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Potential applications of mussel modelling

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Abstract Mussels are extensively cultivated worldwide and are of growing economic importance. However, constraints on the exploitation of wild mussel resources have necessitated the need for tools to improve the management of mussel cultivation towards increased production. Ecological models are increasingly being used as a management tool, and therefore the existing approaches to modelling mussels have been reviewed with respect to their possible application to the improvement of shellfish management strategies. We suggest that dynamic energy budget (DEB) models have the greatest potential in this area, and discuss the mussel DEB models that have been developed to date in terms of their physiological complexity, accuracy of prediction of individual mussel growth and ability to predict mussel population production. Individual mussel production has been predicted; however, the focus of many of the models has been on the growth and reproduction of a single mussel and therefore population effects generally have not been included. Other models at the population level have included only limited population effects, and this has reduced the capacity of many of the models to accurately predict mussel production at the population level. Interactions at the population level (self-thinning and predation) are discussed and the models that describe the consequences of these processes are examined. In future DEB models will need to include the ability to parameterise population level processes if we are to have greater confidence in their application to shellfish management.

Keywords Mussel · Models · Dynamic energy budget · Cultivation

Introduction

Mussels (Bivalvia: Mytilidae) are distributed globally and are a conspicuous feature of many intertidal habitats on both hard and soft substrata (Seed 1976). Mussels are often the dominant organism in terms of their biomass and form a key component of many marine communities (Seed 1976; Herman 1993). Mussel beds support their own diverse communities as the mussel matrix, composed of layers of mussels with accumulated sediment and debris, provides numerous microhabitats and an organically enriched environment (Ragnarsson and Raffaelli 1999). The diversity of the associated invertebrate communities increases with the size and age of the mussel beds, as the latter is proportionally linked to the structural complexity and thickness of the bed (Tsuchiya and Nishihira 1985, 1986).

The dynamics of the mussel bed will be related to spat supply and recruitment. Supply limitation, as is demonstrated in other species with similar life histories (e.g. barnacles; Roughgarden et al. 1988), could therefore be significant for mussel bed structure. Predators can also be important structuring agents of mussel beds. Many of the classical studies that demonstrate zonation patterns of intertidal mussels have focused on the effects of mussel/predator interactions [e.g. with starfish (Seed 1969; Paine 1976) and lobster (Elner and Campbell 1987; Robles 1987) interactions]. Where they occur, the abundance and high biomass of mussels means that they provide an abundant food resource for a wide variety of marine invertebrate and avian predators (Seed 1993). The main invertebrate predators of mussels in Northern Europe include gastropods, starfish and decapod crustaceans (Seed 1993), while vertebrate predators include birds such as oystercatchers (*Haematopus* spp.) (Meire and Eryvynck 1986; Cayford and Goss-Custard 1990) and eider ducks (*Somateria mollissima*) (Dunthorn 1971;

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Guillemette et al. 1992), fish (Dare and Edwards 1976) and even seals, walrus and turtles (Seed 1993). Furthermore the mussels themselves can serve as self-structuring agents through self-thinning. This is thinning imposed by a population on itself at high density with an observed negative relationship between individuals per unit area and average individual mass (Westoby 1984).

As with other reef-forming bivalve molluscs, such as oysters, mussels play an important role in the exchange of material between benthic and pelagic systems (Asmus and Asmus 1993). The filter-feeding activities of bivalve beds can process large bodies of water in a short time span. For example the volume equivalent to South San Francisco Bay is filtered at least once a day by its resident filter feeders (Cloerne 1982), and in one area of the Potomac River, Maryland, the volume of water could be pumped through the population of Asiatic clam (*Corbicula fluminea*) in 3–4 days (Cohen et al. 1984). Consequently, filter feeding by mussels is a major mechanism for the removal of suspended material such as phytoplankton, detritus and inorganic seston from the water column to the benthos. In addition some species have been shown to actively absorb organic compounds dissolved in coastal waters (Manahan et al. 1982). In turn, mussels output faeces and pseudofaeces that enrich the surrounding sediments, where the nutrients are remineralised by microbial activity (Dame 1993). Mussel metabolites (e.g. ammonium and orthophosphate) are also released into the water column and provide an accelerated link of nutrients to primary producers. Thus mussels form an integral part of the ecosystem in which they occur. They provide unique habitats that are generally higher in diversity than surrounding sediments, exert a major influence on overlying primary producers, are important in the biogeochemical cycling of minerals, nutrients and energy within the system and are a major food resource for many other species.

