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Modelling carrying capacity of bivalve aquaculture: a review of definitions and methods

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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

The need to develop sustainable activities in the coastal zone that are compatible with other uses is key for minimizing controversy among stakeholders and consequently for marine spatial planning. In aquaculture, carrying capacity (CC) has traditionally been regarded as a useful concept for maximizing stocking biomass and profitability at the farm scale. Over the past decades the concept itself and its level of complexity have substantially evolved, prompting the creation of different CC components: physical, production, ecological, social and governance. These components provide a holistic approach to the analysis of aquaculture and its interaction with the ecosystem, economy and society. With respect to ecological and production CC, a series of indices and complex mathematical models have been developed. Nevertheless, there is still no consensus regarding criteria and thresholds, a situation that often limits the application of these new tools to management. In this document, we review the current understanding of CC for bivalve aquaculture, with emphasis on the modelling techniques that are available for inferring ecological and production CC.

Modélisation de la capacité de charge de l'aquaculture des bivalves : un examen des définitions et des méthodes

RÉSUMÉ

Il est essentiel de planifier des activités durables qui sont compatibles aux autres utilisations dans la zone côtière de manière à minimiser toute controverse parmi les intervenants, permettant ainsi la planification spatiale maritime. En aquaculture, la capacité de charge a traditionnellement été un concept utile afin de maximiser la biomasse en production et la rentabilité à l'échelle de l'exploitation. Toutefois, au cours des dernières décennies, le concept lui-même et son niveau de complexité ont considérablement évolué, entraînant du même coup la création de différents aspects de la capacité de charge : physique, production, écologique, social et gouvernance. Ces aspects offrent une approche holistique à l'analyse de l'aquaculture et de ses interactions avec l'écosystème, l'économie et la société. En ce qui concerne les aspects écologique et relatif à la production de la capacité de charge, une série d'indices et de modèles mathématiques complexes ont été mis au point. Pourtant, il n'y a pas encore de consensus en ce qui a trait aux critères et aux seuils; cette situation limite souvent l'application de ces nouveaux outils dans un contexte de gestion de l'aquacuture. Dans le présent document, nous passons en revue la compréhension actuelle de la capacité de charge par rapport à l'aquaculture des bivalves en mettant l'accent sur les techniques de modélisation disponibles afin d'inférer les aspects écologique et relatif à la production de la capacité de charge.

INTRODUCTION

The rapid growth of aquaculture at a worldwide scale (Costa-Pierce 2010) has generated concerns about the impacts of the activity not only on local environments but also at the social scale, as aquaculture competes for space and resources with traditional users of land, water and coasts (Byron and Costa-Pierce 2013). Carrying capacity (CC) is one of the most useful concepts to assess the development of shellfish mariculture, but remains contentious due to the lack of a clear and concise definition (McKindsey et al. 2006). The importance of CC is reflected in the growing number of reviews on the subject (McKindsey et al. 2006; Grant and Filgueira 2011; Byron and Costa-Pierce 2013; Ferreira et al. 2013; McKindsey 2013). In this document, we provide an overview of the current understanding of CC, particularly ecological and production CC, by focusing on the methodologies that are presently available for their inference. We present this information using the following structure:

- Bivalve aquaculture and the environment
    - Pelagic environment
    - Benthic environment
    - Habitat modification/creation
- Definition of carrying capacity
- Inferring carrying capacity: indices, models and thresholds of sustainability
    - Indices
    - Farm models
    - Spatial models
    - Food web models
- Conclusions

BIVALVE AQUACULTURE AND THE ENVIRONMENT

Bivalves act as ecosystem engineers or foundation species by influencing habitat and resources available for other species (Jones et al. 1997). This section has been divided into three sub-sections. The first addresses the direct role of bivalves on the pelagic environment with emphasis on bivalve-phytoplankton trophic interaction as well as nutrient cycling and particle dynamics. The second sub-section concerns the effect of bivalves on the benthic environment with emphasis on potential modification of the characteristics of the seafloor and associated communities. The third sub-section focuses on the potential consequences of culturing bivalves on habitat. In each section we have also discussed the most significant impacts that bivalve aquaculture may exert on the environment, which have been identified by McKindsey (2013) as: food depletion in the water column; enhanced localized biodeposition and the concomitant alteration of nutrient, oxygen fluxes, and community composition; and transfer of diseases and hitchhiking species. Although we focus on the major potential impacts, the different stages of the aquaculture process can lead to different impacts (Table 1). In addition to McKindsey (2013), a series of reviews with focus on the potential environmental impacts of bivalve aquaculture have been recently published. Dumbauld et al. (2009); Forrest et al. (2009) and McKindsey et al. (2011) provide a detailed list of potential effects and environmental interactions with clams, oysters and mussels, respectively. Cranford et al. (2012) also provides a general overview for bivalve aquaculture without emphasis on any particular species, and summarizes a series of indicators of benthic and pelagic impacts.

PELAGIC ENVIRONMENT

The cultivation of bivalves at high densities can exert a significant effect on flows of matter and energy in coastal marine ecosystems (Figure 1.1 in Cranford et al. 2006) (Dowd 2003; Cranford et al. 2012). The most obvious effect of introducing a large biomass of filter-feeders is the interaction with phytoplankton populations. Bivalve filtration activity may exert a top-down control of phytoplankton populations (Dame 1996; Dame and Prins 1998; Newell 2004; Petersen et al. 2008; Huang et al. 2008), to the extent that if bivalve culture consumes the phytoplankton faster than it can be replaced by advection or local production, the resulting depletion can compromise bivalve performance itself (Bacher et al. 2003; Strohmeier et al. 2005; Ferreira et al. 2007; Duarte et al. 2008). The concept of “depletion” though commonly used in the bivalve literature could be mistakenly understood as having a negative connotation. The term should not be interpreted as a near-total absence of phytoplankton cells. Instead the term simply refers to a reduction of phytoplankton concentration attributed to bivalve grazing, a phenomenon that naturally occurs over dense bivalve beds (Dame et al. 1991; Dolmer 2000). In addition to reducing phytoplankton concentrations, filtration activity can alter the structure of phytoplankton communities. For example, in light-limited systems, filtration can decrease turbidity and facilitate a shift towards faster growing algal species (Prins et al. 1995). Also, the progressive increase of bivalve retention efficiency from small to large particles (Strohmeier et al. 2012) can result in increased picophytoplankton abundance (Olsson et al. 1992; Vaquer et al. 1996; Dupuy et al. 2000; Souchu et al. 2001; Cranford et al. 2008; Smaal et al. 2013; Froján et al. 2014). Although most research on bivalve feeding behaviour has been focused on the interaction between bivalves and phytoplankton, there is support in the literature that detritus can also be important in bivalve nutrition (Hawkins et al. 2002; Navarro et al. 2009). Consequently, selective retention efficiency could lead to an alteration of the structure of the phytoplankton community, as well as an alteration of detritus size spectra, both of which may alter the available seston for other consumers (Prins et al. 1998; Dupuy et al. 2000; Pietros and Rice 2003; Leguerrier et al. 2004). Despite the breadth of research on bivalve feeding behaviour including feeding rate, retention efficiency, particle sorting and digestive processes, there are still major knowledge gaps in our understanding of what bivalves eat. This also includes their interactions with marine aggregates, commonly known as marine snow, which can be ingested by bivalves (Newell et al. 2005) and may play a key role in benthic-pelagic coupling.

