes around 80% of the shellfish aquaculture landed value in Canada.

Determining the net impact of shellfish aquaculture on fish habitat, community structure and ecosystem productivity is complex and requires an objective and holistic approach. Indeed, a number of studies (see McKindsey et al., 2006a) consider the beneficial “impacts” of shellfish aquaculture. This area was considered beyond the scope of this current report but is recognized as an area that should be investigated further.

Concerns have been raised about the possible effects of extensive shellfish culture operations on coastal marine ecosystem and the related risks to the ecological functioning and sustainability of these regions. In their extensive review, Cranford et al. (2006) identified that shellfish aquaculture operations can result in alterations to nutrient pathways by three basic mechanisms:

1. The biodeposition, accumulation and remineralization of organic matter in shellfish feces and pseudofaeces can alter benthic habitat by changing biogeochemical properties and biological community structure (flora and fauna of all sizes);

2. The removal of a significant fraction of the total natural seston in a bay to support the growth of cultured shellfish can alter the water column habitat bio-diversity, particle size, and trophic structure and its suitability for other marine organisms;

3. The translocation of organic matter remineralization from pelagic to benthic food webs and the excretion of ammonia by culture shellfish can alter the nutrient dynamics (e.g., recycling rates, retention of nutrients in coastal systems, nutrient ratios) and affect habitat and community structure.

Cranford et al. (2006) pointed out that under some conditions all three mechanisms, in addition to potentially altering community structure, can also influence biological productivity, with potential cascading effects on ecosystem structure and function. Examples of potential effects of aquaculture on productivity include:

- stimulation of primary productivity due to increased nutrient availability and cycling rate associated with the effects of shellfish grazing (Cranford et al., 2003);
- decline in the productivity of benthic infauna in the presence of toxic sulphides (Cranford et al., 2003); and
- increase in the productivity of demersal and macrobenthic predators attracted to feed on cultured species, fouling organisms, and on small polychaetes, typically found in organically enriched sediments (ICES, 2005).

Cultured shellfish (for the purpose of this review including only bivalve molluscs) and associated rearing structures have the potential to impact the environment in positive and negative ways. Four basic areas of concern are the effects of bivalve culture on: (1) suspended particles, particularly in terms of food resources; (2) sediment geochemistry/benthic habitat; (3) nutrient cycling; and (4) benthic and pelagic population dynamics/community structure. Cranford et al. (2006) illustrated general shellfish aquaculture – environment interactions reproduced in Figure 2.

This current review examines the activity Site and Stock Management of shellfish aquaculture operations, linked to the stressor category of release/removal of nutrients, non-cultured organisms and other organic matter.

The following sections review the pathways of effects associated with nutrient removal; nutrient release to the water column and benthos and a discussion of the environmental consequences of these releases. A final summary section reviews the data gaps and future research needs.

REMOVAL OF NUTRIENTS

The influence of bivalve filter feeding on the pelagic ecosystem is very well studied and is well reviewed in, among others, Dame (1996), Prins et al. (1998), and Newell (2004). Dense bivalve populations, which in this review focuses mainly on mussels, have an exceptional capacity to filter large volumes of water and, as opportunistic feeders, exert a strong influence on suspended particulate matter (seston) concentrations.

Bivalves live in a highly dynamic physical environment with both temporal and spatial variability in the quantity and quality of available food (Prins et al., 1998). Advective processes, resuspension and wave action can all affect temporal and large-scale spatial variability in food supply (Berg and Newell, 1986; Fréchette et al., 1989; Asmus et al., 1990; Prins et al., 1996; Smaal and Haas, 1997). The types of food utilized include phytoplankton, ciliates, flagellates, zooplankton and detritus (Bayne et al., 1989; Dame, 1993, 1996; Jorgensen, 1996; Smaal et al., 1997) which occur within a diverse and variable seston mixture of organic and inorganic materials (e.g., Trottet et al., 2008).

Filter-feeding by mussels naturally results in some local reduction (depletion) of those particulates consumed and thus imposes a change to the overall composition the seston. This process may also alter primary productivity, change algal community composition (Prins et al., 1998), and modify the fluxes of material and energy though the ecosystem (Cloern, 1982; Officer et al., 1982; Cohen et al., 1984; Yamamuro and Koike, 1993; Dame, 1996).

Particle depletion was characterized by Cranford et al. (2006) as a significant reduction in suspended particulate matter resulting from consumption by cultured shellfish – with a specific cautionary note that the word "depletion" should not be perceived as having a negative connotation as food consumption by any filter feeder results in some level of depletion. However, in cases where bivalve feeding rates exceed the replenishment rate mediated through tidal flushing and phytoplankton growth, then the mussels will become food limited and production/productivity will be less than maximal (Cranford et al., 2008).