In addition to the significant ecosystem services that they provide, mussels are also the focus of important artisanal and commercial fisheries. The wide distribution of mussels has resulted in their cultivation throughout much of the world including Europe, Asia, and North America, using a variety of methods such as longline, raft and on-bottom culture (Hickman 1992). The extensive cultivation of mussels has become an activity of growing economic importance (Smaal 1991), with world-wide mussel landings increasing by 25% between 1994 and 1998. Despite the relatively buoyant nature of mussel fisheries, mussel stocks are able to sustain only limited levels of exploitation. In situations where mussels are relaid for on-growing from wild stock this resource/stock is subject to natural fluctuations in recruitment and hence will be susceptible to over-exploitation. Furthermore, suitable sites for relaying may themselves be a limited resource.

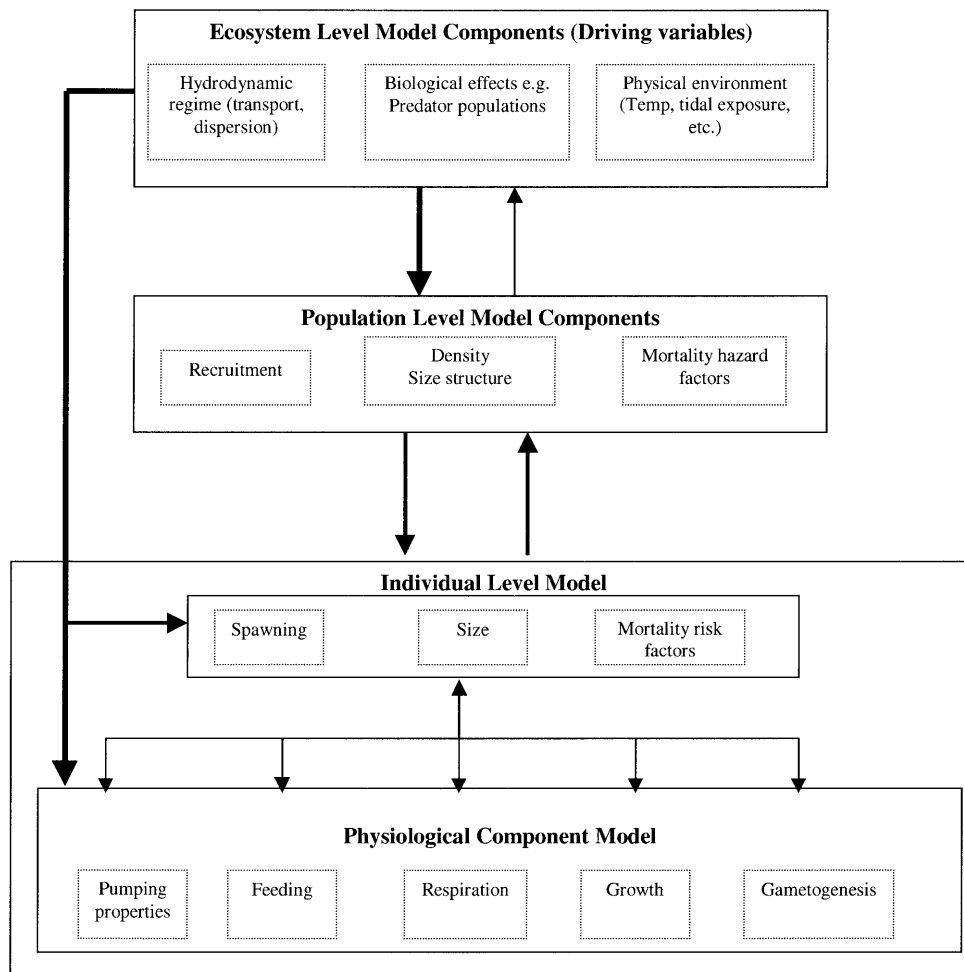
These constraints on the exploitation of wild mussel resources have prompted the necessity for tools to improve the management of mussel cultivation. In order to improve the use of the limited mussel resources avail-

able, one management objective may be to improve yield (the ratio of kg/m² of marketable mussels to kg/m² seed mussels laid). To achieve this aim, it is necessary to understand the complex suite of biological and physical factors that ultimately affect mussel growth and survival. From a commercial perspective, this information needs to be integrated in such a way that it can be used to predict the outcome of various management regimes on the growth performance and yield of cultivated mussels. One way that such predictions might be achieved is through the development of ecological models that link interactions between the key factors that impinge upon growth and survival.