During the feeding process, phytoplankton and particulate organic matter are consolidated into pseudofaeces (uningested) and faeces (unassimilated). Remineralization of nutrients in pseudofaeces and faeces in the water column, and particularly in the benthos (Grant et al. 1995; Newell 2004; Carlsson et al. 2010; Jansen et al. 2012), as well as bivalve ammonia excretion can be directly used by phytoplankton (Dame et al. 1991, Smaal and Prins 1993, Prins et al. 1998; Mazouni 2004; Asmus and Asmus 2005; Sará 2007; Cranford et al. 2007). The ecological significance of nutrient regeneration consists of a relaxation of nutrient limitation for phytoplankton, which may result in enhanced primary production at the local scale (Smaal 1991; Prins et al. 1995; 1998; Pietros and Rice 2003), a process that is more significant in nutrient-limited environments. Therefore, cultured shellfish can also exert a bottom-up nutrient control on phytoplankton populations (Ogilvie et al. 2000; Cranford et al. 2007; Trottet et al. 2008; Froján et al. 2014), which is considered to be an important feedback of bivalves on their own food source (Smaal et al. 2001). These processes have been demonstrated in mesocosm studies with the clam *Mercenaria mercenaria*, which showed that a relatively low abundance of clams can double primary production and alter the community structure of phytoplankton (Doering and Oviatt 1986; Doering et al. 1989). However, this positive feedback on phytoplankton populations is limited and increasing bivalve biomass will reach a point at which grazing on phytoplankton begins to reduce primary production (Smaal et al. 2013).

According to this, the most studied pelagic impact of bivalve farming is related to the top-down pressure that bivalves can exert on phytoplankton (see above). Top-down pressure can reduce phytoplankton concentrations to below natural levels, a situation that is commonly referred to as “phytoplankton or seston depletion”. Percent depletion within bivalve farms can range from nearly undetectable levels to 80% (Petersen et al. 2008; Duarte et al. 2008; Cranford et al. 2014). Seston depletion can be enhanced by the filter-feeding activity of fouling organisms and other biota associated with bivalve aquaculture (Mazouni et al. 2001; Mazouni 2004; Decottignies et al. 2007). A more intense phytoplankton depletion is expected at the local scale in the vicinity of farms (Gibbs 2007; Grant et al. 2007; Dumbauld et al. 2009; Lin et al. 2009) but at a lower intensity, effects may also extend to a larger spatial scale (Prins et al. 1998; Cerco and Noel 2007; Coen et al. 2007; Grant et al. 2008; Lin et al. 2009; Filgueira and Grant 2009; Filgueira et al. 2014a). Intense depletion is expected at shallow sites characterized by long water residence times and high bivalve densities, such as densities found within three-dimensional culture systems (Rodhouse and Roden 1987; Heral 1993; Comeau et al. 2008). Depletion may lead to increased competition for phytoplankton, which may ultimately have a significant effect on bivalve growth rate and performance (Filgueira et al. 2013; 2014a). Depletion can also negatively affect other grazers in the surrounding ecosystem, such as wild populations of filter feeders (van Strahlen and Dijkema 1994), including zooplankton (Gibbs 2007). Consequently, farmed bivalves can redirect energy away from zooplankton, replacing the ecological role of zooplankton in the ecosystem by grazing on phytoplankton (Jiang and Gibbs 2005; Gibbs 2007). Bivalves can also directly predate on zooplankton populations, although this pathway of effect has not been extensively documented (Davenport et al. 2000; Trottet et al. 2008). Perturbations at the zooplankton trophic level can alter the energy transfer to higher trophic levels because zooplankton is preyed upon by small fishes, especially fish larvae (Gibbs 2007), but cultured bivalves are generally not preyed upon by small fishes (Gibbs 2007).

BENTHIC ENVIRONMENT

Faeces and pseudofaeces sink to the seafloor (Newell 2004; Dame 1996) and redirect part of the pelagic energy flow towards benthic food webs (Leguerrier et al. 2004; Cranford et al. 2007; Lin et al. 2009) where they can be further recycled (Cloern 1982; Dumbauld et al. 2009). These vertical fluxes of wastes (generally referred to as biodeposits) can potentially increase the accumulation of organic material in the vicinity of the aquaculture site (McKindsey et al. 2006), which can alter benthic habitat and communities. Although, the main source of organic loading is in the form of biodeposits, the fall-off of farmed bivalves and associated fouling can also constitute a significant contribution (McKindsey et al. 2011). Biodeposits are generally organic-rich, fine particles and consequently the seabed can become organically enriched and fine-textured relative to surrounding areas. The effects of the biodeposits on the benthos depend on local environmental characteristics and the intensity of farming activity (Giles et al. 2009).

