1 **Title:** A simulation model of carrying capacity for mussel culture in a Norwegian fjord:
2 role of induced upwelling

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ABSTRACT

Shellfish carrying capacity is determined by the interaction of cultured species with the ecosystem, principally constrained by environmental characteristics, especially food availability. A recent experiment carried out in Lysefjord (SW Norway) has shown that induced upwelling of nutrient-rich deeper water stimulated phytoplankton growth, potentially increasing the carrying capacity for mussel cultivation. With the aim of assisting in development of sustainable mussel culture in Lysefjord, an object-oriented model of aquaculture-environment interactions and mussel carrying capacity was constructed. A multiple box ecosystem model was developed within the visual simulation environment of Simile software allowing explicit coupling between boxes, which represent regions of the fjord. Once the box model was developed and calibrated, subsequent application of PEST (Parameter ESTimation) allowed optimization of different parameters of the model in order to manage mussel production according to carrying capacity criteria. The Simile model and the simultaneous application of PEST allowed several scenarios taking into account different stocking densities, upwelling alternatives, and the creation of new cultivation areas.

Key Words: Ecosystem model; Ecosystem management; Shellfish aquaculture; Carrying capacity; Phytoplankton; Fjord, Norway

1. INTRODUCTION

Primary production of marine systems depends in part on physical processes that regulate light and nutrients. There is a strong linkage between productivity and water column stability, affecting nutrient supply and cell distribution in the water column. The pycnocline also limits the exchange of nutrients from below the euphotic zone, and summer nutrient depletion is a common feature of temperate water columns (Steele, 1974). In many coastal areas primary production is periodically enhanced by mixing of nutrient-rich deep waters or a shallow pycnocline (see review in Pennington et al., 2006). Fjords are an extreme example of these conditions, since they are often deep, with huge reservoirs of nutrient-rich subsurface water and a strong pycnocline that maintains stratification for long periods. Stratification is primarily a result of freshwater runoff, heating and calm wind conditions that restrict vertical mixing of nutrients into the euphotic layer (Aure et al., 1996; Asplin et al., 1999). Nutrients derived from freshwater runoff and intermediate water inflow from coastal waters are generally less important than vertical nutrient flux (Aksnes et al., 1989). During the summer, water circulation in fjords is characterized by strong stratification that restricts the vertical exchange and the supply of nutrients from deep waters to the euphotic layer (Aure et al., 1996; Asplin et al., 1999). Consequently, primary production is based on nutrient regeneration rather than a new supply (Skjoldal et al., 2004), which implies a depletion of nutrients and a sharply limitation of primary production.

Shellfish aquaculture is dependent on phytoplankton and the reduction of new primary production during summer becomes an important bottleneck for mussel farming, resulting in the principal limitation of carrying capacity. Despite the potential for aquaculture in many pristine Norwegian fjords, summer nutrient limitation is a

73 significant impediment to large scale production. The low seston concentrations found
74 in these environments (Strohmeier et al., 2009) elevate the risk of food depletion that
75 can reduce bivalve growth, particularly when they are kept at high stocking density in
76 culture. The possibility of manipulating the fjord water column to make deeper water
77 nutrients available is compelling experiment in coastal biogeochemistry and
78 hydrodynamics. The CANO project (CARRYing capacity in NORwegian aquaculture)
79 involves a large scale experiment carried out in Lysefjord (SW Norway) in order to
80 determine the potential impacts of induced upwelling on phytoplankton biomass,
81 production and composition (Aure et al., 2007a). Induced upwelling was generated at a
82 single location near the head of the fjord by pumping brackish water from the surface to
83 depth (30 m), with a large diameter pipe (1.25 m). Although this could not break the
84 pycnocline, it increased local vertical transport of nutrients resulting in a tripling of
85 mean chlorophyll a and related primary production during summer (Aure et al., 2007a).
86 This study also documented the horizontal and vertical spread of nutrients and
87 chlorophyll, indicating the widespread potential for enhancing food supplies of cultured
88 suspension feeders.

