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**Vertical distribution of feeding- and mortality rates of *Calanus finmarchicus* in the Norwegian Sea**

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**Abstract**

From net-catches and echo-sounder data, we estimate the vertical distribution of environmental parameters and potential food and predators for *Calanus finmarchicus* at a station in the Norwegian Sea. These profiles are combined with mechanistic models of prey- and predator encounter- and feeding rates to produce vertical profiles of growth- and mortality rates of *C. finmarchicus*. The mortality rate varied by orders of magnitude through the water column, while modest variation in temperature and food availability led to moderate differences in growth rate between depths. Herring was pointed out as the most important predator, while blue whiting, lanternfish and krill were the main predators below 120 m. We argue that combining mechanistic models of feeding processes with real data of *in situ* situations is an approach that could increase our understanding of ecosystem functioning.

## Introduction

Trophic interactions are fundamental in ecology, and knowing and understanding who eats whom and when it happens is an absolute prerequisite for understanding the functioning of ecosystems and the dynamics of populations (Kerfoot & Sih 1987, Williamson 1993,). A number of mechanistic models for predator-prey encounters and feeding in the pelagic have been developed over the last few decades, covering both perception of predators and prey through different sensory cues and escapement- and capture probabilities (e.g. Aksnes & Giske 1993, Kiørboe & Visser 2000, Visser 2001, Fiksen & MacKenzie 2002, Titelman & Kiørboe 2003).

Mechanistic models are characterized by their inclusion of parameters and variables with explicit biological or physical meaning. As opposed to statistical models, they are also valid outside the domain of observations, and can therefore be used to analyse how systems respond to situations that have never been observed (Mangel et al 2001). However, mechanistic feeding models are rarely thoroughly applied to or tested against observations from natural environments, with multiple predators non-uniformly distributed in spatially heterogeneous environments. The reasons for this are probably the discrepancy between the extensive need for high resolution data and what is typically obtainable, insufficient parameterisation for application to complex systems, and possibly also differing traditions between field- and theory-oriented biologists.

Here we present a framework for data driven mechanistic analyses of trophic interactions in pelagic communities. By applying quantitative models of feeding-, growth- and predation processes to data of distributions of organisms, we estimate growth- and mortality rates of *Calanus finmarchicus* late copepodids (CIV).

## Data

Data were collected from RV "G. O. Sars" in the Norwegian sea, 70.1N, 4.0E, on the 24th of May 2004. Surface light was logged continuously. Vertical temperature profile was measured with a CTD. Water samples from attached Niskin bottles were used to measure total pigments ( $chl = chl_a + phaeopigments$ ). Due to lack of deep sampling at the station, chl-values below 100 meters are uncertain.

Species composition, length distributions and depth-specific densities of fish and macroplankton were estimated from trawl catches and Simrad EK 60, 38kHz echosounder data. An Åkra-trawl (400 m<sup>2</sup> opening area) was used for fish sampling, and a smaller (60 m<sup>2</sup>) krill-trawl with 5 mm mesh size was used to quantitatively sample macroplankton. Mesozooplankton were sampled with MOCNESS, but these data are not yet ready.

Evident from trawl catches, Norwegian spring spawning herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), northern lanternfish (*Benthoosema glaciale*) and the euphausiid *Meganyctiphanes norvegica* were the main potential predators on late *C. finmarchicus* copepodides. Acoustic registrations from the upper 120 m collected in the time interval 1200-1800 were ascribed to herring. Blue whiting and lanternfish abundances and distributions were estimated from echo-registrations collected during the time interval 15:08-15:46, corresponding with a mesopelagic trawl-haul. A surface trawl haul caught herring with an average length of 31 cm,

corresponding to a TS (target strength) of -41.4 dB. Blue whiting had an average length of 25 cm, corresponding to a TS of -42 dB. TS of 6 cm *Benthosema glaciale* was set to -60dB. The abundance of each species was estimated from volume back scattering values at different echogram thresholds. Figure 1 shows echograms from the upper 500 meters. Through most of the water column, we were unable to extract macroplankton acoustic signals quantitatively, so average *M. norvegica* densities were calculated from krill-trawl catches alone. Vertical distributions of temperature, chlorophyll and main predators are shown in Figure 2.