The production rate of biodeposits is directly dependent on the stocking density of a cultured population (Forrest et al. 2009; Dumbauld et al. 2009; McKindsey et al. 2011) and the organisms associated with the farmed population (Stenton-Dozey et al. 2001; Giles et al. 2006; McKindsey et al. 2009). Other important factors that determine how biodeposits are deliverd to the benthos are their sinking velocity, which is dependent on a bivalve’s diet (Chamberlain 2002; Giles 2006), and the physical flushing of the water in the embayment. The sinking velocity and physical flushing will determine the dispersion of the biodeposits (Pearson and Black 2001; Grant et al. 2005). Note that physical flushing may also be affected by the farming structures themselves, since they can alter hydrodynamics (Plew et al. 2005; Petersen et al. 2008;

Stevens et al. 2008; Strohmeier et al. 2008; Comeau et al. 2014). In general, the deposition of biodeposits of bivalves and associated fauna is restricted to the area directly below the farm and its proximal vicinity, where sedimentation rates can be significantly enhanced compared to reference sites outside the farm (Tenore et al. 1982; Hatcher et al. 1994; Hartstein and Stevens 2005). However there are potentially serious issues associated with sampling designs and reference sites. Recently, Guyondet et al. (2014) stated that the increase in sedimentation is confined to the central zone of the farmed areas while a reduction is expected outside the farms. This highlights the serious issues associated with sampling designs and establishing reference sites.

The ultimate effects of the organic loading depend on :

1) the characteristics of the biodeposits (Giles and Pilditch 2006; Carlsson et al. 2010), which can greatly vary both spatially and temporally (Bayne et al. 1993);
2) local sediment characteristics such as grain size, temperature, dissolved oxygen, presence/absence of seagrass, infauna, etc.; but also
3) the coupling with the water column, e.g. oxygen fluxes.

Together, these variables ultimately determine the assimilative capacity of the sediments (Kusuki 1981; Souchu et al. 2001; Mitchell 2006). In general, the increase in organic loading can alter benthic sediment geochemistry (Dalhlbäck and Gunnarsson 1981; Mattsson and Lindén 1983). The organic matter can be consumed by benthic feeders, mitigating the effects of organic loading (Valdemarsen et al. 2010), but it can also be decomposed by microbes following a series of oxidant reductions (Figure 2 in McKindsey et al. 2011). When the decay of biodeposits consumes oxygen at a rate greater than that of renewal by water exchange, this can create anoxic conditions and induces sulfate reduction near the surface of the sediment (McKindsey et al. 2011). Concomitant with the increase in organic matter, an increase in anoxic conditions and total free sulphides as well as a reduction in redox potential may occur beneath a bivalve farm (Tenore et al. 1982; Hargrave et al. 2008). Consequently, fluxes of ammonium, nitrate/nitrite, phosphate and silicate can be enhanced below bivalve farms (Giles et al. 2006; Carlsson et al. 2009; Dumbauld et al. 2009; Alonso-Pérez et al. 2010). Organic loading can create, in a worst case scenario, locally anoxic sediments (Forrest and Creese 2006; Nizzoli et al. 2006; Mesnage et al. 2007; Richard et al. 2007; Hargrave et al. 2008) and increasing local sulfide concentrations (Holmer et al. 2005; Vinther and Holmer 2008; Vinther et al. 2008).

The chemical changes as well as the physical changes in the sediment characteristics potentially enhance differences between benthic communities within and outside of culture sites (McKindsey et al. 2011). These changes can significantly affect habitat characteristics and ultimately infaunal communities (Mirto et al. 2000; Christensen et al. 2003; Beadman et al. 2004; Callier et al. 2007; Murray et al. 2007). The response of benthic communities follows the classical conceptual model of succession proposed by Pearson and Rosenberg (1978). These effects range from no discernible effects in the infaunal community (Crawford et al. 2003; Mitchell 2006) to significant alterations of the infaunal assemblage (Castel et al. 1989; Nugues et al. 1996; Hartstein and Rowden 2004), including intermediate situations in which moderate effects have been identified (Forrest and Creese 2006). The effects can also be significant in microbial and meiofaunal communities (Mirto et al. 2000). Another key aspect is related to the potential effects on bioturbators, which have a great impact on oxygen dynamics in sediments (Norkko and Shumway 2011). Gibbs (2007) suggested that benthic communities could shift from filter- to deposit-feeders. In general, the response of the macrobenthic community to the increase in organic loading follows these steps (Cranford et al. 2012):

- a decrease in species richness and an increase in the total number of individuals as a result of the high densities of a few opportunistic species;
- a general reduction in biomass for most species, although there may be an increase in total biomass corresponding to the presence of a few opportunistic species;
- a decrease in body size of the average species or individual;
- a shallowing of that portion of the sediment column occupied by infauna; and
- a shift in the relative dominance of trophic groups.

Ultimately, in a worst-case scenario, the sediment may become anoxic and dominated by microbial mats such as *Beggiatoa* spp (McKindsey et al. 2011; Norkko and Shumway 2011). *Beggiatoa* spp may also be present in early stages of benthic degradation.

HABITAT MODIFICATION/CREATION

In addition to the modification of benthic habitat via organic loading (see above), bivalve aquaculture can exert other modifications in both benthic and pelagic habitat. The increase in light penetration (Cerco and Noel 2007; Schröder et al. 2014) and/or sediment nutrient enrichment (Reusch and Williams 1998; Peterson and Heck 1999; 2001) promoted by cultured bivalves can enhance the productivity of seagrass in shallow coastal ecosystems (Peterson and Heck 2001; Carroll et al. 2008). For example, it is predicted that the increase of water clarity from bivalve aquaculture and/or oyster restoration may lead to an increased biomass of submerged aquatic vegetation (Newell and Koch 2004; Cerco and Noel 2007; Wall et al. 2008). A recent study conducted in Atlantic Canada showed a positive relationship between farmed oyster biomass and eelgrass (*Zostera marina*) biomass (Andrea Locke, personal communication). In addition to the direct effect on benthic habitat caused by the proliferation of submerged aquatic vegetation, a reduction of phytoplankton production in the water column is expected, due to the direct competition for nutrients (Souchu et al. 2001; Newell 2004; Porter et al. 2004).