89
90 The development of sustainable aquaculture in the Lysefjord and similar fjords
91 appropriate for induced upwelling requires a study of environmental-mussel interactions
92 and mussel carrying capacity. The creation of a new culture area introduces a large
93 biomass of filter feeders which can exert an important effect on the dynamics of
94 particles and nutrients in marine ecosystems, potentially altering the flow of matter and
95 energy (Dowd, 2003). This is especially important in fjords, which are characterized by
96 low seston concentration (Strohmeier et al., 2008) and a relatively small component of
97 native filter-feeders. Because the induced upwelling will enhance new production in the

fjord, introduction of suspension feeder biomass must be proportionate as to not over-exploit the base of the fjord food chain. In this way, carrying capacity studies can be useful decision-making tools for managing aquaculture activity (Bacher et al., 1998; Ferreira et al., 1998; Duarte et al., 2003; Grant et al., 2007) and increasing the profit in new cultivation areas (Héral, 1993).

This balance can be achieved through mathematical models used to assess these potential interactions in marine ecosystems (Dowd, 2005). The possibility of running alternate scenarios provides potential information to explore the consequences of changing nutrient conditions, the standing stock of mussels, or the distribution of both within the fjord. This kind of models requires the coupling of a physical submodel to describe the water exchange within the study area and an ecophysiological submodel to describe the physiology of different organisms and the interactions between them and the environment. However, the information required to set up the model is sometimes difficult to obtain. In the case of Lysefjord, a physical model is available to calculate the water exchange between different areas of the fjord (Asplin, unpublished data), and there is an appropriate chlorophyll dataset (Aure et al. 2007a). Moreover, the properties of the induced upwelling have been well documented (Aure et al. 2007a).

In the present study, an ecosystem box model based on PNZ-type dynamics (Phytoplankton –Nutrients – Zooplankton) with the addition of mussel and seston submodels has been applied to Lysefjord with the aim of assessing the spread of nutrients and chlorophyll as a function of induced upwelling, and assisting in development of sustainable mussel culture in this manipulated ecosystem. The focus of the model was carrying capacity of the fjord and not bivalve growth, and for that reason

a constant levels of mussel biomass have been implemented in the model domain, such that mussel biomass interacts with the ecosystem model as a forcing function (Dowd, 2005, Filgueira and Grant, 2009). This approach (1) increases the robustness of the results in new aquaculture areas in which a non-groundtruthed mussel submodel potentially introduces uncertainty related to biomass-dependent processes and (2) simulates the most conservative scenario from the ecosystem point of view because the mussel standing stock can be considered the maximum biomass that can be sustainably supported by the ecosystem and therefore cannot be exceeded. Different scenarios were run in order to explore the effect of different stocking densities and locations. Ultimately, the standing stock of mussel biomass that represents the ideal scenario according to a predefined carrying capacity criterion was estimated using optimization. We emphasize optimization as a major advance in these types of models applied to aquaculture.

2. MATERIAL AND METHODS

2.1. Study site and boundary conditions

Lysefjord is located on the southwest coast of Norway (59°0'N, 6°16'E). The fjord is between 0.5 and 2 km wide and approximately 40 km long although the study area is limited to the first 6 km nearest to the head (Fig 1). The sill depth is 14 m, maximum depth is 460 m and the average depth in Box 1, 2, 3 and 4 (defined below) is 130, 160, 150 and 100 m respectively. The surface area of the fjord is 44 km², while the study area located in the head is about 5 km². Water exchange of the study area and the outer part of the fjord is 260 m³ s⁻¹ (Aure et al., 2007a). The freshwater input to the fjord is from a river that empties in the head of the fjord (Box 4) and hydroelectric discharge in

the North bank of Box 3 (Fig 1). The fjord is bounded by steep cliffs of up to 800 m over most of its length.

The induced upwelling system is located near to the hydroelectric discharge (Box 3, Fig 1) and consists of an electrically powered pump on a raft that takes brackish water from the surface (0-3 m depth) and forces it down ($2 \text{ m}^3 \text{ s}^{-1}$) to 30 m depth. Due to differences in buoyancy, the submerged brackish water rises to the surface and mixes with more saline water, carrying deeper nutrients up to the euphotic zone. The rising plume will intrude at depths where the density equals the density of the ambient water. A detailed explanation of pump technical characteristics and the effect of the pumped water are given in Aure et al. (2007a).