In cases where the spatial scale of phytoplankton depletion includes a significant fraction of a coastal inlet or embayment, Cranford et al. (2011) suggest that effect may lead to broader consequences ("ecological costs") to other components of the ecosystem. It is in such cases where the culture activity has been described as exceeding the 'carrying capacity' of the area (see McKindsey et al. (2006b) for broader discussions on the different types and definitions of carrying capacity issues).

The removal of particulate matter may be beneficial in preventing eutrophication in estuaries where agricultural runoff results in additions of dissolved nutrients that stimulate phytoplankton production (Cranford et al., 2003; Newell, 2004). Indeed, the introduction of shellfish filter feeders to eutrophic coastal regions has been widely promoted as a potentially valuable tool for mitigating or buffering the negative habitat effects of nutrient enrichment (e.g., Rice, 2001). Shellfish aquaculture in nutrient enriched systems has the benefit of not only controlling excess phytoplankton biomass but also results in the removal of excess nutrients from the region in the shellfish harvest.

The capacity for shellfish feeding to deplete particles is controlled, in part, by the efficiency of the gill to capture particles. Suspension feeding bivalves are able to retain suspended particles larger than 3-7 μm with 100% efficiency (varies with species). There is a steep decline in retention efficiency below this size range and less than 50% of 1 μm particles are retained by mussels and oysters (Møhlenberg and Riisgard, 1978). Most picoplankton (0.2 to 2.0 µm) are therefore not effectively captured as a food source by bivalve filter feeders. The upper limit to particle consumption by shellfish is between 0.5 and 6 mm (500 and 6000 µm; Karlsson et al., 2003), which includes mesozooplankton (100 to 1000 µm). The potential importance of size selectivity of feeding activities on broader ecosystem functioning was described in Cranford et al. (2008). Differences in the size spectra of resident phytoplankton was noted between bays that contained farms (dominated by picophytoplankton) and those that were unfarmed (dominated by microphytoplankton). The study showed a close relationship between the average bay-wide picophytoplankton contribution and the risk of bay-scale seston depletion by mussel culture (Figure 3). They suggested that such changes in the size spectra of phytoplankton could result in changes to predator-prey relationships and overall nutrient flux dynamics.

It is important to note that in addition to the process of feeding, 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; Jorgenson, 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) has been recommended. For example, 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. A range of estimates from median to maximum clearance rates all show that dense populations of bivalves can control the phytoplankton over large scales under certain conditions. A metaanalysis of published clearance rate data (Cranford et al., 2011) was conducted to aid modellers select rates that represent average conditions in nature (e.g., Figure 4).

Although not usually considered in “ecosystem modelling” for bivalve culture carrying capacity studies (but see Dowd, 2005; Jiang and Gibbs, 2005), a large concentration of filter-feeding bivalves in the water column, as is found in bivalve culture operations, may have an influence on zooplankton communities. Bivalves may filter out an unknown proportion of the zooplankton in an area, including typical zooplankton species as well as meroplankton of fishes and other commercially important species (Gibbs, 2004). Dame (1993) suggested that bivalves are largely assumed to filter out mostly small organisms from the water column. For example, Lam-Hoai et al. (1997) and Lam-Hoai and Rougier (2001) reported that the abundance of microzooplankton was reduced in areas with bivalve farming, relative to sites without it, suggesting that this was due to grazing by the bivalves in culture and their associated fauna. However, other work has shown that bivalves may also be consumers of larger benthic and pelagic organisms (Davenport et al., 2000; Lehane and Davenport, 2002). Davenport et al. (2000) showed that 30-35 mm mussels (*M. edulis*) could consume both 300 μm *Artemia* sp. nauplii and 1-1.2 mm copepods in the lab. Field studies reported in the same study found that mussels consumed (based on stomach content analysis) copepods (< 1.5 mm), crab zoeas (2 mm), fish eggs (1-2 mm), and even amphipods (5-6 mm). Subsequent to this, Lehane and Davenport (2002) showed that mussels consumed organisms up to 3 mm in length and that cockles (*Cerastoderma edule*) and scallops (*Aequipecten opercularis*) are also capable of consuming considerable quantities of zooplankton, both when suspended in the water column and when on the bottom.

ECOLOGICAL CONSEQUENCE

Shellfish farms have the potential to significantly alter the pelagic ecosystem. Depending on site-specific conditions, there is potential for bivalve farming operations to exceed the ecological carrying capacity of the body of water in which they are located owing to the ecological effects of suspension feeding. Ecological carrying capacity may be defined as the stocking or farm density above which unacceptable ecological impacts begin to manifest (see McKindsey et al., 2006b). This happens when the removal of seston by all bivalve farms in a water body, including any individual lease being assessed, outstrips the capacity of the ecosystem to replenish the supply, resulting in adverse conditions for wild and cultured populations.