Another effect of bivalve aquaculture on habitat availability is related to the deployment of three-dimensional physical structures in the ocean (Costa-Pierce and Bridger 2002; Olin 2002, Davenport et al. 2003; McKindsey et al. 2011). The physical structure can provide refuge from predators and/or food sources (see McKindsey et al. 2011), which can attract new species (Gibbs 2004; Jiang and Gibbs 2005; Clynick et al. 2008). For example, Tenore and González (1976) found that mussel rafts in Ría de Arousa (Spain) provided habitat and food resources that enhanced secondary productivity. Tallman and Forrester (2007) show that oyster grow-out cages provide quality habitat for fishes associated with hard-bottom habitats. Physical structures such as farms or docks can also create shaded areas (Everett et al. 1995; Burdick and Short 1999; Thom et al. 2005), which can negatively impact photosynthetic organisms, such as seagrass (Skinner et al. 2013; 2014). The structures can alter hydrodynamics (Plew et al. 2005; Petersen et al. 2008; Stevens et al. 2008; Strohmeier et al. 2008; Comeau et al. 2014), causing erosion or deposition, depending on local characteristics (Dumbauld et al. 2009; McKindsey et al. 2011). These structures can also generate attachment points for epiphytic species, including macroalgae (Dumbauld et al. 2009) but also invasive species, including tunicate ascidians such as *Ciona intestinalis* and *Styela clava*. The latter species cause serious problems for aquaculture operations worldwide by increasing operational costs and/or causing direct competition for food with cultured bivalves (Karayucel 1997; Uribe and Etchepare 2002; Carver et al. 2003; Lambert 2007; McKindsey et al. 2007).

Marine species have been transported for aquaculture purposes since at least the 1700s (Padilla et al. 2011), which has facilitated the spread of non-indigenous species, from macroanimal and macroalgal to microparasites, including toxic microalgae and diseases (McKindsey et al. 2007; Forrest et al. 2009; Padilla et al. 2011). Ruesink et al. (2005) have estimated that more than 40% of non-indigenous marine species in Europe, the western United States, and the North Sea may have been introduced by oyster aquaculture. These species can be harmful to humans, other species, and the cultured species themselves (McArdle et al. 1991; Lilly et al. 2002; Cohen and Zabin 2009; Hégaret et al. 2009). New guidelines for transfer protocols of non-indigenous species have likely reduced the transfer of unwanted organisms, especially at international scales (McKindsey et al. 2007). However, secondary transfers from aquaculture facilities, which act as reservoirs of non-indigenous species, to other locations at regional or local scale still constitute a pathway to new invasions (Forrest et al. 2009). This is related to the fact that aquaculture facilities promote the aggregation of living biomass in the ocean:

1) aquaculture implies by definition the culture of organisms at high densities;
2) farming structures are deployed in the ocean, which generate new habitats (refuge and food) that trigger the aggregation of pelagic species; and
3) fouling species can colonize cages, ropes and other gear, increasing the biomass density (Carver et al. 2003; Ramsay et al. 2008).

The biomass aggregates can act as reservoirs of non-indigenous species and increase the risk of disease development/transmission, which could transfer to new locations by secondary pathways such as hydrodynamics or local vessels.

DEFINITION OF CARRYING CAPACITY

Sustainability is easier to plan than to retrofit (Ferreira et al. 2010), which makes a case for the analysis of CC at the ecosystem scale (Ferreira et al. 2013). Inglis et al. (2000) and McKindsey et al. (2006) have defined four types of CC:

- Physical CC describes the area that is geographically available and physically/chemically adequate for a certain type of aquaculture. It is useful to quantify the potential area available for aquaculture but it provides little information for management/regulation.
- Production CC has been defined from different perspectives:
    1) from a biomass perspective as the maximum level of aquaculture production (Inglis 2002);
    2) from an economic perspective as the standing stock at which the annual production of the marketable cohort is maximized (Bacher et al. 1998; Smaal et al. 1998). Given the trade-offs between bivalve growth rates, market tastes, economic returns, etc., production CC is not necessarily the greatest biomass that can be farmed (McKindsey 2013); and
    3) from a trophic web perspective as the biomass that could be theoretically produced if the pelagic food web were collapsed down into a nutrient-phytoplankton-bivalve loop (Gibbs 2004).
- Ecological CC is defined as the magnitude of aquaculture production that can be supported without leading to unacceptable changes in ecological process, species, populations, or communities in the environment (Byron and Costa-Pierce 2013). While production CC focuses only on the target species and associated processes that support production, ecological CC should, in principle, consider the whole ecosystem and all the activities involved in the aquaculture process (McKindsey et al. 2006).

- Social CC can be defined as the amount of aquaculture that can be developed without adverse social impacts. The determination of social CC requires the involvement of multiple stakeholders, that is, scientists, farmers, regulators, NGOs, etc. (See Fig. 3 in Byron et al. 2011a). Communication between scientists and stakeholders is a key aspect of this process to obtain the expected outcome for sustainable management of resources and equity of all users (Byron et al. 2011a). Social CC is still in its infancy (Byron et al. 2011a) and analytical methods to estimate it are yet under development (Byron and Costa-Pierce 2013).

Recently, regulatory or governance CC has been added to this framework (Byron and Costa-Pierce 2013; Ferreira et al. 2013). Regulatory CC establishes the legal framework and communication protocols among stakeholders to ensure a smooth integration of the aquaculture activity into the coastal zone, minimizing potential conflicts. Governance is not usually limited by a lack of legal instruments but often by their adequacy and acceptance by stakeholders (Ferreira et al. 2013).

Assuming that physical CC cannot be used in the management/regulatory process and in many respects is encapsulated in the production CC (Ferreira et al. 2013), social CC is the most restrictive type of CC in Europe and North America (Figure 2 in Byron and Costa-Pierce 2013), where social opposition is at the forefront of decision-making (Ferreira et al. 2013). In other locations such as China and Southeast Asia, where food production is the paramount concern, social pressure adopts an entirely different perspective, acting as a driver for increased aquaculture for reasons of economy and food security (Ferreira et al. 2013). Consequently, constraints depend on social and political standpoints and cannot be homogenized worldwide. Nevertheless, a common framework for CC has been suggested following the three principles of the Ecosystem Approach to Aquaculture (EAA) (FAO 2008; Soto et al. 2008):

- aquaculture should be developed in the context of ecosystem functions and services with no degradation of these beyond their resilience capacity;
- aquaculture should improve human wellbeing and equity for all relevant stakeholders; and
- aquaculture should be developed in the context of (and integrated to) other relevant sectors.

The application of the EAA principles is a strategy for the integration of the activity within the wider ecosystem in such a way that it promotes sustainable development, equity, and resilience of interlinked social and ecological systems (Soto et al. 2008).