Outside the model domain, boundary time series (between Julian day 84 and 264) of chlorophyll, total particulate matter, surface and deep nutrients and temperature were obtained at Stn 17 (Fig 1) in a multi-year study (see Aure et al., 2007a for methodological details). The data from several cruises (Aure et al., 2007a; Aure, unpublished data) was pooled and averaged resulting in a time series with a sampling frequency of 7-15 days. Linear interpolation was used to reconstruct the time series between sampling dates. Chlorophyll concentration was converted to carbon units assuming carbon:chl of 50:1. Detrital carbon was calculated by multiplying the POM value by 0.5 and subtracting the phytoplankton carbon. Nutrients values were taken from 10 m depth data. The local freshwater induced production was not considered in the model because it was negligible compared to the induced upwelling production inside the influence area. No other model quantities were considered to be altered by upwelling besides nutrients. A time series of nitrate concentration in deep waters

(average between 15 and 20 m depth) was used to characterize available nutrients from depth, and only nitrate was considered.

Inside the model domain, an independent dataset of five CTD vertical profiles collected in two samplings dates (with induced upwelling: 22 July 2005 and without induced upwelling: 30 August 2005, Aure et al. 2007a) were used to estimate the water exchange in the fjord.

2.2. Ecological model

A multiple box ecosystem model was developed with highly configurable GUI-based software (Simile v5.3, <http://www.simulistics.com>) that allows explicit coupling between boxes, which represent regions of the fjord. The model was based on the classical PNZ model (Phytoplankton (P) – Nutrients (N) – Zooplankton (Z)) with the addition of mussel (M) and detritus (D) submodels. Given that the phytoplankton growth rate is high enough to dominate the biomass renewal in fjords (Asknes et al., 1989) and the minimal impact of the zooplankton compartment on the results, the later submodel was turned off in subsequent scenarios in order to simplify the global model. All the submodels are characterized in terms of mg C m^{-3} , with the exception of dissolved nutrients, which is characterized in terms of mg N m^{-3} . The equations of the model are based on Kremer and Nixon (1978) and a detailed description is given in Grant et al., (1993, 2007, 2008) and Dowd (1997, 2005). Brief descriptions of the differential equations that define the submodels are given by:

$$\frac{dP}{dt} = +\text{growth} - \text{mortality} - M \text{ grazing} \pm \text{mixing} \quad (\text{Eq. 1})$$

$$\frac{dN}{dt} = +induced\ upwelling + M\ excretion - P\ uptake \pm mixing \quad (Eq. 2)$$

$$\frac{dD}{dt} = +M\ feces + P\ mortality - sinking - M\ grazing \pm mixing \quad (Eq. 3)$$

$$\frac{dM}{dt} = +seeding + net\ growth - mortality - harvesting = 0 \quad (Eq. 4)$$

The mixing term includes the exchange between boxes and the exchange with the far field. Light photoperiod and intensity were adapted in the model to reproduce the local conditions observed in the fjord. The following modifications for particle dynamics have been applied in this study. With regard to detritus equation, a fraction of the mussel faeces and dead phytoplankton are routed to the detritus compartment instead of the bottom. Fifty percent of mussel faeces are directed to the detritus compartment, assuming that water movement can disperse faeces, which remain in suspension. A sensitivity test showed that a variation of 10% in this rate causes a maximum change of 0.38% in the results of detritus submodel. In addition, 80% of dead phytoplankton is transferred to the detritus compartment, assuming that water movement is enough to maintain small dead cells in suspension. A sensitivity test showed that a variation of 10% in this rate causes a maximum change of 0.15% in the results of detritus submodel.

The mussel compartment maintains a constant biomass through time. The term that interacts with the ecosystem, net growth of mussels (ingestion minus respiration and defecation) is balanced by farming practices (seeding and harvesting) and mussel mortality. The constant biomass assumption was achieved by (1) maintaining a constant number of mussels in the modelled population, that is, seeding, harvesting, reproduction and mortality were not considered; and (2) resetting the mussel weight to the initial value after each time step.

2.3. *Exchange between boxes*

The ecosystem model is defined by four boxes of 5m depth (1: 12 668 286 m³, 2: 5 317 975 m³, 3: 3 983 529 m³ and 4: 2 736 965 m³) connected according to Figure 1. The lower layer of water >5m depth is external to the domain. Each box is assumed to be internally homogeneous and the horizontal exchange between adjacent boxes is regulated by an exchange coefficient K , which can be interpreted as an inverse time scale for the flushing of the box (see Appendix A in Dowd (2005) for mathematical explanations). Given that the volume of the boxes were different, two different coefficients were calculated for each boundary between boxes in order to conserve water, solutes, and particles.