The definition of a model is a simplified (often mathematical) description of a system, created in order to assist in understanding calculations and predictions. Models are particularly useful in the identification of areas that require further research but are also useful for practical management of complex systems. Each model is developed from a particular perspective and with a particular set of objectives in mind. These objectives to a large extent will define the limitations of that model. Historically mussels have been extensively researched and this knowledge base has no doubt influenced the extensive range of modelling approaches used to study their ecology (Gosling 1992). With the increasing interest in more applied aspects of mussel ecology, we thought it timely to review the existing approaches to modelling mussels and to see how these might be applied to improving their management. Models that will be useful in a management context will permit production (growth and reproduction) to be forecast as a function of food supply and other environmental factors. Dynamic energy budget (DEB) models are a plausible approach. However, complicated interactions at the population level (mortality – self-thinning and predation) requires that we integrate models of individual production (e.g. DEB models) with models that describe the consequences of these processes on the production of mussels at the population level. To better describe the levels of model complexity, Fig. 1 illustrates a hierarchy of modelling. Figure 1 demonstrates how with the need to represent important processes at higher levels in the hierarchy (e.g. population level), the potential complexity of the modelling task increases. As a consequence there is a need to consider the appropriate level of detail required of the physiological DEB model, while meeting the objectives of a useful and ecologically relevant management tool. Thus, with the increasing complexity of the models, simpler model components may be required.

For discussion purposes this review has been divided into two main sections that address DEB models, and a broader group that encompasses other models. However, the review is focused towards DEB modelling, as this is the area, in our opinion, with the greatest potential for synthesising our understanding of processes governing the energetic and population dynamics of mussels.

Fig. 1 Hierarchy of mussel modelling, showing components at each level and interactions between levels. The strength of interactions is indicated by the thickness of the arrows. Collectively the physiological components determine the size and reproductive capacity of a mussel. The individual mussels in turn interact at the population level influencing both the size structure and recruitment to the population. The mussel population will have a limited effect on the ecosystem through providing a food source for predator populations and by altering local topography. The ecosystem provides the largest influence from population level to component level as the driving force providing food and the environmental conditions in which the mussel population is situated



Dynamic energy budget models

There are a number of DEB models specifically designed to represent mussel growth (Table 1). Each of these seeks to represent mussel growth as the balance between components of feeding, respiration and reproductive output. Within each model this is achieved with differing levels of complexity of mussel physiology and by the inclusion of various physical and biological factors (Table 2). The differences between each of the models occur as a direct result of the approach taken during the development of the model and are to some extent dependent on the specific aim(s) of the model.

The most sophisticated model, in terms of physiological complexity, is that of Scholten and Smaal (1998). This model was developed to simulate the growth and reproduction of a subtidal mussel incorporating all the available ecophysiological knowledge. Specifics in the model are detailed from filtration through to ingestion, absorption [incorporating the optimal feeding model of Willows (1992)], respiration and excretion. Energy flow is represented by carbon and nitrogen fluxes between the five main compartments in the model: blood, body tissue, storage products, the organic component of the shell, reproductive tissues and activity (gametes and

spawning). Growth and reproduction are ascertained from the rates and efficiency of the physiological processes that vary with seasonal variation in temperature, food quality and quantity, and metabolic demands. The incorporation of all the available knowledge on the ecophysiology of mussels resulted in a highly complex and over-parameterised model, which is difficult to calibrate (Scholten and Smaal 1998). The complexity has also made the model unidentifiable i.e. there are redundant or ambiguous hypotheses within the model (Scholten and Smaal 1998), and this must be addressed before further meaningful development of the model can occur. However, Scholten and Smaal (1998) state that at present there is insufficient knowledge of mussel ecophysiology to rectify the situation. Nonetheless, the model predicted growth well for the site for which it had been calibrated and moderately well for another site with a high seston level. However, it was not successful in predicting growth at an alternative site that had a low seston and food inputs. This may be as a result of the adaptation of the mussels to their environment of low total particulate matter (TPM). To overcome this problem would require either a separate calibration of the model with adapted mussels for use in low TPM environments, or further complexity added into the model to