INFERRING CARRYING CAPACITY: INDICES, MODELS AND THRESHOLDS OF SUSTAINABILITY

The EAA concept can be applied following different frameworks (Walker et al. 2003; Nobre et al. 2009; Ostrom 2009; Cranford et al. 2012; McKindsey 2013) in which CC estimations play a key role. In this review we have focused on the two types of CC that can be estimated using mathematical modelling, that is, production and ecological CC (Ferreira et al. 2013). Models are powerful tools for exploring ecological CC, allowing for the study of stocks, energy fluxes and potential interactions in complex ecosystems (Dowd 2005). Models integrate time and space, which is critical for understanding ecological dynamics and therefore how natural systems provide ecosystem services (Palmer et al. 2004). In addition, scenario building (“what if” scenarios) allows the exploration of future situations where unanticipated stressors generate new risks or opportunities, and is thus an important tool for managing those changes (Nobre et al. 2010). Modelling is also among the few tools capable of assessing aquaculture sustainability while also considering the cumulative effects of additional human activities (e.g. eutrophication, climate change) and resident and invasive suspension-feeding species (Cranford et al. 2012). When modelling is combined with stakeholder input, the resulting ecological CC calculations are exceptionally powerful in the management arena (Byron et al. 2011a). In addition, models could be used to address the principles of EAA by:

- exploring the effects of aquaculture activity on the resilience of a relevant process of the ecosystem;
- providing objective scientific knowledge, which facilitates the communication among stakeholders; and
- exporting the outputs of the model to marine spatial planning processes in order to ensure aquaculture is compatible with other activities.

As stated above, production CC models can be limited to the target species and associated processes that support production, but ecological CC should in principle consider the whole ecosystem (McKindsey et al. 2006), that is, benthic and pelagic environments. Although both environments are obviously linked, the impacts on the benthos are usually restricted to the vicinity of the farm (Hargrave et al. 2008; Cranford et al. 2009; Guyondet et al. 2014). By contrast, the impacts on the pelagic environmet can reach a larger spatial scale due to effects on the base of the trophic web, that is, phytoplankton populations. The potential larger impact of bivalve aquaculture on the pelagic environment and the need to reduce model complexity as well as scientific uncertainty (FAO 2008) have been used as rationale to focus CC models on the pelagic environment. Actually, most CC modelling to date has been focused on the pelagic environment, with emphasis on food depletion, rather than on the benthic environment (McKindsey 2013). The methodological approaches to study CC from the pelagic perspective can be summarized in indices, farm models, spatial models and food web models.

INDICES

Indices based on the comparison of key oceanographic and biological processes have been used to assess the CC of bivalve aquaculture sites. These indices generally consider the bay as a homogenous system (1 box) and consequently lack spatial resolution (Grant and Filgueira 2011). However, their simplicity and the fact that the demand for data is relatively easy to fulfill, have resulted in their popular use in the literature (Incze et al. 1981; Cloern 1982; Officer et al. 1982; Carver and Mallet 1990; Smaal and Prins 1993; Heip et al. 1995; Comeau et al. 2008; Comeau 2013) as well as in certification programs such as the one by the Aquaculture Stewardship Council (ASC 2012). Such indices were used to explore production CC (e.g. Newell and Shumway 1993) as well as ecological CC (e.g. Gibbs 2007). Although there are slight variations, the common rationale of CC indices relies in comparing the energy demand of bivalve populations (based on filtration rates) and the ecosystem’s capacity to replenish these resources, which depends on advection and local production. For example, Dame and Prins (1998) proposed indices of depletion based on ratios among water residence time (RT), primary production time (PT) and bivalve clearance time (CT). Using these indices they evaluated the ecological CC of several bivalve aquaculture sites across the world. Their study has become well known, and their indices are now commonly referred to as ‘Dame Indices’. They provide a simple way to gauge the influence of bivalves on ecosystem processes, namely phytoplankton communities (Grant and Filgueira 2011).

Cranford et al. (unpublished manuscript) have calculated Dame Indices for embayments in Prince Edward Island, Québec and Nova Scotia (Table 2). The interpretation of Dame Indices could follow Gibbs (2007), who established specific thresholds for ecological and production CC. Gibbs (2007) suggested that when value of the ratio of carbon extracted by bivalves to carbon produced by phytoplankton (CT/PT in Table 2) is close to 1.0, the culture has reached production CC because the pelagic food web has collapsed down into a nutrient-phytoplankton-bivalve loop (Gibbs 2004). Smaal and Prins (1993) and ASC (2012) have also defined sustainable aquaculture (~ecological CC) in terms of the CT/PT ratio, namely for situations where internal food production, as opposed to water advected from outside the system, primarily regulates CC. They suggest that the CT/PT threshold for ecological CC should in reality be above 3 since it allows for an algal buffer stock to realize a certain level of primary production and also to take into account the occurrence of other unknown grazers in proximity to the bivalve farming operations. The lack of strong rationale for establishing this threshold was emphasized by ASC (2012), in which it is stated that the threshold is considered as a practical figure for management, monitoring and certification rather than an ecological fixed requirement.

In regards to ecological CC, Gibbs (2007) suggested that water residence time / bivalve clearance time (RT/CT) ratio values below 0.05 indicate that the culture will not be able to induce significant changes to the pelagic functioning, thereby meeting the definition of ecological CC. Note that Cranford et al. (unpublished manuscript) have calculated the inverse of that ratio, that is, CT/RT (Table 2), which based on Gibbs (2007) should be above 20 to meet ecological CC. However, the Gibbs' threshold of ecological CC (RT/CT < 0.05 or CT/RT > 20) is not based on any strong and objective ecosystem criterion. For example, it has been argued that bivalves naturally exerted a dominant effect in some coastal systems prior to the development of aquaculture. Historical (c. 1880–1910) baselines for North American oyster reefs suggest CT/RT values ≤ 1 for six of eight estuaries in the Gulf of Mexico (zu Ermgassen et al. 2013). A similar top-down control by oysters likely existed during pre-colonial times for some estuaries on the North Atlantic coast (Newell 1988; Mann et al. 2009a; 2009b; zu Ermgassen et al. 2013).