The exchange with the far field is carried out in Box 1, the induced upwelling is located in Box 3, and Box 4 represents the inner part of the fjord. Horizontal water exchange between the four boxes of the model was estimated using PEST (Model-Independent Parameter Estimation, Watermark Numerical Computing, <http://www.sspa.com/pest/>), an optimization utility that uses the Gauss-Marquardt-Levenberg algorithm to estimate the value of a parameter, minimizing the discrepancies between the model results and a dataset chosen by the user. Water exchange between Box 1 and 2, 2 and 3 and 3 and 4 was estimated in order to achieve the chlorophyll gradient observed when the upwelling pump was turned on specific to 22 July 2005 by (Aure et al. 2007a). A relative longitudinal gradient was calculated by dividing the integrated values of chlorophyll profiles in different locations that represent the different boxes. The time series used to force the model for PEST simulations are from an independent multi-year dataset different to Aure et al. (2007a), so the parameter estimation is independent from the 22 July 2005 observations.

Subsequently, the initial conditions inside the model domain must be adapted to the new situation created by the induced upwelling, requiring an iterative process with the estimation of water exchange because the initial conditions depend on water exchange and vice versa. The iterative process has three steps:

1. Running the model using PEST to determine the exchange coefficients, which simulate the gradient of chlorophyll in the fjord (Model set up: Boundary conditions: Multi-year time series between Julian day 84 and 264; Time Step: 1 d; Simulated submodels: phytoplankton, nutrients and detritus).
2. Running the model with the exchange coefficients estimated in the first step. In this step, the boundary conditions were set up as a constant time series with similar values to the observed ones during the first day of the modelled period (Julian day 84). The aim of establishing constant forcing time series was to determine the initial conditions in each box that were in equilibrium with the far field at the beginning of the simulation period (Julian day 84). Given that the boundary conditions were constant the results provided an asymptotic value for phytoplankton, nutrients and detritus in each box. (Model set up: Boundary conditions: constant time series with similar values to Julian day 84; Time scale: until reaching asymptotic values in the simulated submodels; Time Step: 1 d; Simulated submodels: phytoplankton, nutrients and detritus).
3. Repeat the first step using as initial conditions in each box the asymptotic values generated in the second one. Repeating the process until achieving constant values for initial conditions and for exchange between boxes.

2.4. Carrying capacity criterion

The carrying capacity criterion can be defined as the standing stock of mussel biomass that grazes the additional phytoplankton produced by induced upwelling back to a chlorophyll concentration that would be observed in the absence of aquaculture and induced upwelling (“background” chlorophyll). The chlorophyll background values in each box were calculated by running the model without induced upwelling and aquaculture activity.

The mussel biomass that fulfils this carrying capacity criterion was optimized by PEST by minimizing the discrepancies between the background chlorophyll time series and the one observed with aquaculture activity and induced upwelling. In this mathematical process, all days have the same contribution in the minimization algorithm, however, from an ecological standpoint, a day with low chlorophyll may be more consequential. In order to explore this potential problem, four carrying capacity weightings (Factor 1, 2, 3 and 4) were analysed in terms of chlorophyll depletion. With Factor 1, PEST was used to minimize the discrepancies between the model and the background chlorophyll time series and estimate the mussel biomass that compensated the induced upwelling. In Factor 2, 3 and 4 criteria, the background chlorophyll time series used by PEST were modified depending on the daily chlorophyll content. With Factor 2 criterion, the highest chlorophyll value was weighted by 1 and the lowest one by 2 (multipliers of 3 and 4 in Factor 3 and 4 respectively). Linear regression was used to determine the multiplier used in other values of the dataset. This procedure increased the relative significance of low chlorophyll in the background datasets. These modified datasets were used by PEST to optimize the mussel standing stock biomass.

