5 Discussion

In this section we make observations regarding the details of the three models, and the simulation results. Ecological implications of these results are discussed briefly in the following section.

5.1 General comments

There are several small shellfish farms in the Tamaki strait area and further up the coastline of the Coromandel peninsula. Our models take no account of these. Firstly, many would be outside the models' domains, and secondly experience in the Marlborough Sounds and elsewhere suggests that the far-field impacts of such small farms are negligible (Ross, A.H. & Hadfield, M.G. 2003). This is also evident in our simulations: scenario 0 (existing farms) includes not only the Wilson Bay farms, but also nine small farms around Waimangu point – yet the influence of these latter farms is barely perceptible.

Drag associated with farms may have a significant effect on current velocities in and around farms. Measurements indicate that much of the water which would have passed through the volume occupied by the farm instead flows (rather faster) around and under the farm, whilst water within the farm moves more slowly than would otherwise be the case. The hydrodynamic model which produced the currents etc. used to drive the biological models takes no account of these drag effects. Whilst we have no data with which to make quantitative statements regarding what would happen in the Firth of Thames, scaling arguments suggest that flow modification will extend to a distance comparable to the dimensions of the farm itself – (C. Stevens, NIWA, *pers. comm.,* see also Plew et al. (in review)). This implies that flow around both Wilson Bay and the modelled Western Firth AMA may be altered somewhat. Even in the absence of quantitative information on flow modification, we can make some qualitative statements. The steep horizontal and vertical velocity gradients across a farm's perimeter will tend to enhance dispersive mixing. Depending upon whether nutrient concentrations outside the farm are higher or lower than those within the farm, this will either promote or suppress phytoplankton growth within the farm. Similarly, the enhanced dispersion will tend to counter phytoplankton depletion (percentage) when phytoplankton within the farm is lower. Reduced advection through a farm will tend to reduce the far-field impacts of the farm, but increase the magnitude of any local-scale impacts. Nonetheless, when measured at the firth-scale, reduced advection through the farms is likely to result in a lower total rate of removal of phytoplankton from the water-column by mussels.

In both the logistic plankton model and the biophysical model, plankton abundances in the extreme south of the firth often fall as the simulation progresses (snapper larvae are not found in this region at any time). This decline is expected. The firth is an estuarine system, with most of the riverine input entering in the southern firth. Thus, there is a net export of water (and associated plankton) from the southern firth. Populations will persist there only if the local rates of population growth and horizontal dispersion are high enough (Speirs, D.C. & Gurney, W.S.C. 2001).

The western firth AMA is usually predicted to have greater impact (nutrient enhancement, plankton depletion/enhancement) than are the Waimangu Point and Wilson Bay developments. There are several reasons for this. Firstly, the western firth AMA is much larger, so there is greater scope for effects to compound. Secondly both peak and tidal residual current velocities tend to be lower in this region. Thus, residence times per unit farm-volume tend to be longer. Once again, this implies that effects have more chance to compound. Finally, in comparison with the Wilson Bay AMA, the western firth one sits in comparatively shallow water. It was agreed that dropper lines should extend to the same depth (below sea-surface) in both regions. This implies that there is less ‘farm-free’ water below the Western Firth farms. This is important because this ‘farm-free’ water operates to buffer (or mask) the farm effects when depth-averaged quantities are considered.

5.2 Over-estimation of mussel ingestion rates

We have already alluded to the likelihood that the models are overestimating the quantity of material which is filtered from the water-column by mussels. There are two reasons for this. The first of these applies to both the empirical model and the biophysical model. The second applies to the snapper and logistic plankton models only.

An important reason that all three models are likely to overestimate mussel filtration is that there is a mismatch between the spatial scales that the model is able to resolve (at best: 750 x 750 x 2 m), and the scales at which mussel feeding currents operate. In reality, mussels filter only the water in their immediate vicinity. If the water is not replaced (by advection or turbulence), they will quickly clear their neighbourhood of particles. In the absence of replenishment, they can then consume no more material no matter how hard they filter. Furthermore, in a longline system, much of the water that flows past a mussel may already have been filtered by its upstream neighbours. In the model, however, these fine-spatial scale effects are not represented. Instead, the mussels perceive the control-volume (750 m x 750 m x layer-thickness) average particulate concentration – it is not feasible to explicitly represent micro-scale depletion around the dropper lines within models having domains as extensive as ours. The implication of this scale-mismatch is that, in regions where advection/turbulence is weak, (simulated) mussels have access to more food than corresponding living mussels would perceive. Recent small spatial-scale modelling work suggests that micro-scale depletion around mussel droppers can be significant, particularly when currents are weak (Smith, A. 2003). It is difficult to quantify the degree to which the models will over-predict consumption but we note that it is likely to be more of a problem in the area of the western firth AMA than in the Wilson bay area (because the latter area has higher peak and tidal residual current speeds).