In summary, the lack of established thresholds for Dame-type indices presently limits their broad applicability. Another current drawback of these indices is their lack of spatial resolution, thus eliminating the possibility of differentiating areas within embayments. Inner and outer areas of an embayment, for example, are typically very different in terms of physical properties such as water renewal time. To address this issue, Guyondet et al. (2005; 2013) integrated a 3D circulation model into one of the Dame indices (CT/RT), thus allowing the calculation of the index in different sub-regions of an estuary. Results highlighted the spatial variability of the index, which was driven by variability in water residence time.

FARM MODELS

Production and ecological CC are strongly related (McKindsey 2013). In fact, the mathematical models that explore production and ecology can share the same core biogeochemical and hydrodynamic equations. However, farm-scale models restrict the model domain to the extent of the farm (Figure 1 in Ferreira et al. 2007), preventing the possibility of a general overview/assessment of the ecosystem. For this reason, farm-scale models are limited to production CC. Nevertheless, some modelling approaches at the farm scale can provide valuable understanding of farm- to ecosystem-scale impacts of bivalve culture (Cranford et al. 2014). All farm models are focused on the interaction bivalve-phytoplankton, since phytoplankton depletion is most obvious at this local scale (Grant et al. 2007; Duarte et al. 2008; Cranford et al. 2014). At the farm scale, phytoplankton dynamics are dominated by physical (advection) rather than biogeochemical (primary productivity) processes (Duarte et al. 2005). Consequently, farm-scale models usually include a hydrodynamic model to describe water circulation through the farm and a bioenergetic model to describe bivalve filtration and growth. The bioenergetic model is usually based on the Scope For Growth (SFG) approach (Winberg 1960) or a Dynamic Energy Budget (DEB) approach (Kooijman 2010). However, when the model is focused only on phytoplankton depletion, a simple flow equation based on average clearance rate of the bivalves is used to describe the phytoplankton-bivalve interaction. In the latter case, the model lacks the capability to predict bivalve growth (e.g. Incze et al. 1981). Farm models are generally considered useful for optimizing lease geometry and configuration (Pilditch et al. 2001; Aure et al. 2007; Rosland et al. 2011) as well as aquaculture husbandry (Duarte et al. 2008). They are especially useful when coupled to economic models, since they allow the estimation of optimal production based on economic profit (FARM™, Farm Aquaculture Resource Management; Ferreira et al. 2007).

SPATIAL MODELS

This category is the broadest among CC models. It includes a variety of approaches that share the same philosophy but with modelling schemes that vary in spatial resolution and complexity. Two main classes of spatial models can be established, box and fully-spatial models. The main difference between these approaches is the spatial resolution of the model. In a box model, the domain is divided into few large areas that are considered homogeneous. In fully-spatial models, a grid with hundreds or thousands of polygons is defined to represent the model domain. Consequently, the spatial resolution of box models is coarser than for fully-spatial models. Resolution has also a direct implication for how hydrodynamics are prescribed in each type of model. Box models need to accommodate the circulation of a large area of the ocean by using averaged values for each box. On the contrary, fully-spatial models are usually built using the grid that was used to develop the hydrodynamic model, making the coupling process between the hydrodynamic and biogeochemical models straightforward in terms of spatial resolution.

High spatial resolution is consistent with ecosystem-based management goals that involve marine spatial planning (Douvere 2008). In addition, spatial resolution can have implications for model predictions (Melbourne-Thomas et al. 2011), especially when processes are dependent on concentration (Fennel and Neumann 2004). Thus, the highest spatial resolution is always desirable, but complex fully-spatial models can require a significant amount of data in order to create and test the model. However, the ecological information available for validation of the performance of models is usually sparse in space and time (Kremer et al. 2010). While increasing model complexity attempts to bolster ecological realism, imperfect knowledge of relationships and parameters may also lead to greater scientific uncertainty (FAO 2008). Therefore, the assumption that extra detail is always beneficial can be flawed when applied at the scale and number of dimensions of end-to-end models (Fulton 2010). This implies that modelling should restrict its focus to relevant components and critical dynamics, which must be defined based on the management question to be addressed, available data, the important system features (including forcing conditions) and the appropriate scales (FAO 2008; Fulton 2010). Ferreira et al. (2013) summarized the desirable properties of a modelling system to address CC (Table 3).

Box and fully-spatial models share the same biogeochemical core, which can vary in complexity, ranging from simple nutrient-seston-bivalve interactions to complex models in which multiple ecosystem processes are considered (Figure 1.1 in Cranford et al. 2006). Hydrodynamics are parameterized as integrated water exchange coefficients among large areas of the domain in box models (Dowd 2005) or by coupling a hydrodynamic model to the biogeochemical one. The hydrodynamic model can be 2D or 3D depending on the characteristics of the modeled system, and the coupling can be performed offline or online (Filgueira et al. 2012). In offline coupling techniques the physical model is run first and the biogeochemical model is run subsequently using the physical outputs from the different time steps. By contrast, online coupling dictates that both hydrodynamic and biogeochemical models are performed simultaneously. The complexity of the model in both biogeochemical and hydrodynamic submodels can be simplified depending on the objectives of the study. For example, Guyondet et al. (2013) coupled a 2D hydrodynamic model to a simplified biogeochemical model in which only seston was considered, and parameterized the balance between seston production and bivalve consumption to explore food depletion and optimize shellfish culture. Dowd (2003) limited spatial resolution to a longitudinal transect of a bay with concomitant simplification of hydrodynamics. Therefore, although model complexity varies significantly, box and fully-spatial models have been used to explore both production and ecological CC. Examples of such investigations are listed in Table 4.

Most CC models have focused on the dynamics of phytoplankton or seston and their interaction with bivalves. Specifically, most studies have examined to which extent bivalves deplete these food resources and therefore become susceptible to reduced growth (Grant and Filgueira 2011). This assessment is often carried out within the context of production CC. However, food depletion can also be used as a benchmark for ecological CC, given that phytoplankton constitutes the primary step in marine food webs and that their preservation is an important tenet of ecosystem-based management (Crowder and Norse 2008). The main shortcoming regarding application of these models is that the criterion or threshold for whether CC has been reached is typically subjective (Grant and Filgueira 2011). In the case of production CC, the definition of the threshold depends on a farmer’s judgment, which obviously relies on economic criteria as well as social values.

