Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea – results of the INFERNO project

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EDITORIAL

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The Norwegian Sea (NS) is the feeding ground for some of the largest fish stocks in the world, including Norwegian spring spawning (NSS) herring (*Clupea harengus* Linnaeus, 1758; Figure 1), blue whiting (*Micromesistius poutassou* Risso, 1827) and the Northeast Atlantic (NA) mackerel (*Scomber scombrus* Linnaeus, 1758). These planktivorous stocks have substantial spatial and dietary overlap (e.g. Nøttestad et al. 1997; Dalpadado et al. 2000; Kaartvedt 2000), and are often collectively referred to as the 'pelagic complex' in the Norwegian Sea. Due to their high abundances, they can potentially have a strong ecological impact on the ecosystem and each other (Skjoldal et al. 2004a). The NSS herring collapsed in the late 1960's and rebuilt during the 1980's (Dragesund et al. 1997). Following the herring collapse, high abundances of blue whiting were discovered in the Norwegian Sea (Misund et al. 1998), and it has been speculated that the blue whiting population increased concurrently with the collapse of the NSS herring (Skjoldal et al. 1993), but the evidence remains inconclusive (Daan 1980). Since the late 1980s the abundance of fish in the NS has increased steadily and this has increased the potential for interactions between the planktivorous stocks (Figure 2). This was the background for seeking funding for the INFERNO project 'Effects of interactions between fish populations on ecosystem dynamics and fish recruitment in the Norwegian Sea' submitted to the Research Council of Norway (RCN) in 2005. The main hypothesis to be addressed in the INFERNO project was that *the planktivorous fish populations feeding in the NS have interactions that negatively affect individual growth, mediated through depletion of their common zooplankton resource.* The project was funded and lasted for the period 2006–2009 and nine papers from the INFERNO project and associated research are presented in this thematic issue of *Marine Biology Research.* Many of the principal investigators of the project worked at the Institute of Marine Research (IMR), but the project also benefitted strongly from interactions and exchange of data and ideas with scientists from Russia (Alexander Krysov and Vladimir Zabavnikov), the Faeroe Islands (Jan Arge Jacobsen) and Iceland (Torstein Sigurdsson and Gudmundur Óskarsson). The international partners have participated actively in the project through project meetings and as co-authors of papers.

During the project period the trend of a decreasing zooplankton biomass in the NS continued and the biomass now remains low (Figure 2). The fish biomass peaked in 2004 and has since decreased somewhat, but remains fairly high. The abundance of blue whiting increased until 2004, and the range of the horizontal distribution expanded in a north-westerly direction during this period. Strong year classes of mackerel from 2001 and 2002, together with increasing temperatures, resulted in an increased number of mackerel in the Norwegian Sea (Payne et al. 2012; Utne et al. 2012a). Furthermore, there were rather substantial changes in the migration pattern of herring during the study period and thus high interannual variability in horizontal overlap between the species. There was a relatively high spatial overlap between the species during the 1990s, with a southern centre of gravity (for all three species), but due to the northern displacement of

Figure 1. Herring (*Clupea harengus*) represents an important component of the pelagic complex of the Norwegian Sea. Photographer: David Shale (www.deepseaimages.co.uk).
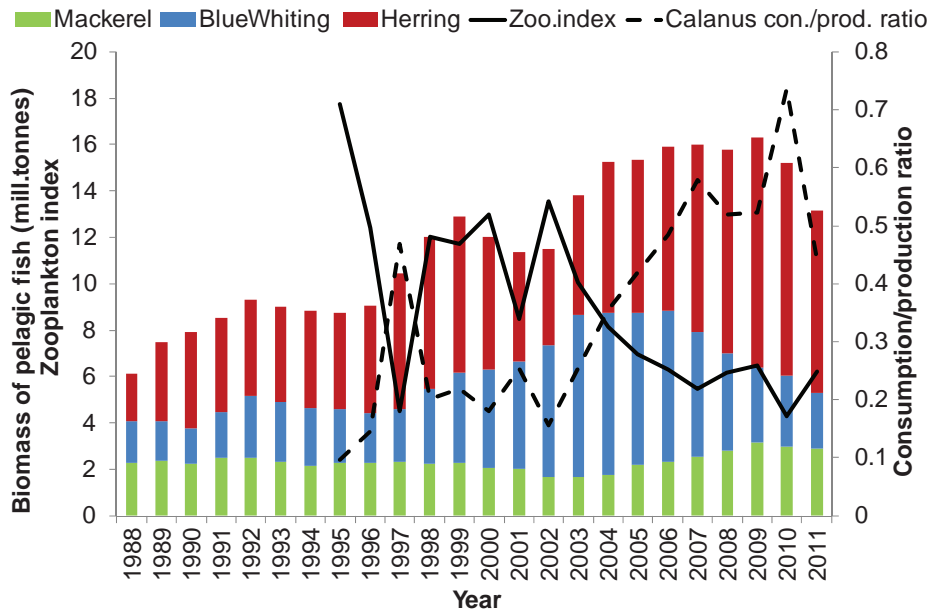
Figure 2. Developments in fish biomass, plankton biomass and ratio of estimated fish consumption of *Calanus finmarchicus* divided by the estimated *C. finmarchicus* production for copepodite stage 4 to adult. The annual consumption estimates are based on consumption/biomass relations and diet data in Skjoldal et al. (2004), and the annual production estimates are based on the total *Calanus* production estimate in Skjoldal et al. (2004) divided by stage using data from Aksnes & Blindheim (1996) multiplied by the zooplankton index relative to the maximum value.

especially herring and blue whiting, the overlap decreased in the early 2000s. As mackerel stayed mainly south of 70°N and NSS herring north of 70°N, the horizontal overlap between these species was limited (Utne et al. 2012a; Utne & Huse 2012). The horizontal overlap between blue whiting and mackerel was extensive in some years, but because the blue whiting prefers deeper water than mackerel, the vertical overlap is low. There was pronounced inter-annual variability in the vertical distribution of blue whiting and herring (Huse et al. 2012). The vertical distribution appears to be linked so that herring occurs shallower when the abundance of blue whiting is high. This indicates that there is interaction between those species.