3. RESULTS

3.1. Calibration and sensitivity analysis of water exchange

The application of the iterative process based on the spatial gradient of chlorophyll provided the following exchange coefficients between boxes ($K_{\text{entry-exit}}$): $K_{1-2} = 1.95 \pm 0.017 \text{ d}^{-1}$, $K_{2-3} = 2.55 \pm 0.042 \text{ d}^{-1}$, $K_{3-4} = 4.84 \pm 0.171 \text{ d}^{-1}$. The reverse coefficients, K_{2-1} , K_{3-2} and K_{4-3} , were calculated taking into account the above values and the volume of the different boxes. Although the exchange coefficients were determined from upwelling conditions, a test of their validity was undertaken by predicting the chlorophyll gradient in comparison to observed values in the absence of induced upwelling (Aure et al., 2007a). Figure 2 shows the ratio between chlorophyll in Box 4 and chlorophyll in the remaining boxes in two scenarios, with (22 July 2005) and without (30 August 2005) induced upwelling. The modelled ratio is in very good agreement with the observed value in the whole upper fjord with both scenarios, showing no statistical differences (t-test, $p > 0.05$). In both situations the chlorophyll pattern shows an enrichment of chlorophyll in the inner part of the fjord. However, the enrichment gradient is more abrupt in the upwelling scenario, with Box 4 containing 1.63 times more chlorophyll than Box 1, whereas in the non-upwelling scenario this ratio is reduced to 1.10 times.

In order to test the sensitivity of estimated exchange coefficients on model results, several scenarios were run increasing the value of the coefficients by 100% and reducing them by 50%. The small change in chlorophyll content when K_{3-4} is changed suggests that the results of the model are not sensitive to changes in the exchange between Box 3 and 4 (Table 1). The scenarios indicate that the model is more sensitive to a reduction of the exchange between boxes than to an increase. The maximum change in chlorophyll content with an increase in K of 100% is 12.5%, but a reduction of 50%

caused a change of 32% in chlorophyll content. The comparison of exchange coefficients indicates that the exchange between Box 2 and 3 is the most sensitive.

3.2. Background Scenario

The chlorophyll background values in each box were calculated by running the model without induced upwelling and aquaculture activity. Phytoplankton populations inside the fjord are regulated by advection, i.e. exchange with the far field, and the nutrient supply. Figure 3 shows the chlorophyll content and nutrients in the four boxes and far field. This scenario is the base for the different carrying capacity criteria.

3.3. Carrying capacity criterion

The use of PEST allows estimation of the maximum mussel biomass in the fjord to remain below the chosen carrying capacity criterion (Table 2). A common pattern in the four criterion weightings is that mussel standing stock must be minimal in Boxes 1 and 2, and the bulk of biomass must be located in Box 4, the inner box of the fjord. The results show important differences between the different criteria: the standing stock biomass to satisfy Factor 1 criterion is 3620 tons wet weight while Factor 4 criterion allows a biomass of only 482 tons. We emphasize that these biomass estimates are not simply linear multipliers of the criterion weighting system, since the weights interact with the seston time series.

The impact on the ecosystem of each scenario was analyzed by means of two indicators, the percentage of days in which the chlorophyll is depleted compared to background values and the maximum depletion observed during the simulated period. The four scenarios show the same pattern and both indicators demonstrate how the impact on the

ecosystem increases from the outer part of the fjord to the inner one in which mussel biomass is located. Therefore, the ecosystem effects are emphasized in Box 4. In terms of depletion, Factor 1 and 2 scenarios showed a similar impact on the ecosystem, 88 and 80% of days in which depletion is observed and a maximum depletion of 68 and 64% respectively. Factor 3 scenario showed lower values: 55% of days showed depletion and the maximum extent was 42%. Factor 4 scenario is the most conservative for the environment with percentage of depletion days = 27%, and the maximum depletion, 12%. Factor 4 scenario was considered as the most acceptable on this basis.

The chlorophyll pattern in Factor 4 scenario is fairly similar to that observed in the background scenario, however the former is enriched (Figure 3 and 4). Factor 4 scenario shows the clear gradient observed by Aure et al. (2007a), accumulation of chlorophyll in the inner part of the fjord (Box 4), and a reduction towards the mouth (Box 1). This pattern is more evident during phytoplankton bloom events, between day 94 and 108 and day 144 and 188.

4. DISCUSSION

One of the novel points of this work is the use of an optimization tool like PEST to estimate the water exchange between the boxes of the model. We are effectively using the chlorophyll gradient as a conservative tracer, assuming that the gradient is due to diffusion-advection over short time scales. Other studies have used tracers such as temperature for the same purpose (Dowd, 2003). This was only possible due to the steep difference in chlorophyll in the fjord established by induced upwelling and quantified in Aure et al. (2007a). In addition, these authors observed a negative relationship between water transport and chlorophyll content within the fjord. In the same way, the sensitivity