The definition of objective thresholds for ecological CC is still in its infancy and, in common with all questions in conservation ecology, the challenge lies in the quantitative identification of a conservation problem, that is, the precise definition of the limits at which ecosystem health is not compromised (Duarte et al. 2003; Fisher et al. 2009). These limits are known as tipping points, or the critical thresholds at which a small perturbation can qualitatively alter the state or development of a system (Lenton et al. 2008). When a perturbation is beyond a tipping point, the resilience of the system is exceeded and the system reorganizes (Crowder and Norse 2008), altering ecosystem functioning and consequently ecosystem services. Precautionary definitions of these tipping points are crucial in order to optimize ecosystem functioning. Grant and Filgueira (2011) have defined objective precautionary thresholds based on the natural variability of phytoplankton biomass, based on the premise that cultivated bivalves should not be allowed to graze primary producers down to a level outside their natural variability range. In other words, these thresholds consider whether aquaculture signals can be detected against the ecosystem background noise (Ferreira et al. 2013).

Tett et al. (2011) have defined a framework for CC and assimilative capacity based on dose-response curves following a DPSIR methodology (Drivers-Pressure-State-Impact-Response, Luiten 1999). Other ecological status evaluation methods such as ASSETS (Assessment of Estuarine Trophic Status, Bricker et al. 2003) or DDPSIR (Delta DPSIR) have also been applied to CC studies (e.g. Ferreira et al. (2007) and Nobre (2009), respectively). In Tett’s framework (Figure 1 in Tett et al. 2011), CC is defined as the stock that can be kept and the harvest that can be extracted without damaging the health of the ecosystem or interfering with other human uses of that system. This statement highlights how several components of CC can converge into a common definition. Setting thresholds is also complicated by the fact that an ecosystem’s response to a disturbance may be an increase in variability, such that no change is observed in the mean values (Cranford et al. 2012). Such issues have led to thresholds of potential concern (TPC), which are a set of operational goals along a continuum of change for selected environmental indicators. TPC values can change when new ecological information is available, allowing managers to distinguish normal ‘background’ variability from a significant change (Cranford et al. 2012).

FOOD WEB MODELS

Mass-balance food web models have also been used to explore the influence of bivalve aquaculture on food web dynamics. The most popular tool for food web modelling is EwE , which has three main components: Ecopath – a static, mass-balanced snapshot of the system; Ecosim – a time dynamic simulation module for policy exploration; and Ecospace – a spatial and temporal dynamic module primarily designed for exploring impact on and placement of protected areas. The combination of these three different components of EwE allows for solving different research questions by adjusting the approach/complexity of the model. Early models were developed exclusively in Ecopath, providing a static snapshot of the ecosystem, but with limited applicability due to the impossibility of simulating dynamic processes through time (Grant and Filgueira 2011; McKindsey 2013), which is key for coastal zones. In addition, Ecopath was not able to provide spatially-explicit outcomes, another handicap for its applicability (McKindsey et al. 2006). However, the addition of Ecosim and Ecospace avoids these limitations. EwE outcomes provide valuable information about ecosystem functioning in terms of energy flows towards different species across several trophic levels (e.g. Wolff 1994; Wolff et al. 2000; Taylor et al. 2008). Although Wolff (1994) explored CC with Ecopath, three main studies, Jian and Gibbs (2005) and Byron et al. (2011b and 2011c) have specifically focused on production and ecological CC and all of them reached the same conclusion: production CC, defined as the level of production at which the trophic web is reduced to nutrient-phytoplankton-bivalve, is higher than ecological CC, defined as the level of culture at which there are no major changes in the structure and energy fluxes of the food web. The main advantage of food web modelling is that it allows the study of many species and trophic levels at the same time, a task that is very difficult to achieve with any of the models previously described. Therefore, this modelling approach is very useful when species from different trophic levels are involved in the CC goals, such as in the fishery of an economically/socially relevant species. The drawback is that EwE uses a largely top-down mass-balance approach and poorly represents bottom-up effects, which are critical in bivalve aquaculture sites due to the impact of cultured biomass on nutrients and detritus (McKindsey 2013).

CONCLUSIONS

Impacts related to bivalve aquaculture may occur in both benthic and pelagic environments. It appears that direct impacts on the benthic environment are limited to the vicinity of the farm (Hargrave et al. 2008; Cranford et al. 2009; Guyondet et al. 2014). Impacts on the pelagic environment may trigger larger ecosystem effects, potentially affecting phytoplankton populations and concomitantly higher trophic levels that depend on phytoplankton production. CC is one of the most useful concepts for assessing the impact of bivalve aquaculture development. The different components of CC allow the inclusion of ecological, economical and societal elements into the assessment. For this reason multiple stakeholders, including scientists, farmers, regulators, NGOs, etc., must take part in an integrated management process (Byron et al. 2011a). Two CC components, production and ecological, are typically investigated using mathematical models that integrate complex interactions between aquaculture and the environment. Due to the significant influence of local environmental conditions on ecosystem functioning, CC studies are site specific (Cranford et al. 2012). Spatially-explicit models are particularly desirable due to their more accurate description of complex hydrography and straightforward applications of outcomes to marine spatial planning processes. Nevertheless, spatially-explicit models demand a high level of complexity, which in turn can increase scientific uncertainty of the outcomes. Accordingly, the modelling approach as well as spatial scale and resolution of the model must be adjusted to the goals of the study. For example, the Canadian Fisheries Act emphasizes protecting the productivity of commercial, recreational and aboriginal fisheries (DFO 2014). Thus, exploring ecological CC under the umbrella of this goal would call for (1) an analysis of energy transfer through the trophic web using food web modelling; and/or (2) a strong focus on the dynamics of phytoplankton, which constitutes the primary step in marine food webs, when using other modelling approaches. Therefore, indices, farm models, spatial models and food web models are useful tools for exploring CC and all of them present advantages and disadvantages. The main challenge in the estimation of ecological CC is the definition of acceptable/unacceptable ecological impacts. Identifying tipping points of ecological resilience is critical for identifying thresholds and advancing the application of ecological CC.

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TABLES

Table 1. Activities related to bivalve culture that may influence the ecological carrying capacity in coastal areas (from McKindsey 2013).