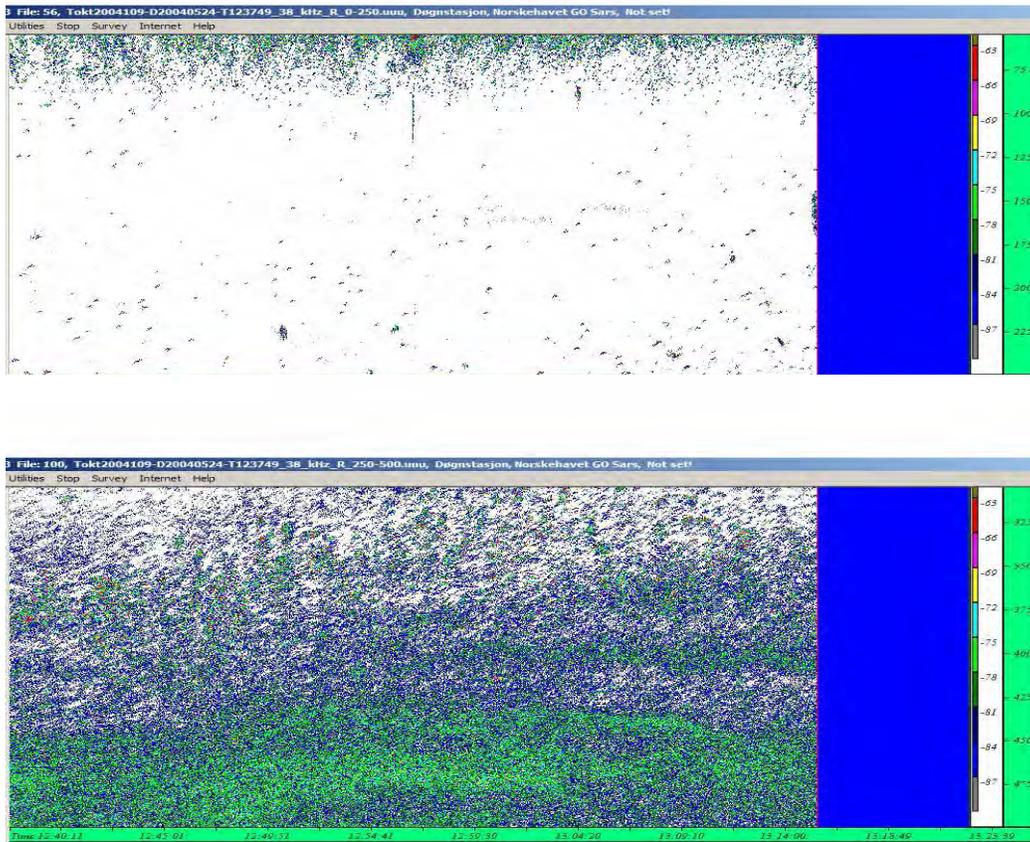


Figure 1. Echograms from 0-250 (top) and 250-500 meters (bottom), sampled between 12:37 and 13:15.