The nature and scale of effect of any individual or multiple shellfish farming operations on phytoplankton and seston are predictable as the major site specific variables affecting the spatial and temporal characteristics of the effect are well known. Relatively simple modeling approaches for assessing the risk of far-field pelagic effects are available that include a comparison of the major physical (bay flushing time) and biological processes (water clearance time and primary production turnover time) that largely determine the ecological risk. The effect on higher trophic levels is much less certain although destabilization of phytoplankton biomass and composition at the scale of coastal ecosystems will have significant ecological consequences.

RELEASE OF NUTRIENTS

There is an extensive literature describing how high numbers of filter-feeding shellfish can alter nutrient dynamics in their environment (see Dame, 1996 and Cranford et al., 2003). Shellfish consume the organic nutrients in the organisms and detritus upon which they feed, excrete dissolved nutrients in their metabolic wastes, and deliver organic materials containing nutrients to the benthos in their faeces and pseudofaeces. The rate of nutrient cycling may be increased both by the excretion of dissolved wastes and by the more rapid remineralization of organic wastes in organically enriched environments, both in the community surrounding the cultured organisms and in the underlying benthos. Nutrients released by these processes may stimulate primary production. Dense bivalve populations and communities are known to have a dominant influence on the nitrogen cycle in coastal ecosystems with the degree of control depending largely on site-specific hydrographic conditions (Dame, 1996; Newell, 2004; Cranford et al., 2007). Bivalves exert “bottom-up” nutrient control on the phytoplankton by (1) the excretion of large amounts of nitrogen (primarily ammonia) and (2) by depositing organic matter from ingested phytoplankton and detritus (also includes remnants from ingested auto- and heterotrophic microplankton and zooplankton), which facilitates the benthic recycling of nitrogen. The increased organic loading of sediments from biodeposition may enhance the retention of nutrients, coming from both the sea and land, in coastal systems and stimulate mineralization and nitrogen release rates (Newell, 2004; Nizzoli et al., 2006). Accelerated nitrogen cycling and coastal nitrogen retention directly attributed to bivalve excretion and biodeposition may significantly accelerate phytoplankton turnover and production (Doering and Oviatt, 1986; Doering et al., 1989; Asmus and Asmus, 1991; Prins et al., 1995).

Addressing the issue of linking shellfish culture to biological productivity requires close attention to the spatial scale in question. As noted above, aquaculture can accelerate nitrogen cycling and coastal nitrogen retention, but the increase in primary production is at the lease to coastal ecosystem scale. The enhanced primary production and more rapid sedimentation of organic matter to the seabed may, depending on site-specific conditions, intensify biofouling, demersal, and macrobenthic production and likely even increases shellfish production carrying capacity. However, this bivalve-mediated creation of a productivity “hot spot” has to be balanced by a reduction in primary to tertiary production in the far-field. Conversely, the shellfish harvest removes nutrients from the environment and therefore will decrease overall production levels accordingly if nutrients are limiting production. The significance of this later effect has not been studied beyond the application of shellfish culture for mediating excess nutrient release from land run-off.

There is ample empirical evidence to show that aquaculture may change the functioning of the food web by translocating production from one trophic level and habitat to another. For example, bivalve grazing and biodepositIon takes production from the pelagic environment and channels more of it through benthic communities. The increased local benthic production likely comes with the cost of decreased micro- to mesozooplankton production. Trophic interactions in planktonic food webs are highly complex, but when the zooplankton are treated simply as a functional ecological group, the outcome from decreased zooplankton production is predictable at higher trophic levels.

TO THE WATER COLUMN

Shellfish excrete ammonia and other nutrients and, if excreted in sufficient quantities under some conditions, can significantly impact coastal nutrient dynamics. Specific impacts discussed by Cranford et al. (2006) include:

- Increased ammonia levels may promote phytoplankton production and/or alter phytoplankton species composition which may in turn affect grazer species composition and abundance.
- Increased rates of nitrogen cycling in coastal regions due to the more rapid deposition of suspended organic matter and the subsequent nutrient regeneration in sediments.
- Increase in local nutrient availability as less material is exported from the system.
- More frequent algal blooms due to the greater availability of nutrients. Importantly, although there has been much speculation on the contribution of bivalve culture to the incidence of harmful algal blooms (HABs), there is no evidence supporting a direct link.
- Harvesting of bivalves contributes to the removal of excess nutrients from eutrophicated coastal systems, but effectively represents a net loss from nutrient-limited systems.