test (Table 1) suggests that an increase or decrease of the exchange can cause a reduction or increment respectively of the chlorophyll content. The optimized exchange coefficients were compared to the values calculated using physical modelling and current meter data collected within Lysefjord (Asplin, unpublished data). These latter values, $K_{1-2} = 2.69 \text{ d}^{-1}$, $K_{2-3} = 3.52 \text{ d}^{-1}$, $K_{3-4} = 3.61 \text{ d}^{-1}$, are in good agreement with the optimized values. This procedure allows us to introduce the hydrodynamics in the biogeochemical model without development of a separate physical model. We note that this approach essentially solves for the physical exchange rather than utilizing a separate circulation model. Despite the obvious 3D structure of the water column, we treat the system as 2D in terms of advection since horizontal transport exceeds vertical transport by a factor of 10 (Aure et al., 2007b). Vertical transport of nitrogen is considered to be important only in Box 3 where the upweller is located. In this case, it is parameterized as a flux of nitrogen based on vertical exchange induced by the upweller and a time series of deep-water nitrogen (Aure et al., 2007a). This is an entirely appropriate approach in a box model, where there are quantities available to act as tracers.

In addition to nutrients, several factors can exert influence on phytoplankton populations, including horizontal advection, turbidity, and grazing (Cloern, 2001; Jassby et al., 2002) as well as light availability. However, the supply of nutrients is one of the most important influences, for example explaining 36% of the variability of phytoplankton production (Borum, 1996). In the case of Lysefjord, the rising plume of induced upwelled water cannot break down the pycnocline, but causes a change in nutrient diffusion that exerts a bottom-up control of phytoplankton populations (Aure et al., 2007a). In addition, the creation of new cultivation areas will introduce a large biomass of mussels that can exert a second control on phytoplankton populations, e.g. a

top-down regulation of primary production (Cloern, 1982; Dame and Prins, 1998). In fact, suspension-feeders have been proposed as a solution to excess phytoplankton blooms caused by eutrophication (Kangas, 2003). In addition, they can accelerate the nitrogen cycle via ammonia excretion (Dame et al., 1991), which can enhance regenerated production although does not represent a net food source (Grant et al., 1998).

In the background scenario where mussels are absent, the interplay of nutrient supply and horizontal transport seems apparent (Figure 3). When the concentration of nutrients in the far field is below $\approx 5.5 \text{ mg N m}^{-3}$, chlorophyll content is regulated by advective processes (for example between days 94 and 108), generating a homogeneous distribution of chlorophyll in the whole upper fjord. In contrast, when nutrients are higher than this threshold, phytoplankton populations seem regulated by nutrient supply. This could explain the phytoplankton bloom observed between day 144 and 188, which causes an enrichment of chlorophyll in the inner part of the fjord compared to the far field. After day 248 onwards, the same pattern would be expected but the time series is too short (only 16 more days until the end of the time series, Julian day 264) to allow the development of a phytoplankton bloom. When different levels of mussel biomass are introduced in the fjord, the top-down regulation induced by grazers is apparent. Our carrying capacity criteria showed how varying standing stock of mussels causes differing degrees of chlorophyll depletion in the fjord (Table 2). When nutrients from depth are introduced into the system, horizontal transport becomes less important and the previous advection event between days 94 and 108 is now influenced by nutrient supply, with a gradient between the inner part of the fjord and the far field (Figure 4). Therefore, an ideal scenario for mussel farming is the stocking density,

which achieves a balance between bottom-up control from upwelled nutrients and top-down control by mussels feeding.

Previous definitions of carrying capacity focused on aquaculture involve the maximum standing stock that may be kept within an ecosystem without negative impact on mussel growth rate (Carver and Mallet, 1990) or the standing stock at which the annual production of the marketable cohort is maximized (Bacher et al., 1998). Further evolution of the concept involves division of the carrying capacity concept in four categories: physical, production, ecological and social (Inglis et al., 2000). McKindsey et al. (2006) reviewed these concepts and suggested that one area for improvement is a greater understanding of environmental interactions. Ecosystem modelling allows investigation of production and ecological carrying capacity by means of models focused on mussel growth and interactions between culture and the ecosystem. In this context, our research emphasized ecological carrying capacity, investigating chlorophyll depletion, a flux that is at the confluence of two anthropogenic effects on the system: nutrients input and mussel culture. Previous studies of mussel culture in natural upwelling areas have sought to balance stocking density with new production (Grant et al., 1998). Taking into account these effects, we could define a carrying capacity criterion based the stocking density at which a defined measure of ecosystem health is not compromised (Grant et al., 2007). However this acceptable limit is difficult to define (Duarte et al., 2003). Given that the particular conditions of Lysefjord culture, and the dual interaction that human activity exerts on the ecosystem, we propose a specific definition of carrying capacity criterion as the standing stock of mussel that consumes the new production generated by the induced upwelling and maintains the chlorophyll concentration in a similar level to background values. This carrying

capacity criterion is the most conservative that we can generate because it implies no impact at all in phytoplankton populations after establishing new aquaculture areas.