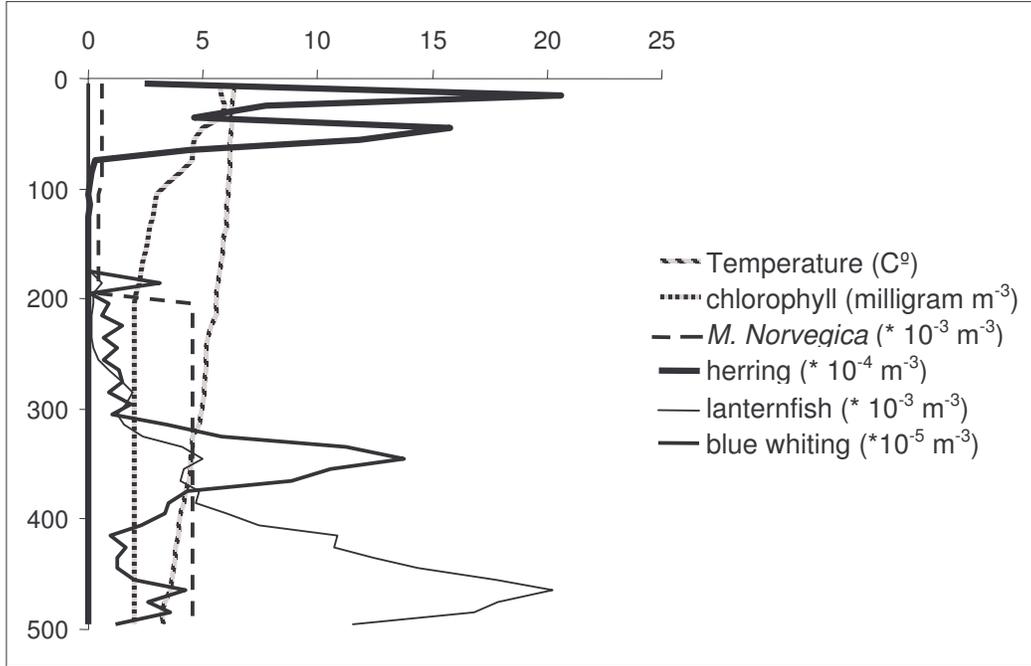


Figure 2. Vertical distributions of temperature, chlorophyll and predators.

### Models

A model was developed to calculate growth- ( $g$ ) and mortality ( $m$ ) rates ( $\text{h}^{-1}$ ) of *C. finmarchicus* CIV copepodids in the environment presented in Fig. 1.

Surface light was modelled from above surface light at noon, and light extinction through depth follows the relationship

$$I_z = I_0 \int_0^z e^{-k_z z} dz, \text{ where}$$

$$k_z = 0.07 + 0.054 \times chl_z^{\frac{2}{3}} + 0.0088 \times chl_z.$$

We did not attempt to build a mechanistic model for growth rate of *C. finmarchicus*. For comparison with mortality profiles, we built a simple temperature- and food dependent growth model, based on results and parameter values of Vidal (1980), Carlotti & Wolfe (1998), Harris et al. (2000) and Hygum et al. (2000). Maximum growth rate at 15°C ( $g_{15}$ ) was set to be 0.254  $\text{day}^{-1}$ , and  $q_{10}$  to be 2.1. Food limitation was modelled as a Michaelis-Menten function, and the half-saturation constant increases with increasing temperature, conforming to the results of Vidal (1980). The half-saturation concentration at 15°C ( $k_{15}$ ) was set to 3.0  $\text{chlorophyll m}^{-3}$ .

$$g_z = \frac{g_{15}}{24} \times q_{10}^{\frac{T_z - 15}{10}} \times \frac{chl_z}{chl_z + \frac{k_{15} \times T}{15}}$$

Mortality rates were found by summing up predation rates from present predators. The vertical profile of mortality rates is therefore dependent both on the vertical

gradient of the relevant environmental factors (light) and the vertical distribution of potential predators.