High concentrations of shellfish can influence dissolved concentrations of inorganic forms of nitrogen, phosphorus and silicate: ammonia and phosphate are excreted, and ammonia, phosphate and silicate are released from benthic environments by the decomposition of shellfish biodeposits (Dame et al., 1991; Smaal and Prins, 1993; Prins and Smaal, 1994; Strain, 2002). Excretion of ammonia by dense bivalve populations appears to exert a controlling influence on nitrogen concentrations in some coastal regions (Dame et al., 1991), including a mussel culture site in Nova Scotia (Strain, 2002), and this aspect of bivalve culture may have a positive effect on the phytoplankton (Maestrini et al., 1986; Dame, 1996). The relative importance 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 remains the subject of ongoing and future research. Excretion could result in a change in the composition of the inorganic forms of nitrogen, resulting in increasing ammonium:nitrate ratios relative to natural ratios. Ammonium is preferentially utilized by the small pico-phytoplankton (Wafer et al., 2004) that are not efficiently grazed by shellfish. Ammonia is also an important nitrogen source for heterotrophic bacterial growth (Kirchman, 1994). 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). Thus, not only do shellfish selectively graze the larger phytoplankton forms, they also enhance the growth of the smaller forms through their excretion products.

Because nitrogen is usually considered to be the nutrient limiting primary production in coastal ecosystems, the most attention has been paid to nitrogen cycling. However, shellfish culture also has the potential to affect nitrogen:phosphorous (N:P) and nitrogen: silicon (N:Si) ratios, with the speculation of possible consequences for phytoplankton dynamics and development of Harmful Algal Blooms (Cranford et al., 2006).

The additional flux from fouling organisms and water column regeneration of trapped organic matter will increase the potential for significant ecological outcomes from shellfish aquaculture. The remineralization of nutrients in egested organic matter that becomes trapped around the bivalves will result in additional, potentially limiting, nutrients becoming available to phytoplankton. Nitrogen fluxes from the recycling of biodeposits trapped within suspended bivalve culture ropes and other structures have been found to be ecologically significant and can be higher than benthic fluxes (Mazouni, 2004; Richard et al., 2006; Nizzoli et al., 2006).

Finally, dense concentrations of cultured bivalves may have very high reproductive output capacity. The relative importance of the addition of this mass of larvae into the receiving ecosystem, both in terms of nutrients and biologically active particles, remains virtually unknown.

ECOLOGICAL CONSEQUENCE

Nutrient releases to the water column can constitute a major ecosystem flux depending on specific site conditions. There is little empirical information available on localized or ecosystem effects of nutrient releases to the water column from shellfish farming operations (excretion by shellfish and epifauna and remineralization of trapped organic matter). Assessment of ecosystem level outcomes overlaps with effects from the shellfish nutrient release to the benthic remineralization pathway. However, ecosystem modelling has shown that excretion by shellfish culture alone constitutes a major nitrogen flux relative to natural pelagic pathways. Clear stressor-impact linkages are difficult to make at this time, largely as a result of the complexity of the issue and interactions between multiple aquaculture and other nutrient releases in the coastal zone.

TO THE BENTHOS

One of the primary ways that suspended shellfish aquaculture may modify the ecosystem is by increasing the downward flux of organic matter. By filtering suspended organic matter and changing the packaging to larger, more rapidly sinking particles (faeces and pseudo-faeces), the shellfish can enhance the flux of organic material to the bottom. Bivalves effectively remove natural suspended matter with particle sizes greater than 1 to 7 µm diameter (see discussion above in removal of nutrients section), 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). In depositional environments, this increased flux can result in a significant organic enrichment of the sediments beneath the culture operation, increasing sediment oxygen demand and, in extreme situations, enhancing the risk of bottom anoxia.

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.

The effects of increased sedimentation, through biodeposition processes, from suspended mussel cultures, on their surrounding benthic environment, have been considered in a number of studies and are reviewed in detail in Mckindsey et al. (2006a) and Cranford et al. (2006).

Reported effects vary considerably between studies, with descriptions of the physico-chemical and biological structure of the proximal seabed ranging from no observable effect (Crawford et al., 2003b; Danovaro et al., 2004), through slight modifications to the benthic status (Baudinet et al., 1990; Grant et al., 1995), to highly impacted and enriched conditions (Dahlback and Gunnarson, 1981; Stenton-Dozey et al., 2001). Interestingly, when observed, the location of benthic effect is generally confined to a small area extending no more than a few tens of metres from the farm boundary (Mattson and Linden, 1983; Chamberlain et al., 2001; Hartstein and Rowden, 2004, Weise et al., 2008). Hatcher et al. (1994) suggested that as mussel faeces and pseudofaeces are derived from phytoplankton and suspended sediment, they would have similar organic matter to natural sedimentation. Hence, a large volume of mussel biodeposits found beneath a site would represent an increase in total organic deposition driven by a total increase in sedimentation. Consequently, increased sedimentation through biodeposition processes may effectively lead to organic enrichment of the seabed surrounding mussel farms with a subsequent alteration in the physico-chemical and biological status of the proximal seabed conditions.