A further reason that the snapper and logistic plankton models may over-estimate mussel clearance rates is that these two models take no account of the organic detritus within the water-column. This is a major constituent of the total organic particulates in the water-column, and is certainly filtered (and a fraction of it may be assimilated) by mussels. There is evidence that mussel clearance rates are unimodal functions of the organic matter abundance within the section – being maximal at intermediate concentrations of organic matter (Hawkins, A.J.S. et al. 1999). By failing to account for the organic detritus content of the water, we may have induced our model-mussels to pump water at a higher than normal rate (though not higher than they are physiologically capable when the situation demands). If they have filtered at an overly high rate, they will have consumed too many snapper eggs/larvae and too much plankton. Note, however that all three models took account of the influence of suspended inorganic matter upon mussel filtration rates. These generally dominate the total particulate concentration in this region. Hence, the filtration rate will have been only marginally over-estimated.

5.3 Snapper Model

The initial conditions for each age-class reflect the assumption that eggs are produced at a rate of 350 eggs m^{-2} d^{-1} in water between 10 m and 30 m depth. Naturally, such an assumption implies that, in the absence of transport, egg concentration will be higher around the 10 m contour than around the 30 m contour. The initial conditions ignore the influence of transport upon an individual's location. At the start of the simulation, a 7 d old individual is assumed to be in the location where it was born 7 d earlier. Thus, at the start of the simulation, the spatial distribution of the older age-classes is overly tight. The influence of the initial conditions upon the distribution of the model's oldest larval age-class (6-7 d post-spawn) declines to zero during the first seven days of the simulation.

Though less evident in the long-term-average results (Figure 2) than in the time-series of results, comparison of the springtime and summertime simulation results for ENE and WSW winds reveals that distributions are usually more diffuse in the spring. This is a consequence of two factors: both related to the lower degree of spring-time water-column stratification. Firstly, the horizontal circulation patterns are more complex but vertically more uniform (Stephens, S.A. & Broekhuizen, N. 2003). Secondly, because the vertical mixing is stronger in spring, eggs/larvae do not aggregate so strongly near the surface (despite their buoyancy). Consequently, though weaker in absolute terms, vertical shear (differing patterns of horizontal transport in each layer) influences a larger fraction of the larval population in the spring. We note that the times which we have chosen to simulate (September and March) correspond to the very beginning and very end of the snapper spawning season (Francis, M.P. 1993). It is possible that they provide a deceptive indication of farm impacts upon snapper during the bulk of the spawning season; however given the similarity of the estimated incremental mortalities under 6 differing circulation/stratification conditions, and under three different egg/larval ascent speeds, we consider this unlikely.

At times, the differing circulation patterns that evolve under the same wind conditions in spring and summer can induce differences that are more extreme than mere greater horizontal dispersion of the larvae. For example, 6-7 d old larvae are abundant throughout the central firth on day 15 during the springtime prevailing WSW simulation, but almost absent during the summertime WSW simulation. In the latter case, the larval population (which aggregates near the surface when the water-column is strongly stratified) has been exported out of the firth in the strong surface currents which developed over the preceding few days of strong winds from the SW (Stephens, S.A. & Broekhuizen, N. 2003).

For snapper eggs/larvae, it is not surprising to find that the farms induce increasing depletion within a cohort as it ages. By the time the cohort reaches 7-8 days of age (approximate age at first swimming), depletion could be up to 50% within the modelled Western Firth AMA – though this figure varies through time in response to preceding currents and assumes maximal relative vulnerability to mussel grazing. Larvae may not be as vulnerable as eggs or phytoplankton – in which case, this will be an overestimate. Depletion within the farms is minimal at times when the preceding currents were such that either: (a) there are no larvae within the modelled AMA, or (b), those larvae present have spent most of their preceding life outside the farm.

5.4 Logistic Plankton model

As with the snapper, there are reasons to believe that the model will over-predict the extent of mussel predation upon plankton (see section 4.2).