Fish were assumed to feed visually on *C. finmarchicus*. Visual range ( $r$ ) was modelled following Aksnes & Utne (1997). Eye sensitivity and light saturation parameters for the different species were based on estimates for pearlside from Giske & Aksnes (1992), and the eye sizes and habitats of the species. These estimates carry considerable uncertainty. We assumed that blue whiting and lanternfish also perceive *C. finmarchicus* through mechanical cues at close range, and therefore has a light-insensitive minimum search rate corresponding to  $r = 1.5$  and  $0.5$  cm respectively. All encountered prey were assumed to be captured and eaten with a handling time ( $h$ ) of 2 seconds. *C. finmarchicus* and predators were assumed to have a swimming velocity of 1 body-length per second. Feeding rate ( $f$ ) of predator  $P$  at depth  $z$  was found from the classical Holling disc equation:

$$f_{Pz} = \frac{h^{-1} \times n_z}{(h \times v \times r_z^2 \times \tau)^{-1} + n_z},$$

where  $v$  is the velocity of predators relative to prey:  $v = (v_{predator}^2 + v_{prey}^2)^{0.5}$ ,  $\tau$  defines the section of the visual field that is efficiently scanned, and  $n_z$  is the number of prey at depth  $z$ . Fish were assumed to be able to digest all captured prey. *M. norvegica* was assumed to have a constant reactive distance of 1.7 cm, independent of light. Mortality of prey at depth  $z$  follows the equation:

$$m_z = \sum_{P=1}^{P_{max}} \frac{f_{Pz} \times N_{Pz}}{n_z},$$

where  $N_{Pz}$  is the density of predator  $P$  at depth  $z$ . The risk dilution effect experienced by prey when density of prey is high, depends on predator search rate, which for visual predators depend on light and hence depth. To explore the effect of *C. finmarchicus* abundance on mortality, densities of 1, 10, 100 and 1000  $m^{-3}$  were modelled. The low search rate of *M. norvegica* prohibits handling limitation at the *C. finmarchicus* densities in question.

## Results

Mortality rate varied with orders of magnitude through depth. Because of the small vertical differences in temperature and chlorophyll, growth rate varied with a factor of only 2.2. However, when we crossed the study area a week before sampling, surface chlorophyll was more than an order of magnitude higher. Several days of storm probably caused aggregation and large sinking losses of the algae. Assuming a surface chlorophyll concentration of 8  $mg\ m^{-3}$ , gradually decreasing towards 100 m, the potential growth rate becomes significantly higher in upper waters. Figure 3 shows vertical distribution of growth rates.