Differences in the magnitude of a farm's influence likely depend on farm (e.g., farm size, stocking density and age of operation) and site (e.g., bathymetry and hydrodynamic regime) characteristics (Black, 2001; Chamberlain et al., 2001; Hartstein and Rowden, 2004; Hartstein and Stevens, 2005).

However, as previously noted, these effects are not always observed – biodeposits from mussel farms thus may, or may not, have significant effects on the benthos. A number of factors have been suggested to account for the disparate observations of effects of farms on their local environment. Chamberlain et al. (2006) considered that these factors may be combined into three broad categories that are characterized by how they influence the potential effect:

- Group A: quantity and quality of material exiting the farm
- Group B: dispersion of material exiting the farm
- Group C: fate of waste material post-deposition

Indeed, Chamberlain et al. (2001) considered that the production tonnage of a farm and food availability to stock (Group A) and dispersion of biodeposits from the farm site (Group B) were important factors in determining the final fate of faecal material and any subsequent impact on the benthos. They suggested that current velocity variations could explain the differences in the influence on macrofaunal assemblages reported in other studies. Similarly, Hartstein and Stevens (2005) proposed that given a particular rate of ejection of material into the water column, the rate of arrival per unit area will be strongly a function of hydrodynamic factors serving to spread the material (Group B).

Potential impacts on the benthic habitat as a result of organic nutrient release are:

- Recycling of organic biodeposits increases the oxygen demand in the sediments, potentially generating an anaerobic environment that promotes sulfate reduction. This is comparable to the situation under finfish cages.

- Increased sulfide levels and associated habitat degradation lead to a reduction in benthic species abundance and diversity and shifts in benthic community composition.
- Enhanced abundance of fauna associated with low level organic enrichment (i.e., increased food levels for infaunal deposit-feeders and predators).
- Oxygen depletion in the water column. Observations of hypoxic/anoxic conditions resulting from the high Biological Oxygen Demand of biodeposits are limited, but indicate that effects may be limited in time and space with greatest effects localized near the seabed.

Shellfish and epibiont (fouling organisms) fall-off from suspended culture may contribute to the negative impacts of organic loading and/or provide an additional food source for benthic predators.

ECOLOGICAL CONSEQUENCE

Organic Enrichment - Microbial-macrofauna-geochemical variables described above are inter-related and change in a predictable way along an organic enrichment gradient. The gradients appear to be common for a variety of soft bottom marine benthic habitats (Wildish et al., 2001; Holmer et al., 2005). Where these geochemical indicators have been used in locations of shellfish (mussel) aquaculture, benthic enrichment effects have generally only been observed within or close to lease boundaries (Dahlback and Gunnarsson, 1981; Hatcher et al., 1994; Chamberlain et al., 2001; Cranford et al., 2003b). Changes in sediment geochemical variables indicating benthic enrichment associated with shellfish aquaculture are generally either within or restricted close to the edges of leases.

As noted previously, the extent and magnitude of sediment loading around suspended shellfish farms will depend on both the size of the farm and the apparent hydrographic conditions. Hartstein and Stevens (2005) found that organic matter deposition under mussel lines at three New Zealand farms varied inversely with current speed. Crawford et al. (2003b) found few sediment effects associated with shellfish farms along an open coast in Australia. Suspended cultures can also act as a sediment curtain, slowing current speed through the farm and increasing sedimentation rates within its boundaries. For example, Plew et al. (2005) measured a 36- 63% reduction in current speed through a New Zealand mussel farm.

Macrofauna and associated taxa

Most work on the influence of suspended bivalve culture has largely concentrated on benthic processes (physical, chemical and biological) as they relate to increased organic loading associated with the practice (Carroll et al., 2003). With respect to the biological component, typically only infaunal communities are assessed. However, changes to the benthic sediment system may also have major direct and indirect effects on the more mobile and large benthic organisms.

These organisms are not usually considered and yet are what people generally think of when they think of benthic biodiversity. Most work considers only near-field effects, ignoring far-field effects. When they are, typically only negative influences of aquaculture are considered (see, for example, Gibbs, 2004). A more holistic vision of the role of bivalve culture in the ecosystem is clearly needed if management decisions about aquaculture sites are not to be made based on partial information (Davenport et al., 2003; McKindsey, 2005).