Table 1 Dynamic energy budget (DEB) models of mussels

Reference	Aim	Conclusions	Limitations
Scholten and Smaal 1998	To produce an ecophysiological model of the mussel (EMMY), for use as a management tool and to identify knowledge gaps	Complex ecophysiological model developed. No acceptable growth could be predicted for the system under certain conditions. Gaps in knowledge identified	Model developed is complex and unidentifiable
Scholten and Smaal 1999	Assess the effects of different nutrient loads on the growth and reproduction of mussels using the model EMMY	The EMMY model was simplified and good results were obtained to predict mussel growth and reproduction under different nutrient loads	Uncertainty bands within the predictions of the model are large. The model underestimates the adaptability of mussels to poor food conditions
Ross and Nisbet 1990	Develop models to represent growth and reproduction of a mussel population	Mainly successful in predicting growth and reproduction in test populations. Suggested differences in populations largely explained by differences in food and seston dynamics	Simplistic view of feeding used – assumed constant assimilation efficiency and no selection. Assumption that spawning trigger is related to core weight
van Haren and Kooijman 1993	Successfully apply DEB model, previously been used on a variety of other species, to the blue mussel	Varying growth rates in the field described by changes in food density, quality and temperature	Large assumptions of mussel physiology. Complete retention of POM assumed with no loss of organics to pseudofaeces
Grant and Bacher 1998	To test the use of a simple statistical model over a more mechanistic model to simulate growth of a mussel	Statistical model has limited applicability to turbid environments. Mechanistic model reasonably predicts mussel growth	Mechanistic model is still fairly simplistic regarding bioenergetics. Shell growth is not included and absorption efficiency coefficients are not given seasonal variability
Grant et al. 1993	Determine the carrying capacity of a longline commercial mussel farm	Physical – biological model produced with specifics of a field study	Less detailed account of mussel energy budget. No specification of selection or pseudofaeces production. No reproduction
Dowd 1997	Predict the growth of cultured bivalves through a box model approach	General features of mussel growth able to be predicted at test sites by model	Highly sensitive to small changes in physiological parameters of mussel energy budget. Less detailed account of mussel energy budget. Spawning effect averaged
Campbell and Newell 1998	To seed bottom culture lease sites in Maine to their carrying capacity	Demonstrated importance of food quality and quantity in mussel growth. Optimum carry capacity identified using MUSMOD	Not all details of mussel physiology included. Spawning not fully included (not calibrated or validated). Non-transferability

account for mussel functions altered by the adaptation to low TPM.

The Scholten and Smaal (1998) model has since been developed to examine the ecophysiological response of mussels to differing inorganic nutrient loads. In this investigation the model was simplified. The number of compartments in the model was reduced from five to four with the removal of the blood compartments. The complexity of the reproductive mechanism was reduced, with no gamete re-absorption mechanism and no link between respiration and spawning, as had been used in the earlier version of the model. The number of input parameters was also reduced from 38 to 30. The resulting model adequately predicted growth in the various inorganic nutrient regimes, although the uncertainty bands (minimum and maximum values of the simulations) remained rather wide. The model also appears to inadequately represent the extent to which mussels can adjust to poor food conditions, even though a specific

mechanism had been included within the model to allow for adaptation to these conditions.

The models of Scholten and Smaal (1998, 1999) have been designed to be comprehensive, but the approach of including all available mussel ecophysiological information has resulted in models that are complex. The authors recognised the problem identified by Beck (1987) of a comprehensive model that makes correct predictions but with little precision, compared to a simple model that makes incorrect predictions with great precision.

The benefits of simpler models have been investigated by Ross and Nisbet (1990), van Haren and Kooijman (1993) and Grant and Bacher (1998). Ross and Nisbet (1990) developed two models of an intertidal mussel, one a slightly modified version of a model developed by Kooijman (1986) and the other a new model. The two models differed in the partitioning of energy between growth, reproduction and maintenance. In the modified

Table 2 Selected variables included in dynamic energy budget (*DEB*) mussel models

Feature identified	Model									
	Scholten and Smaal 1998	Scholten and Smaal 1999	Ross and Nisbet 1990	van Haren and Kooijman 1993	Grant and Bacher 1998 ^a	Grant and Bacher 1998 ^b	Grant et al. 1993	Dowd 1997	Campbell and Newell 1998	
Physical characteristic										
Temperature	✓	✓		✓			✓	✓	✓	
Water depth									✓	
Water flow							✓	✓	✓	
Water particles										
Total particulate matter	✓	✓	✓	✓		✓	✓	✓	✓	
Particulate organic matter	✓				✓					
Particulate organic carbon	✓	✓		✓	✓	✓				
Particulate organic nitrogen	✓	✓								
Phytoplankton/Chla	✓	✓	✓	✓		✓	✓	✓	✓	
Physiological components										
Selection efficiency	✓	✓		✓		✓		✓		
Ingestion rate	✓	✓	✓	✓	✓	✓	✓	✓		
Absorption efficiency	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Pseudofaeces production	✓	✓	✓	✓		✓			✓	
Respiration	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Basal and active respiration	✓	✓			✓	✓		✓	✓	
Energy partitioning										
Core	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Storage	✓	✓	✓							
Shell	✓	✓							✓	
Reproduction	✓	✓	✓	✓						
Other										
Predation								✓	✓	
Mortality							✓	✓	✓	
Mussel density							✓	✓	✓	