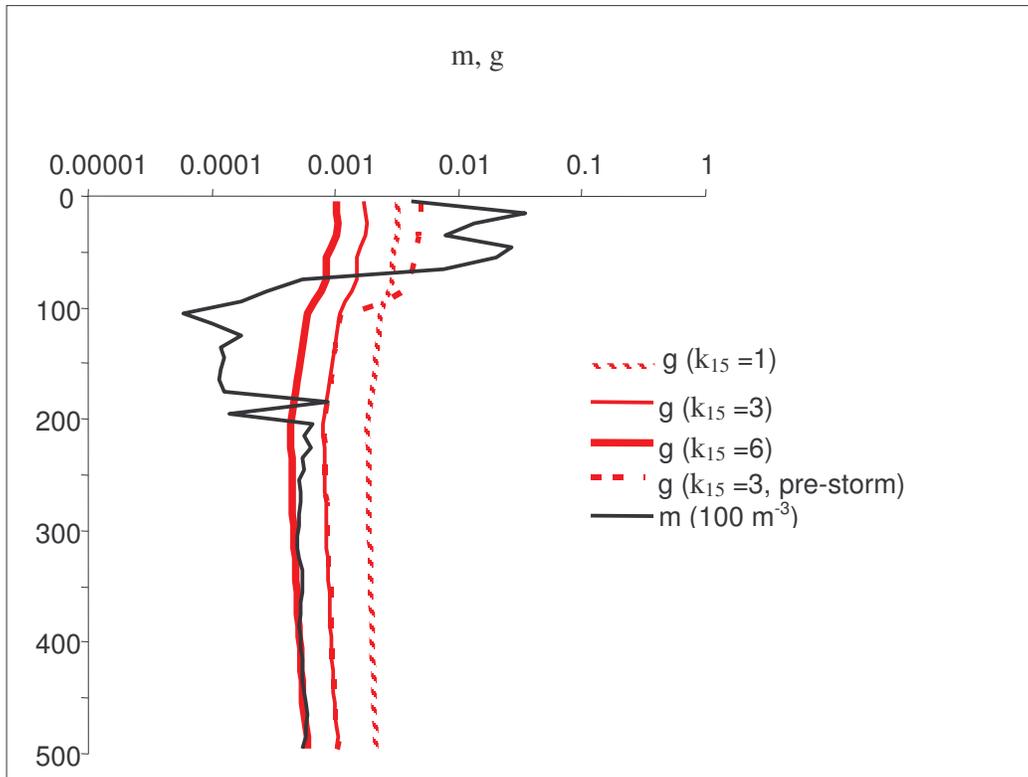


Figure 3. Vertical growth profiles with different food half-saturation values. pre-storm: Higher chlorophyll values in the upper 100 meters before the heavy storm. Mortality rate with 100 *C. finmarchicus*  $\text{m}^{-3}$  is shown for comparison.

Due to the low density of predators between 100 and 200 m, this stratum had the lowest mortality rate. Herring had the highest potential to cause high mortality, while below 120 m, blue whiting, lanternfish and krill were the main predators (Figure 4). In near-surface waters, where search efficiency of herring is high, *C. finmarchicus* experience risk dilution even at modest densities, while at mesopelagic depths, prey handling is of less importance (Figure 5). Hence, in upper waters, the high search rate of herring makes mortality rate orders of magnitude higher than at mesopelagic depths when *C. finmarchicus* are low. At high *C. finmarchicus* abundances, herring, as opposed to the numerically more abundant mesopelagic predators, become handling limited, reducing mortality risk in the upper part of the water column to levels comparable to those at mesopelagic depths.

Mortality varies horizontally due to predator schooling and patchiness. On the echosounder, we observed several swarms of *M. norvegica* at 150-200 m depth, typically with vertical and horizontal extensions of at least 50 m. The numerical densities within these schools were estimated to several hundred  $\text{m}^{-3}$ , and the mortality profile in a location with a swarm with 200 krill  $\text{m}^{-3}$  from 150-200 m is dramatically different (Figure 6).