The companion paper[2] examining organic enrichment effects from finfish farming operations discusses the above issues in more detail and so is not repeated here.

Modeling pathways of effects

Chamberlain et al. (2006) reviewed the state-of-knowledge on modeling approaches towards shellfish aquaculture – environment interactions including many of the pathways of effects identified above. Weise et al. (2008) provided an update on approaches to sedimentation modeling using the Shellfish-DEPOMOD package.

Overall, site specific modelling of pathways of effects may be possible and the level of validation/corroboration is improving over time. However, generic application of these models to 'new' locations is very limited at present.

CONCLUSIONS

A. Removal of Nutrients: Shellfish farms have the potential to significantly alter the pelagic ecosystem. The nature and scale of effect of any individual or multiple shellfish farming operations on phytoplankton and seston are predictable as the major site specific variables affecting the spatial and temporal characteristics of the effect are well known. Practical approaches are available for assessing the risk of these effects and for monitoring the far-field impact. The effect on higher trophic levels is much less certain although destabilization of phytoplankton biomass and composition at the scale of coastal ecosystems will have significant ecological consequences.

B. Release of Nutrients to the Benthos: Shellfish farms have the potential to significantly alter benthic habitat and community structure. The nature and scale of effect of a shellfish farm depends on relatively well known variables and is predictable using the current state-of-knowledge and the Shellfish-DEPOMOD package. Performance-based standards are available that can minimize the potential negative effects of nutrient release/regeneration and thereby manage the ecological outcome within acceptable limits.

C. Release of Nutrients to the Water Column: These releases can constitute a major ecosystem flux, depending on specific site conditions, and often occur directly into nutrient depleted water. There is little empirical information available on localized or ecosystem effects of nutrient releases to the water column from shellfish farming operations (excretion by shellfish and epifauna and remineralization of trapped organic matter). Assessment of ecosystem-level outcomes overlaps with effects from the shellfish nutrient release to the benthic remineralization pathway.

[2] CSAS Working Paper: Page, F., Chamberlain, J., Robinson, S., Reid, G., Chang, B. A Review of the Pathway of Effects Associated with the releases of nutrients and organics from finfish netpen aquaculture.

KNOWLEDGE GAPS AND RESEARCH NEEDS

The separate treatment of stressors (nutrient uptake and release) within this review limits a comprehensive understanding of potential ecosystem consequences of the combined effects of related stressors. More specifically, it is not possible to adequately assesses the effects on one variable (e.g., a limiting nutrient such as nitrate) when that variable is affected simultaneously by more than one POE. In simple terms, an outcome from one POE can lead to another POE. For example, nutrient additions to the benthos and water column (a stressor) may ultimately lead to phytoplankton production (an effect), which comes back around as a stressor (nutrient removal by the shellfish) that contributes to another effect (phytoplankton depletion). The biological implications of these ecological feedbacks are currently a major focus of shellfish aquaculture research, but the consequences cannot adequately be assessed using the POE approach. Excluding potential avenues of secondary/tertiary effects resulting from ecological feedbacks results in an approach that is not ecosystem-based. Uncertainties or knowledge gaps related to feedback effects are a significant hindrance in terms of gaining a more holistic understanding of the effect profiles and the biological implications on overall ecosystem function.