The initial conditions reflect our assumption that carrying capacity has a bivariate normal spatial distribution; however they ignore the consequences of transport. It is not surprising that once the system begins to evolve, this pattern becomes somewhat disrupted. Nor is it surprising that the disruptive effect of transport is greater for slow-growing organisms than it is for the fast-growing ones; however, even for the slow growing plankton, the influence of the initial conditions becomes negligible after 3-5 d.

The parameter *r* defines the (assumed) maximum weight-specific *population* net growth rate. In the absence of any mortality, this would equate to the maximum net rate of individual growth; however in the natural environment, *r* will usually be substantially below the corresponding maximum individual weight-specific growth rate because many juveniles will die (from density independent causes), before attaining maturity. In a recent review Hirst et al. (2003) found that mean (across species) maximum individual growth rate of copepods to be ~0.1 d^{-1} (range 0 – 1.6 d^{-1}). Other metazoan (multicellular, *c.f.* protozoan) zooplankton grew at similar, or higher rates. Our two metazoan sub-classes of logistic plankton (subclasses 4 and 5) are assumed to have maximum weight-specific growth rates of 0.05 d^{-1} and 0.025 d^{-1}. Comparison of these figures with the mean maximum individual growth rate of 0.1 d^{-1} implies that we have assumed a daily weight-specific mortality rate of circa 0.05-0.1 d^{-1}. This is comfortably within the range of values estimated from field data (Corkett, C.J. & MacClaren, I.A. 1979, Eiane, K. et al. 2002).

The logistic model indicates that, when plankton abundance is averaged over periods of several days, there will be little or no evidence of depletion amongst fast-growing, vulnerable plankton; however depletion will occur amongst slow-growing, vulnerable plankton. Depending upon the exact balance between growth rate and relative invulnerability, slow-growing but relatively invulnerable plankton may be depleted by no more than 10%, or they may be depleted by 20% or more within the farms. Unfortunately, the relative vulnerabilities of zooplankton are not well known. Zeldis et al. [, in review #953] found that the relative vulnerability of ciliates was probably similar to that of phytoplankton. Expressed relative to ciliates (*cf* phytoplankton), they found that the relative vulnerabilities of nauplii, copepodites and adult copepods were 0.4 (range 0.2-1.5), 0.2 (range 0.07-0.54) and 0.17 (range 0.01-0.32). They made no measurements of the relative vulnerability of copepod eggs – though it seems likely that these would be at least as vulnerable as nauplii. In a model which lacks any explicit size/age structure (such as the logistic model that we have adopted), the relative vulnerability of each sub-class will be a weighted average of egg, naupliar, copepodite and adult vulnerabilities. The weighting will depend upon the relative durations of each stage – which can be influenced by species, temperature and food abundance.

The simulations conform to the expectation that depletion will be greatest amongst those plankton which have a low net population growth rate (in the absence of mussel grazing). This need not imply that it is only zooplankton that may be suppressed. At times the net population growth rate of phytoplankton can be negative (due to factors such as low light, low temperatures, low nutrient availability and high predation). It is also worth noting that, for slow-growing populations, we anticipate the extent of depletion to be much more sensitive to the relative-vulnerability parameter. Recall that, in the absence of transport, the dynamics of the logistic plankton are governed by Eq. 1. Summing over all particles within a region, the equilibrium solution (i.e., abundance of the sub-class which yields zero net growth) to this equation is:

$$N^{*} = K\frac{(r-f)}{r} = K - \frac{Kf}{r} \qquad \text{Eq. 2}$$

Not surprisingly, the equilibrium plankton concentration declines as *f* (the vulnerability parameter) increases, but note that the slope of this decline is inversely dependent upon *r*. For $r<1$, a small change in the mussel-induced mortality leads to a disproportionately large decline in the equilibrium plankton density.

In reality, phytoplankton removal by mussels may be at least partially offset by an accompanying removal pf zooplankton – thereby reducing the phytoplankton mortality to zooplankton. This effect is not considered in either the empirical (or the biophysical model). The biophysical model also indicates that far-field phytoplankton concentrations may be enhanced in the presence of mussel farms (see below). Given that ambient phytoplankton concentrations may be insufficient to enable zooplankton to grow at their maximal rate (Broekhuizen, N. et al. 2002, p. 79), elevated phytoplankton might promote more rapid zooplankton population growth than we have assumed – thereby reducing the zone of depletion around the farms. Furthermore, if mussels consume sufficient predators of copepods (fish larvae, medusae etc.), this will tend to increase the copepod population recovery rate. Note, however, that these arguments are much more tenuous in the case of snapper because, unlike phytoplankton and zooplankton, fish eggs/larvae do not quickly grow and reproduce.