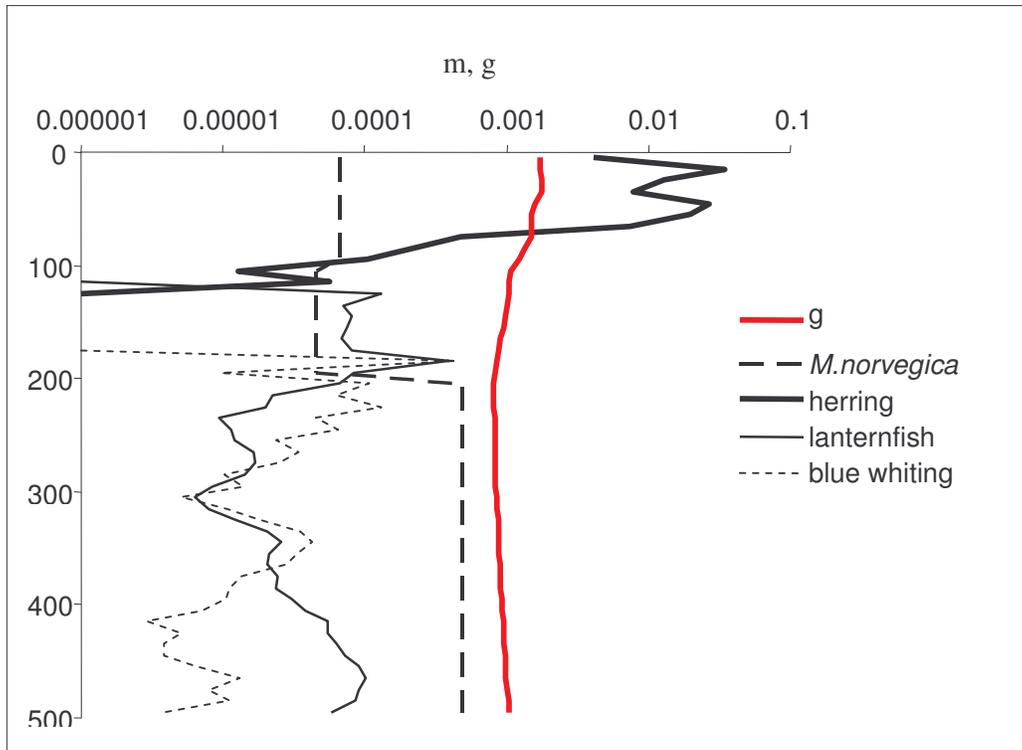


Figure 4. Predicted mortality from the 4 predators. Growth rate is shown for comparison.

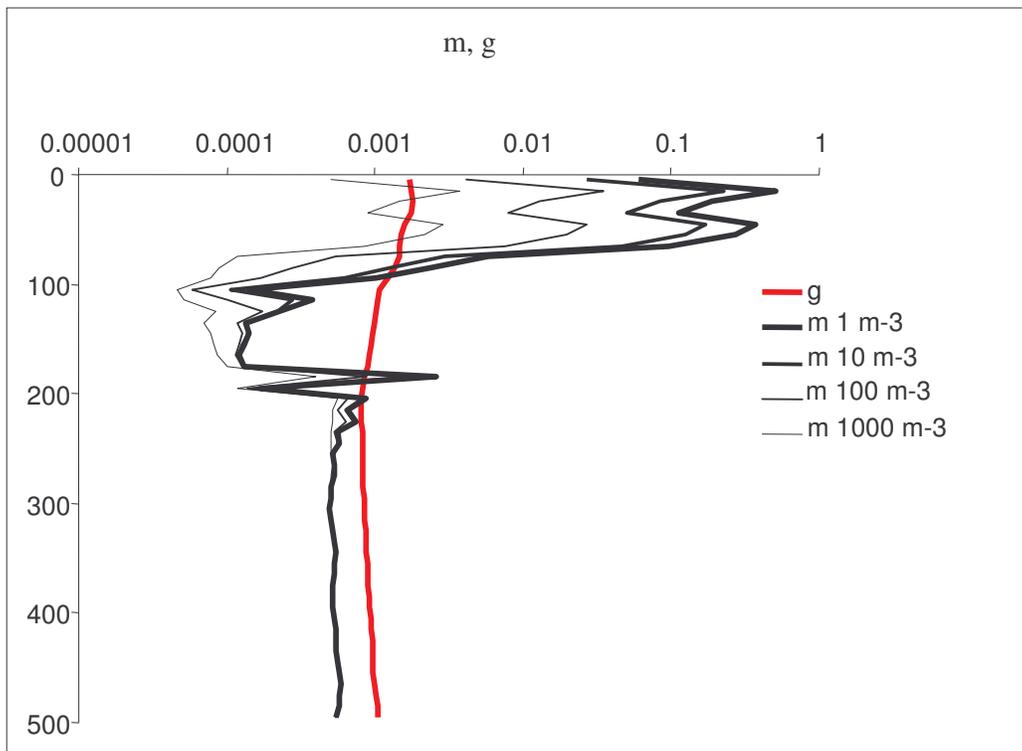


Figure 5. vertical profiles of growth- and mortality rates at different *C. finmarchicus* abundances. Growth rate is shown for comparison.