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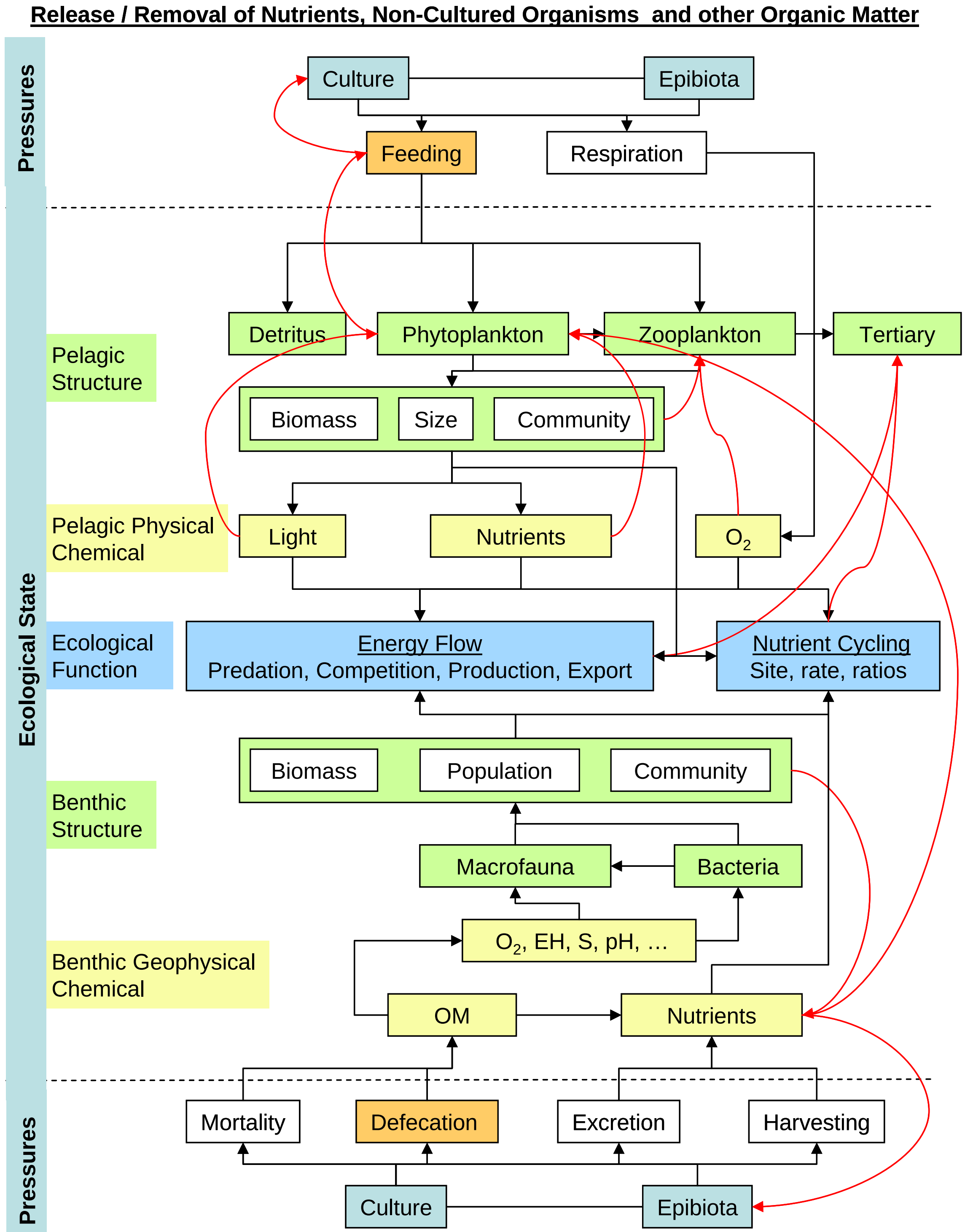

Figure 1: Simplified conceptual diagram of the potential connectivity between shellfish aquaculture pressures and the state of coastal ecosystems (structure and function). Pelagic interactions are illustrated from top to bottom and benthic interactions from bottom to top. Primary effect pathways are shown with solid black lines and secondary effects from ecological feedbacks are shown as red curves. The scale and magnitude of any effects will be site-specific.