^a Statistical model^b Mechanistic model

Kooijman model, the energy assimilated by the mussel initially goes through a storage compartment and is then split between reproduction, overheads of growth and reproduction and growth, with maintenance as a direct expense of growth. The new model differs in that maintenance is taken out of the assimilated energy first, with extra energy provided from storage when the assimilated energy is insufficient. The remaining energy, termed production, is then divided between growth, overheads and storage. The reproductive allocation is taken from storage, but only when storage is above a predetermined level. However, the analysis showed that neither modelling approach was better in terms of its predictive capabilities. Both models predicted growth acceptably well at three test sites, even with the simplifications to mussel ecophysiology of constant assimilation efficiency and no selection of food particles. Neither model was able to predict observed total reproduction for the site where they had been calibrated, and did not predict the observed timing and number of spawnings in another of the test populations. The spawning trigger was related to body tissue weight, and this was accepted as a weak

point in the models. Ross and Nisbet's (1990) main conclusion was that food and seston dynamics are the key factor in growth and reproduction. They identified the interaction between feeding and food/seston concentration as an area of the models that requires further refinement. This is of particular importance since it is also the specific area in the models in which many of their physiological simplifications are apparent.

The significance of the relationship between seston/food concentrations and mussel feeding highlights why physiological simplifications are an important factor when examining the potential of a mussel model to predict growth accurately. Van Haren and Kooijman (1993) devised a model to represent the growth and reproduction of a subtidal mussel by modifying a model that had previously been applied to other species. In their model the relationships between seston/food concentration and feeding are simplified by assuming complete retention of particulate organic matter (POM) and no loss of organic material as pseudofaeces. This assumption has the potential to overestimate the level of organic matter that is assimilated by the mussel and hence overpredict growth.

Other models that demonstrate simplifications in physiological functions are those of Grant and Bacher (1998). They developed two models, a statistical and a mechanistic bioenergetic model, to compare just how complex models need to be to accurately predict mussel growth rate. In the statistical model ingestion was related to a single food source component (POM), which was converted to particulate organic carbon. Absorption rate was then calculated using a constant absorption efficiency. The statistical model was unsuccessful at predicting growth at sites with high water turbidity, and was very sensitive to the absorption efficiency. The mechanistic model, while simpler than that of Scholten and Smaal (1998), was more complex than, and performed better than, the statistical model. Two food components were used, phytoplankton and detrital particulate organic carbon. Clearance, particle rejection and ingestion were then related to turbidity and the availability of these food types. However, the model was sensitive to mussel absorption efficiency, which had two fixed percentage values based on the two food sources. This model would benefit from variable absorption efficiencies related to the quality and quantity of available food. This model was specifically developed with an emphasis on feeding, and for this reason does not include reproduction. Growth is therefore only predicted for juvenile mussels, which means that the application of the model on mussel growth to marketable size is limited since the mussels will have gonads by this stage.