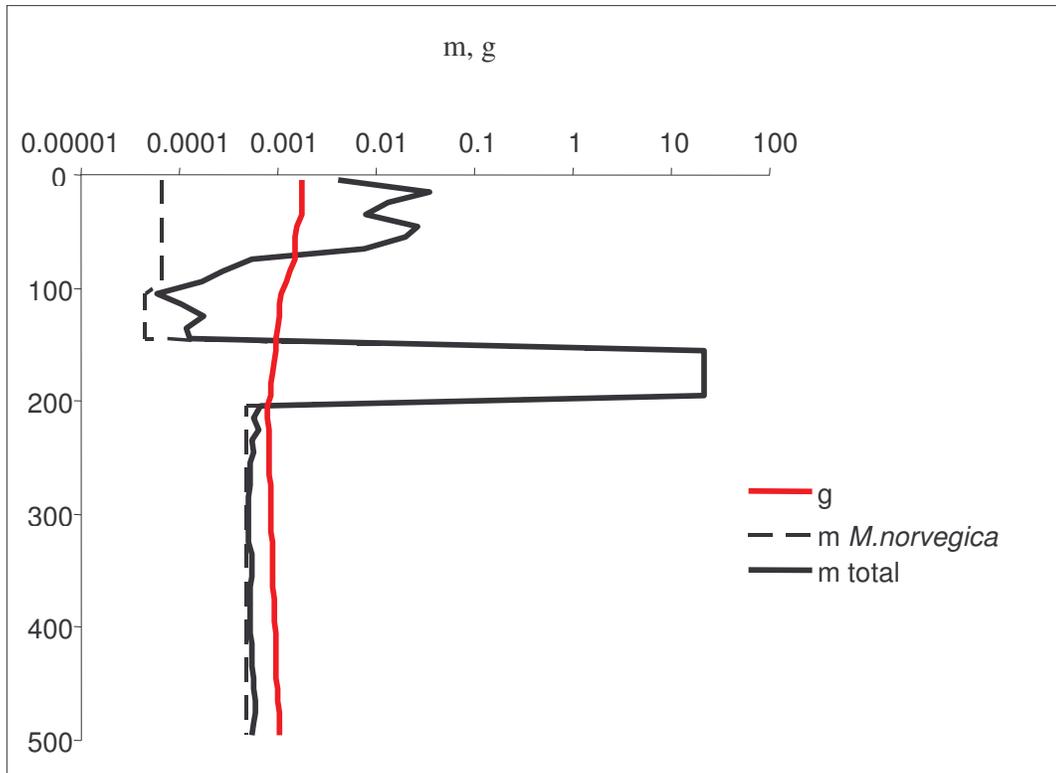


Figure 6. Total mortality and *M. norvegica* inflicted mortality in the presence of a dense ( $200 \text{ m}^{-3}$ ) swarm of krill at 150-200 m.

### Discussion

The dynamics of and interactions between populations are mere results of the processes, physiological and behavioural, of individuals. Whether the goal is to manage exploited populations, to predict ecosystem or population responses to changes in the physical or biological environment, to understand the forcing behind population fluctuations, or to understand why organisms have the life histories and behaviours that they have, we need thorough understanding of the mechanics of the populations' individuals.

Although it may be established that current feeding models give a good approximation to reality when their implicit and explicit assumptions are valid, it is less clear to what extent they actually have the potential to describe the real world variability in feeding. There may well be features of predator- or prey behaviour and distribution, or environmental variables that are important in feeding processes, but not dealt with in feeding models, either due to ignorance or the need for simplification. One approach to answering these questions is to compare predicted feeding rates and diet compositions from data-driven mechanistic feeding models with data on *in situ* feeding of multiple predators on different prey. This requires detailed knowledge about the spatio-temporal overlap between predators and prey, and the values of several species- and habitat specific parameters, and might seem unrealistic. However, many parameters act similarly on similar processes. For instance, light intensity and predator eye sensitivity should have approximately the same effect on visual detection of different items. Further, modern equipment has a high potential for

collecting behaviour and distribution data with high resolution and precision. Thus, by comparing predicted and factual patterns we should be able to investigate to what extent current encounter- and feeding models properly include the important features of organisms and environments.

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