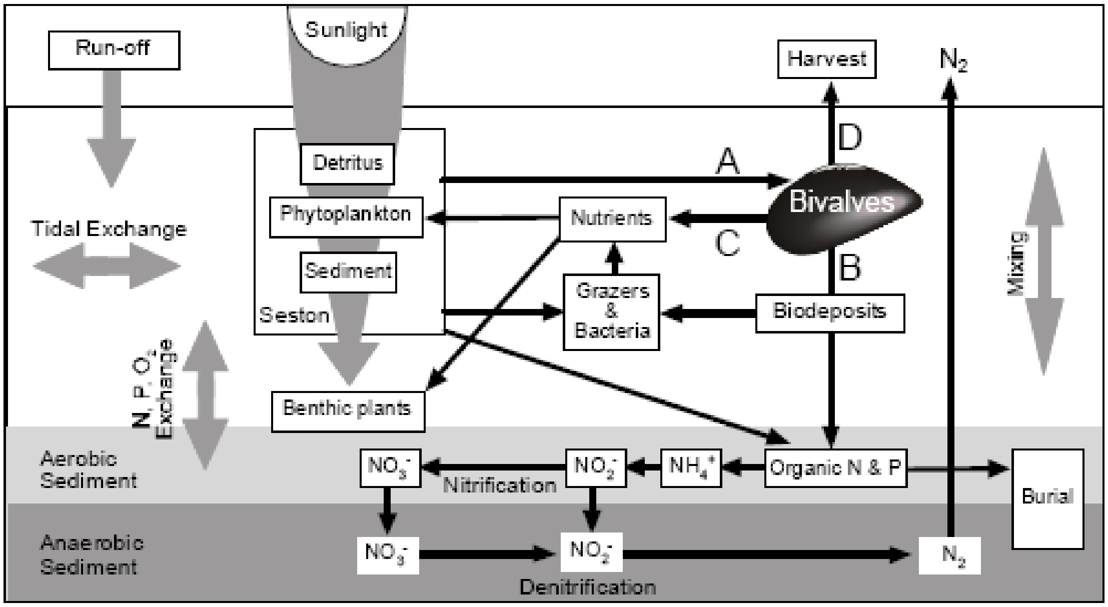

Figure 2: (from Cranford et al., 2006) Conceptual diagram of shellfish (bivalve) aquaculture interactions in coastal ecosystems related to: (A) the removal of suspended particulate matter (seston) during filter feeding; (B) the biodeposition of undigested organic matter in feces and pseudofeces; (C) the excretion of ammonia nitrogen; and (D) the removal of materials (nutrients) in the bivalve harvest.

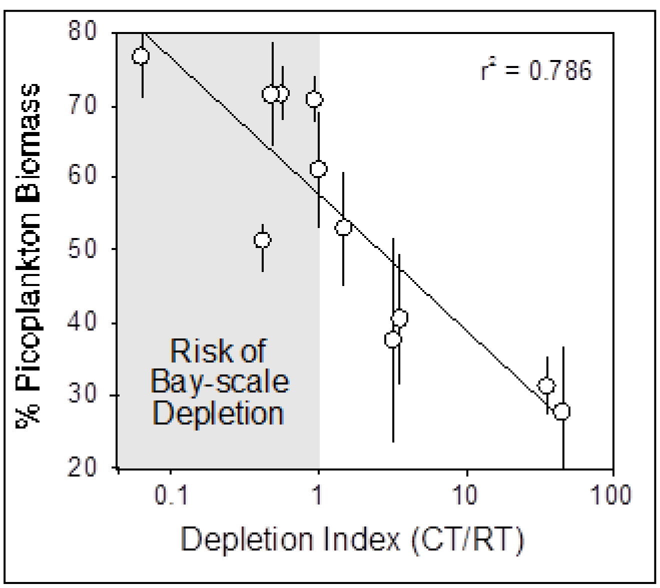

Figure 3: Mean contribution of picophytoplankton in PEI and Nova Scotia mussel culture embayments. The percentage contribution relative to total phytoplankton biomass is plotted against a phytoplankton depletion risk index that compares bay flushing characteristics (residence time; RT) with the biofiltering capabilities of mussel farms (clearance time; CT) (Cranford et al., 2008).

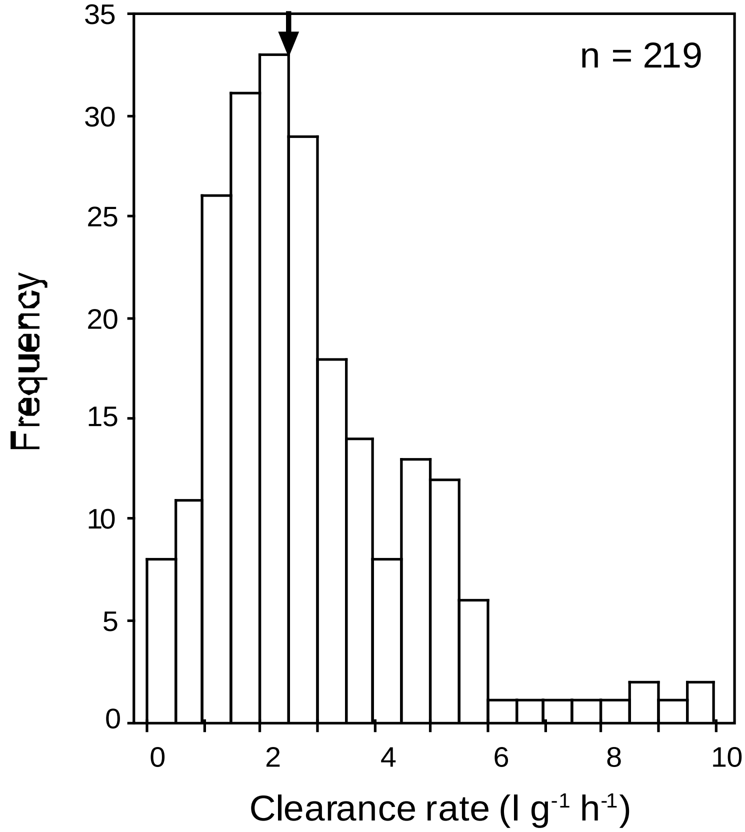

Figure 4: Frequency distribution of 219 published mean clearance rate measurements (weight standardized) on mussels (Mytilus edulis) showing the median value of 2.6 L g^{-1} h^{-1} (arrow) and a smaller mode at 5 L g^{-1} h^{-1} that represent "maximal" rates stimulated by an optimal artificial diet.