Aquaculture process	Aquaculture activity	Impact on ecosystem
Seed collection	Dredging	Disturbance of benthic communities, especially the removal of long-living species Removal of juveniles from wild populations of target species Collection of non-target species Suspension of sediments Depletion of food resources for other species Release of H2S and reduction of dissolved oxygen in the water due to oxygen-consuming substances, release of nutrients
	Artificial collectors	Removal of juveniles from wild population of target species Increasing target and non-target species recruitment success Alteration of the hydrodynamic regimes Acting as fish aggregation devices Risk of entanglement for large vertebrates (e.g., marine mammals, sea birds, turtles, sharks) Foci for nuisance species
	Hatcheries	Chemical pollution (e.g., pharmaceuticals) Genetic selection Spread of diseases
	Importation	Introduction of alien species Genetic pollution Spread of diseases
Ongrowing	Effects common to all techniques	Organic enrichment of seafloor Providing reef-like structures Alteration of hydrodynamic regime (current speed, turbulence) Food web effects: competition with other filter feeders, increasing recycling speed of nutrients, removal of eggs and larvae of fish and benthic organisms Spawning: release of mussel larvae Providing food for predators of bivalves Control of predators and pests
	Bottom culture	Activities to prepare the culture plots (e.g., dredging for predator removal) Placement of protective structures (netting, pipes) Removal of associated organisms by dredging and relaying Competition for space with wild benthos organisms
	Artificial structures for suspended and off-bottom culture (trestles, poles, rafts, longlines)	Acting as artificial reef or fish aggregation devices (attraction/displacement or enhancement of animals) Risk of entanglement for large vertebrates (e.g., marine mammals, sea birds, turtles, sharks) Foci for nuisance species
Harvesting	Effects common to all techniques	Removal of biomass, nutrients Removal of filtration capacity Removal of non-target species Competition with predators
	Dredging	Disturbance of benthic communities, especially removal of long-living species Suspension of sediments Release of H2S and decrease of dissolved oxygen in the water due to oxygen-consuming substances, release of nutrients
	Collection of off-bottom structures	See above
Processing	Dumping of by-catch Relaying near auction houses Depurating	See above

Aquaculture process	Aquaculture activity	Impact on ecosystem
	Dumping of shells Effluents from processing plant Spread of alien species or diseases	

Table 2. Residence time (RT), clearance time (CT), phytoplankton turnover time (PT), CT/RT and CT/PT indices for different embayments of Prince Edward Island, Québec and Nova Scotia. This table summarizes preliminary data (Cranford et al. (unpublished manuscript)).

Region	Site	Residence Time (RT, day)	Clearance Time (CT, day)	Phytoplankton Turnover Time (PT, day)	CT/RT	CT/PT
P.E.I.	Boughton	1.87	4.07	1.70	2.18	2.39
	Brudenell / Montague	2.20	5.78	1.70	2.63	3.40
	Cascumpeque	1.59	130.10	1.48	81.9	87.9
	Cardigan	2.24	1.83	1.70	0.82	1.08
	Malpeque	2.13	16.69	1.70	7.82	9.82
	Murray	1.25	2.41	1.48	1.93	1.63
	New London	2.37	6.47	1.48	2.73	4.37
	Savage	1.52	1.63	1.48	1.07	1.10
	St. Mary’s	1.33	2.97	1.70	2.24	1.75
	St. Peter’s	3.08	2.45	1.48	0.80	1.65
	Tracadie	2.19	1.84	1.48	0.84	1.24
Québec	Grand Entrée	2.17	6.94	0.73	3.20	9.51
Nova Scotia	Lunenburg	2.43	430.12	0.79	177.4	544.5
	Ship	3.21	23.92	0.79	7.46	30.28
	St. Ann’s	5.70	33.25	1.79	5.83	18.58
	Whitehead	4.14	196.29	0.79	47.4	248.5

Table 3. Set of desirable properties when assembling a modelling system to address aquaculture carrying capacity (from Ferreira et al. 2013).

Property	Description
1	No single model solves all problems. Overparameterization and code bloat only make matters worse.
2	Models should only be as complex as the problem requires. In other words, as simple as possible. Increased computational power is no excuse for unnecessary complexity.
3	Models should be able to work independently, present value in doing so, and add further value when working in conjunction with other models.
4	Models should define exactly what problems they can address, as part of the overall questions for an ecosystem, rather than the opposite.
5	Any model in the system must be able to receive input from data or from other models and be able to supply outputs in a form that can be easily used by other models.
6	Different models are appropriate for different scales in space and time. Carrying capacity assessment may require scales as short as a tidal cycle (e.g., for intertidal culture of clams) and as long as a decade (e.g., for coupling ecological models with economic models).
7	Models share a challenge with field sampling with respect to the conversion of data (measured or modeled) into information that is useful for managers; the use of screening models, or other approaches that help to distil data into meaningful information, is a vital component of any system.

Table 4. Publications that present Box models and fully-spatial models for assessing production and ecological carrying capacity (CC).

<table>
<tr><th>Type of model</th><th>Production CC[1]</th><th>Ecological CC[2]</th></tr>
<tr><td rowspan="2">Box model</td><td>Raillard and Ménesguen 1994
Dowd 1997
Bacher et al. 1998
Ferreira et al. 1998
Duarte et al. 2003
Grant et al. 2007
Filgueira et al. 2010</td><td>Chapelle et al. 2000
Dowd 2005
Filgueira and Grant 2009</td></tr>
<tr><td colspan="2">Nunes et al. 2011</td></tr>
<tr><td rowspan="2">Fully-spatial model</td><td>Duarte et al. 2003
Spillman et al. 2008
Maar et al. 2009
Ibarra et al. 2014</td><td>Cugier et al. 2008
Brigolin et al. 2009
Grangeré et al. 2010
Filgueira et al. 2013
Filgueira et al. 2014b</td></tr>
<tr><td colspan="2">Grant et al. 2007
Ferreira et al. 2008
Guyondet et al. 2010
Dabrowski et al. 2013
Filgueira et al. 2014a
Guyondet et al. 2014</td></tr>
</table>

[1] Some models do not focus specifically on production CC but on ecosystem effects or culture-environment interactions, which ultimately would allow the exploration of ecological CC.
[2] Some models do not focus specifically on ecological CC but on aquaculture practices and their effects on production.