5.5 Biophysical Model

The simulation model confirms field observations – that the Hauraki gulf is strongly nitrogen limited during the summer, but much less so during spring. Substantial quantities of DIN enter the SE firth via rivers. This nutrient promotes phytoplankton growth in the southern firth – such that population abundance in the SE firth is often higher than elsewhere in the southern firth. In general, the riverine water moves diagonally north and west across the firth. This pattern is also evident as a plume of elevated phytoplankton abundance. It is satisfying to note that the model predicts that diatom abundance will decline markedly between spring and summer, whilst the densities of dinoflagellates, and more especially, phytoflagellates remain more constant. This pattern is evident in field data from the Hauraki gulf and northern firth of Thames.

Our modelling suggests that phytoplankton abundance is more likely to be suppressed in spring than in summer (when it may be enhanced). This may appear counter-intuitive, but is consistent with field observations in New Zealand (Ogilvie, S.C. et al. 2000) and elsewhere (Prins, T.C. & Smaal, A.C. 1990, Rosenberg, R. & Loo, L.O. 1983). Similar results have also been reported in enclosure experiments (Ogilvie, S.C. et al. 2003, Prins, T.C. et al. 1995). In spring, nutrient is plentiful, so one might expect phytoplankton to be growing rapidly. On the other hand, during summer, ambient nutrient concentrations are very low and, in the absence of farms, phytoplankton growth is very slow. There are two reasons why farm impacts appear to be smaller during the summer. Firstly, despite the plentiful nutrient, (early) springtime phytoplankton growth rates remain relatively low because of the low water temperatures and short day-length. Thus, recovery from grazing is slow. During summer water temperatures and irradiance are conducive to very rapid phytoplankton growth – if nutrient is present. In our 'default' simulations mussels excrete substantial quantities of DIN. This 'fertilizes' the water within and around the farms and promotes very rapid growth of those phytoplankters which survive their passage through the farm. It is worth noting that whilst summertime nitrogen concentrations in the western Firth area increase several fold in the presence of the modelled AMA, the absolute concentrations remain relatively low (~1 mg N m^{-3}). Our sensitivity trials demonstrate that the nature and magnitude of the summertime farm impacts are very strongly influenced by the rate of DIN excretion by mussels. The (relatively high) excretion rates adopted in the default simulations are based upon measurements made in the Marlborough Sounds during March and May (NIWA, unpublished data) when NO_3 was ~10 mg N m^{-3}; NH_4 was reported to be ~20 mg N m^{-3}, however most of this NH_4 may have evolved from degradation of organic matter after the water-samples were collected (M. Gibbs, NIWA, *pers. comm.*). This NO_3-concentration is sufficiently high that phytoplankton would have been under little N-stress. It is conceivable (perhaps, likely) that DIN excretion rates by mussels fall when their prey is N-deficient. Furthermore, it is also probable that the measured rates are atypically high – reflecting a stress response of the experimental mussels (A.H. Ross, *pers. comm.*). In either case, the rates applied in the (default parameter) summertime simulations would be too high. In the sensitivity simulations illustrated in Figure 8d –Figure 11d we assumed that mussels excrete nitrogen only when they absolutely have to do so (in order to prevent their tissue N:C ratio climbing too high). This amounts to assuming that they preferentially meet their respiratory demands by burning carbohydrate or lipid. The resultant DIN excretion rates were much lower than those measured in Marlborough Sounds and were insufficient to stimulate substantial additional phytoplankton biomass development. It would appear that further study of the factors which influence mussel DIN excretion rates are required before we can be confident that mussel farms will enhance phytoplankton populations to the degree suggested in our default simulations, or suppress them to the degree suggested in the sensitivity trial simulations.

Where enhancement occurs, it is only amongst the phytoflagellates and diatoms. Phytoflagellates and diatoms both have much higher maximal cellular growth rates than dinoflagellates. Consequently, they are able to assimilate disproportionately large quantities of the mussel-excreted DIN.

Regardless of whether the farms enhance or suppress the total abundance of phytoplankton, the simulations suggest that the farms will induce a marked shift towards dominance by fast growing taxa (diatoms, phytoflagellates). Once again, this is consistent with experimental observations (Ogilvie, S.C. et al. 2003). If sufficiently large, such a shift may have consequences higher in the foodweb since phytoflagellates and dinoflagellates seem to represent a superior food-type (relative to diatoms) for many zooplankton (Ban, S. et al. 1997, Kleppel, G.S. 1993).