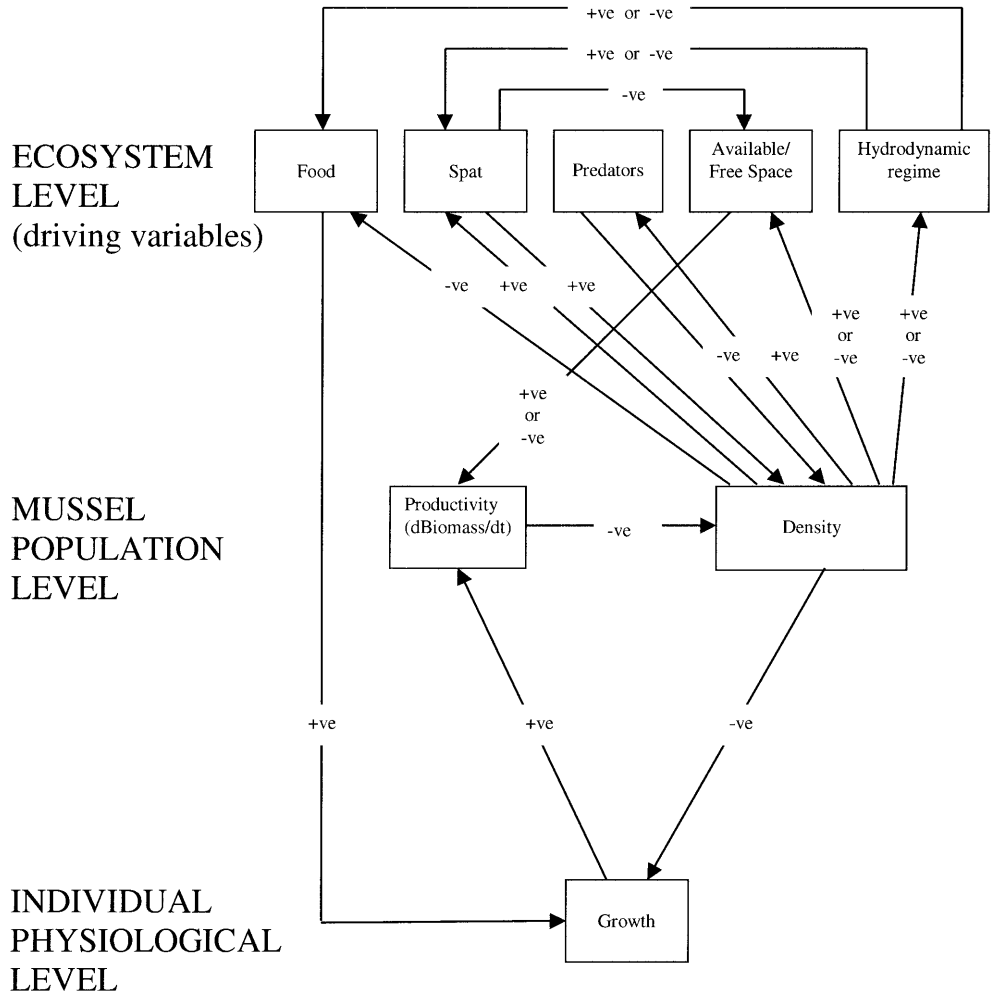
The models discussed up to this point have aimed to accurately represent growth, and in some cases reproduction, of a single mussel. Population level effects need to be included if we are to model the production of a mussel population. This can be achieved by modelling the carrying capacity of a system (but for management purposes requires mussel growth rate in the model to be maintained at a level that compares with cultivated mussels). Carrying capacity modelling has been undertaken for both longline commercial cultivation of mussels (Grant et al. 1993; Dowd 1997) and for a bottom culture site (Campbell and Newell 1998). These models are of intermediate physiological complexity (Scholten and Smaal 1999); however, they also include transport of food within the system. The investigations of Grant et al. (1993) and Dowd (1997) refer to the same study, but have examined it from different perspectives. They used a box model approach to represent the system, with interactions between seston, zooplankton, phytoplankton and mussels. The carrying capacity of the system is defined as the number of bivalves that can be sustained at a specific growth rate. This is determined by predicting the growth rate of a single mussel and then increasing mussel numbers in the system until the specified growth rate is no longer maintained. However, individual mussel growth was found to be very sensitive to specific physiological parameters, such as seston ingestion rate and assimilation efficiency. This model is therefore constrained by a limited inclusion of mussel physiology. The model does not fully incorporate reproduction, but averages out

the effects of weight gain and loss. Dowd (1997) does include density effects of mussel numbers through competition for food, by reducing the concentration of phytoplankton in the water column, an effect that has been demonstrated by Fréchette and Bourget (1985a, b). Others have suggested that direct physical interference between mussels, another example of a population-level interaction, can exert a direct effect on an individual mussel's growth performance and survival probability (Okamura 1986; Fréchette et al. 1992). This has not been incorporated within the model of Dowd (1997), although predator-induced mortality is included through an overall mortality factor, which varies with time, calculated on a site-specific basis. The model was able to predict the general features of mussel growth in the test areas. However, the adaptation of mussels to their environment is an area that was identified as needing improvement to refine the model.

Another model that has been developed to consider carrying capacity is that of Campbell and Newell (1998). This model was developed to be as simple as possible regarding both mussel physiology and physical parameters, with the aim of predicting mussel production using food quality and quantity, water flow and depth. The model of Campbell and Newell (1998) was successful in so much as mussel yields were improved by following the seeding density and timing recommendations of the model. Nonetheless, its predictions were not accurate at one of the validation sites and this was attributed to reproduction not having been included in the original model. The model was modified to include spawning but it was neither calibrated nor validated. At present the model (MUSMOD) cannot accurately predict mussel growth over the entire range of physical conditions where mussels are cultured.