According to the defined carrying capacity criterion and the maximum depletion observed in different scenarios, the Factor 4 Criterion with a maximum chlorophyll depletion of 12%, which is in the range of natural variation in chlorophyll content, provided the optimal biomass that compensated the enhanced new production. Keeping the ecosystem alteration within the bounds of natural variation has been suggested as a decision making criterion for ecosystem based management (Grant and Filgueira, in press) and applied to investigate the change of carrying capacity in a bay in different years (Filgueira and Grant, 2009).

The constant upwelling of deep water with different nutrient concentration during the study period sometimes exceeds the capacity of stocked mussels to exploit the resulting primary production. This causes a net export of chlorophyll towards the mouth of the upper fjord region and a huge enrichment of chlorophyll, particularly in the inner part of the fjord, Box 3 and 4. In order to optimize the use of the pump and reduce the impact on the ecosystem caused by chlorophyll enrichment, a new scenario based on Factor 4 was run in which the pump was turned off when the chlorophyll content in Box 4 was $> 250 \text{ mg C m}^{-3}$. The possibility of switching off the pump allows regulation of the magnitude of the phytoplankton bloom without compromising the yield of mussel aquaculture. In terms of chlorophyll depletion, the response of this scenario (ON/OFF) is similar to that observed in Factor 4 scenario (Figure 4 and 5). The percentage of days in which the chlorophyll content is depleted relative to the background scenario is 9, 10, 20 and 32% in Box 1, 2, 3 and 4 respectively. The maximum percentage of depletion is

3, 6, 8 and 12% in Box 1, 2, 3 and 4 respectively, that is, exactly the same as the original Factor 4 scenario (Table 2). However, attending to the maximum concentration of chlorophyll, both scenarios present a remarkably different performance. Maximum levels of chlorophyll in ON/OFF scenario are significantly lower than in Factor 4 scenario (Figure 4 and 5) and more similar to the background ones (Figure 3).

Chlorophyll content in Box 1 and 4 in the background scenario vs. that observed in the ON/OFF scenario may be compared by regression (Figure 6). The ON/OFF threshold exerts a control on the maximum amount of chlorophyll that can be generated in Box 4, with an expected plateau $\sim 250 \text{ mg C m}^{-3}$. The slopes of the regressions for Boxes 1 and 4 are not statistically different from 1 (t-test: Box 1, $p = 0.30$; Box 4, $p = 0.10$), indicating that mussel grazing is efficiently compensating for increased primary production. The intercept of this line is significantly higher than 0 (t-test, $p < 0.05$), suggesting that the scenario with aquaculture will show a higher ambient concentration of chlorophyll compared to background scenario, although the chlorophyll surplus is rapidly diluted toward the mouth of the fjord. This response will also depend on the dynamics of water exchange rate due to wind and the photosynthetic effectiveness of the phytoplankton community (Aure et al., 2007a). Further adjustment of the pump cycling could be undertaken to tune this scenario even further, providing a sophisticated version of ecosystem-based management.

At the upweller site, there is uncertainty in the mixing depth of upwelled nutrients, as well as the extent of dilution during vertical exchange. This is important because the increase in nutrients is exponential at the top of the nutricline. In our simulations, we used a simple average of nutrients from 15 and 20 m. This resulted in periods in which

our measure of carrying capacity was exceeded, necessitating the factor weighting employed in model output. However, upwelled nutrients from greater depth and concentration would increase subsequent phytoplankton production and thus carrying capacity of mussel production. On this basis we undertook a simple simulation involving a constant value of upwelled nutrients, 105 mg N m^{-3} , which is the average value of the deep nutrient time series used in previous simulations. In this new scenario the standing stock biomass can be increased by 30%, reaching 627 tons of mussels in terms of wet weight. This scenario would maintain the carrying capacity criterion used in the Factor 4 scenario; the percentage of days in which the chlorophyll content is depleted compared with the background scenario is 5, 10, 17 and 28% and the maximum percentage of depletion is 2, 4, 12 and 17% in Box 1, 2, 3 and 4 respectively. Therefore, although the average amount of nutrients used in both simulations is the same, constant time series enhance the carrying capacity of the fjord compared to time series with high temporal variation. The comparison of such simulations can be used to analyse fjords with different sill depth and physical structure that determine the temporal variation of deep nutrients. Similar modelling approaches can support carrying capacity assessments of fjords where induced upwelling is used to promote phytoplankton production and establish aquaculture farms.