The DEB models discussed previously have been shown to predict mussel growth with moderate success and in many cases have been successful in answering the questions that they have been designed to address. Areas in which further research would be advantageous have also been identified. The importance of the relationship between the seston/food concentration and the rate at which carbon or energy is assimilated has been highlighted in many model developments. Much laboratory research has been conducted into this area (e.g. Hawkins and Bayne 1985; Bayne et al. 1987, 1988; Newell and Gallagher 1992; Hawkins et al. 1996, 1998). However, to use this physiological information to manage fisheries, or predict mussel growth *in vivo*, we need to know more about the characteristics of the available food supply. Another area which has been highlighted by both Scholten and Smaal (1998, 1999) and Dowd (1997) is the adaptability of mussels to their ambient environmental conditions, which makes modelling the system more challenging. However, many of the models focus solely upon the growth of a single mussel and so in the cultivation of mussels there are still large areas in which these models do not predict. The mussel models developed to date do not generally include population effects, e.g. re-

Fig. 2 Feedback mechanisms and interactions operating within different levels of mussel modelling. *Arrows* indicate an increase (+ve) or decrease (-ve). The ecosystem provides the driving variables in the system. The hydrodynamic regime influences supplies of food (and hence growth) and spat. Spat settlement is a component in the amount of available/free space. Space limitation can be a significant aspect of self-thinning, and hence may influence population productivity. Density is at the centre of many of the feedback mechanisms as the physical presence of the mussels can affect the hydrodynamic regime, reduce or increase the amount of available/free space and influence spat settlement. The size and number of the mussels will affect the numbers and type of predators, and determine the level of food depletion in the water column



relationships between growth, predation and other sources of mortality which are known to be significant (Goss-Custard and Willows 1996). The lack of population level component within many modelling approaches has precluded the incorporation of feedback mechanisms between the organisms and the environment (Fig. 2). The external conditions are mainly given as conditions that the organism reacts to but does not determine or effect, and this is particularly crucial when field situations and model results are to be compared. Therefore, there is much scope for development of models that better predict mussel production.

Models have been developed that are concerned with population effects, such as predation, particularly regarding birds, and self-thinning. While some of these models are dynamic others are static, but both provide a greater understanding of the interactions that operate within a system. Therefore, if these models could be coupled to, or the processes assimilated within a dynamic model, such a model may allow us to more accurately forecast mussel production. Models that could be used in this capacity are considered in the next section.

Models relevant to the management of mussel production

There is another suite of models that are of particular relevance in the prediction of mussel population production. Fundamentally, these models all address mussel stock-dependent factors and can be separated into three main groups that deal with self-thinning, food/particle depletion, and predation.

Self-thinning is potentially a key component in predicting population productivity, especially under conditions of cultivation. Self-thinning describes the negative relationship that is observed between individual mean size and mean population density in a cohort of growing organisms (Westoby 1984). Self-thinning has been most extensively studied by plant ecologists and has been a subject of interest for the past three decades (Yoda et al. 1963; White 1980; Westoby 1984; Weller 1987), where the limiting factor has been identified as space. The concept has been adapted to sedentary animals by Hughes and Griffiths (1988), who describe a geometry of packing leading to observed self-thinning. Food-regulated self-thinning has also been suggested (Begon et al. 1986; Elliott 1993) but generally has focused on mobile ani-

mals. However, Fréchette and Lefaiivre (1990) have suggested that in benthic suspension feeders both food and space may regulate self-thinning. The cause of self-thinning in mussels is therefore a question that remains unanswered as it may be regulated by food or space limitation (the latter resulting in physical interference).

Nonetheless, models that predict the effect of self-thinning on a population have been devised. Fréchette et al. (1992) developed a hypothesis to explain the change in absolute growth of a mussel resulting from competition for surface space between neighbouring mussels. The change in absolute growth of the mussels is presumed to be brought about through a size-dependent effect of pressure on the mussel shell, resulting in reduced valve gape and hence filtration rate. Guinez and Castilla (1999) proposed a three-dimensional self-thinning model for multi-layered intertidal mussels. This model suggests that density dependence could be more frequent than has previously been indicated by two-dimensional models, and is of particular importance to bottom cultivation, where layering is more likely to occur. Nonetheless, their model is space-driven and does not consider that competition for food resources may influence self-thinning by reducing growth rate.