This study is a unique in that human activity has a dual effect on phytoplankton biomass, promoting enhanced phytoplankton production and introducing mussel populations to compensate for new production. Because the ecosystem is manipulated by the injection of nutrients, an important tool in managing new production toward aquaculture benefit is ecosystem modelling. The model allows the exploration of different scenarios as well as optimization of the mussel standing stock biomass

according a conservative ecological carrying capacity criterion. This task was performed using non-linear optimization processes carried out by using PEST (Parameter ESTimation). Although recently Rosland et al., (2009) used a similar approach to estimate parameters of a Dynamic Energy Budget (DEB) model, optimization algorithms are not commonly applied to aquaculture modelling. However, these tools are extremely useful, being crucial to achieve the main outcome of the study: (1) the estimation of water exchange within the fjord using biological characteristics (chlorophyll gradient), and (2) the optimization of spatial biomass distribution according to a quantitative mathematical carrying capacity criterion. This study shows that ecological benchmarks, scenario building and optimization tools are combined into a robust and effective approach to aquaculture management, highlighting potential of ecological modelling for marine spatial planning.

ACKNOWLEDGEMENTS

This research was funded by the CANO project (CARRYing capacity in NORwegian aquaculture) and a Fundación Juana de Vega fellowship to R.F.

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TABLE AND FIGURE LEGENDS

Table 1. Sensitivity test of water exchange coefficients between the boxes, from Box 1 to the innermost Box 4 in the fjord. Coefficient percentage of change and maximum change observed in chlorophyll results.

Table 2. Estimated standing stock of mussel biomass in different boxes according to different carrying capacity criteria and percentage of days in which is observed chlorophyll depletion compared to the background scenario as well as the maximum percentage of depletion.

Figure 1. Box structure in Lysefjord (SW Norway). Boundary conditions were obtained at Station 17.

Figure 2. Predicted and observed chlorophyll (chl_a) ratio between Box 4 and Box 1, 2 and 3. Scenarios are shown with induced upwelling (solid fill) and without upwelling (shaded fill). Vertical bands represent the standard deviation observed in the model.

Figure 3. Chlorophyll concentration in the background scenario during the simulated period, and boundary conditions of chlorophyll and nutrients.

Figure 4. Chlorophyll concentration according to the Factor 4 carrying capacity weighting during the simulated period, and boundary conditions of deep nutrients.

Figure 5. Chlorophyll concentration according to the ON/OFF Factor 4 carrying capacity weighting during the simulated period.

688

689 **Figure 6.** Linear regression of chlorophyll content in ON/OFF Factor 4 Scenario vs
690 Background Scenario in Boxes 1 and 4. The thick line represents the 1:1 relationship,
691 that is, the ideal situation in which mussel biomass compensates induced upwelling,
692 exerting null impact on chlorophyll concentration. Below (above) that line the ON/OFF
693 Factor 4 scenario is depleted (enriched) in chlorophyll compared to the background
694 scenario.

Figure 1
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Table 1
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Coefficient	% Change	Max. change in chla
K_{1-2}	+ 100%	- 9.0%
	- 50%	+ 20.0%
K_{2-3}	+ 100%	- 12.5%
	- 50%	+ 32.0%
K_{3-4}	+ 100%	- 1%
	- 50%	+ 1%

Table 2
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Carrying Capacity Criterion	Box	Mussel Biomass (Kg Wet Weight)	Days with depletion (%)	Maximum depletion (%)
Factor 1	1	0	54	12
	2	0	77	20
	3	3.09E+05	84	53
	4	3.31E+06	88	68
Factor 2	1	0	38	12
	2	0	58	20
	3	6.49E+03	71	44
	4	2.69E+06	80	64
Factor 3	1	0	29	8
	2	0	33	17
	3	3.97E+03	41	33
	4	1.23E+06	55	42
Factor 4	1	0	6	3
	2	0	7	6
	3	4.32E+03	15	8
	4	4.78E+05	27	12