Self-thinning as a result of food limitation has not been modelled; however, the flow of water over a mussel bed and the corresponding depletion in phytoplankton caused by the filtration of the water has been addressed. Fréchette et al. (1989) developed a two-dimensional model of horizontal advection and vertical diffusion to represent phytoplankton movement within the boundary layer to examine the effect of mussels on phytoplankton distribution. The model has since been modified (Butman et al. 1994) to represent near-bed conditions more accurately. The model allows the prediction of phytoplankton depletion where the filtration rate of the population of organisms is known and where the flow is steady and uniform. Unfortunately this is not a condition regularly found in the field; many mussel beds are found in turbulent conditions. Turbulent conditions can result in the resuspension of sea-bed material (Navarro and Inglesias 1993) and this can provide additional organic material, in the form of organic-rich detritus and benthic microalgae, and promote growth where phytoplankton is limiting (Fréchette and Grant 1991). The resuspension of sea-bed material can also promote the growth of phytoplankton and this is an effect that may be particularly important to bivalve communities on a larger spatial scale, such as whole estuaries, embayments etc. Nonetheless the model of Butman et al. (1994) does provide a line of investigation along which to continue further study.

Apart from mortality that is intrinsic to the mussel population, external sources of mortality must also be addressed, i.e. predation. The most important predators of mussels are starfish, crabs and shore birds (Seed 1969). The impact of these predators can be very seasonal, for example crabs are generally more active in the spring and summer, and in the winter the impact of birds is greater when large flocks temporarily over-winter in coastal areas (Seed and Suchanek 1992).

Predation has been modelled most extensively regarding the effects of birds on mussels. Hilgerloh and Siemoneit (1999) developed a dynamic model of bird predation on mussel beds in the tidal flats of Lower Saxony, Germany. While the quantitative effect was found to be small, it did establish that mussels larger than the mean of the population were more often predated upon. This suggests that where populations suffer significant bird predation the apparent growth of a mussel cohort will be reduced, resulting in a smaller mean mussel size than in a population without predation. Other studies have focused upon single species, for example oystercatchers (*Haematopus ostralegus*). Oystercatcher feeding can be used to calculate the carrying capacity of mussel beds, and formed the basis of a model developed by Goss-Custard et al. (1995), using an empirical game theory distribution model of oystercatchers feeding on mussels. This involves a description of how a population of oystercatchers, in which individual birds vary in their competitive ability and foraging efficiency, becomes spatially distributed over the spatially variable mussel food supply. Manipulation of the model output can produce estimates of the mussel biomass removed from the beds, giving an indication of the effect of oystercatcher predation on intertidal mussel beds.

There is a paucity of specific models relating to invertebrate predation on mussels, although a considerable amount of research has been conducted into this area. Feeding mechanisms by both crabs (Seed 1969; Jubb et al. 1983; Ameyaw-Akumfi and Hughes 1987) and starfish (O'Neill et al. 1983; Norberg and Tedengren 1995) are well documented. Size selection is also demonstrated, with smaller mussels suffering disproportionately high losses from crabs (Seed 1976) and starfish feeding on mussels equal to or larger than the mean size of the mussel population (Dolmer 1998).

There is a distinct relationship between the size of mussel taken and type of predator, with crabs responsible for mortality of the smaller mussels in the population and birds and starfish preying on the larger mussels. Therefore, a way of including predation mortality within a mussel population model may be to apply a size-specific mortality function dependent on the composition of the predator community. The reduction in mussel population density as a result of predation mortality may also have effects on other density-dependent functions operating within the mussel bed, e.g. self-thinning, and thus may require further interactions within the model.

Conclusions

The approach of using DEB models has enabled predictions to be made regarding individual mussel growth and production. This method of modelling is of particular value since it has the capacity to represent changes in the mussel populations resulting from variations in the factors operating on the mussel population. Differing levels of complexity of mussel ecophysiology have been used

and problems have been encountered in both complex (due to over-parameterisation) and simple models (lack of accuracy). Since many of the models were developed to represent the growth and reproduction of a single mussel, population effects have generally been ignored and this reduces their ability to accurately predict population production. However, some of the models have included varying degrees of population effects and models that specifically address these effects have been identified. To enable DEB models to be used in shellfishery management with greater confidence will require models that are not over-parameterised, yet include population level processes. A sensible future approach would be to develop models based on an integration of physiological knowledge of individual processes with a well designed field experiment with the objective of simultaneously estimating predation, density and food limitation effects on growth and mortality. Thus this may allow more of the necessary factors in mussel production to be simultaneously parameterised and incorporated into a model that includes the most important individual and population level processes.

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