The diet of the three species varies between years and with season. The peak feeding season for herring and blue whiting is typically in May–June, whereas for mackerel it is in July. The herring diet is dominated by *Calanus finmarchicus* (Gunnerus, 1770), particularly early in the feeding season (Broms et al. 2012). Later in the season the diet is more varied and less dependent on *C. finmarchicus* (Langøy et al. 2012; Utne et al. 2012b). Krill and amphipods then become more important as prey. The blue whiting has an ontogenetic shift in its diet associated with the move into deeper waters at an age of around two years. The diet shift is characterized by going from a *C. finmarch-icus*-dominated diet to a diet dominated by krill and amphipods. Mackerel seems to be more opportunistic and adjusts to prey availability more than the other two fish species, but the diet is often dominated by *C. finmarchicus* (Langøy et al. 2012).

Due to the dynamic space uses by pelagic fish, one needs to capture their 3D spatial distribution in order to study their interactions. The role of space in ecology remains elusive, and the subject has been referred to as the 'final frontier for ecological theory' (Kareiva 1994). Individual-based models (IBMs) with super-individuals have been developed for the copepod *C. finmarchicus*, the main meso-zooplankton component of the NS, and for the NSS herring, blue whiting, and NA mackerel (Hjøllo et al. 2012; Utne et al. 2012b). These models are coupled with the biogeochemical model NORWECOM and the Regional Ocean Model System (ROMS). The result is an ecosystem model complex that integrates ocean physics, feeding, growth, fine-scale movement and life-history traits of key plankton and fish species with full feedback of energy between different trophic levels. The model system has been developed and is used to simulate the spatial overlap between the stocks on a daily fine-scale basis. Whereas the data analysis discussed above provides snapshots of the distributions, the fish IBM has a daily time step and provides daily predictions of overlap. The migration

model illustrates that the overlap between the species is highly dynamic within the season and varies between years (Utne & Huse 2012). Preliminary model simulations using the fully coupled model system suggest that the planktivorous stocks exert a considerable predation pressure on the zooplankton resources in the Norwegian Sea (Utne et al. 2012b).

During the 1980s the biomass of the planktivorous fish stocks was about a third of the peak biomass in 2004, and the biomass of zooplankton was much higher (Figure 2). The ratio of estimated fish consumption to production ratio for *C. finmarchicus* has therefore been high in recent years and indicates that fish predation has had an increasing impact on the *C. finmarchicus* population (Figure 2). There are uncertainties in the absolute levels of this ratio, but the substantial increase in the recent decade makes it plausible that the reduction in zooplankton biomass seen after 2002 is caused by fish predation. In 1997 there was a very low plankton index value (Figure 2) that was probably not attributed to fish predation, but rather to unfavourable conditions for primary and/or secondary production. The migration pattern of the fish has changed to become extended further to the west during the period and the former main feeding areas in the central Norwegian Sea have virtually been abandoned. The NSS herring has had a downward trend in length at age over time (Figure 3). In recent years the mackerel length at age has decreased concurrently with an increase in the mackerel stock size (Figure 3). For the blue whiting a decreasing trend in length at age shifted to a positive trend in 2008 (Figure 3). In order for species interaction to

Table I. Spearman rank correlations (*p*-values) between fish length at age 6 against intraspecific (single) stock biomass, interspecific biomass (sum of the two other species' stocks), and total fish biomass (sum of all three). For herring the spawning stock biomass was used and for mackerel and blue whiting total stock biomass (1 +) was used. Data from the period 1982–2011 were used with the length data taken from the IMR data base and the biomass data for the period 1982–1987 taken from ICES (2007), and for the period 1988–2011 taken from ICES (2011).

	Herring	Mackerel	Blue whiting
Intraspecific biomass	5.36E-08	0.04889	0.01359
Interspecific biomass	0.004782	0.5869	0.001830
Total biomass	4.96E-05	0.4618	0.0001404

qualify as competition, it has to have a negative impact on at least one of the interacting species. Spearman rank correlations between length at age 6 and stock biomasses are given in Table I. For herring there are clear signs of both intra- and interspecific competition, while for the mackerel only the intraspecific term is significant (Table I). For the blue whiting all the three correlations are significant, but here the interspecific relationships are the strongest. This is in line with the simulation results in Utne et al. (2012b), which indicated that the blue whiting foraging rate was negatively affected by the feeding interaction with the other stocks, whereas the other two stocks were much less affected. The recent increase in the blue whiting length at age is probably due to very low intraspecific competition at the present low stock biomass. So even though the size at age is likely to depend on climatic conditions (Holst et al. 2004), light regime (Varpe & Fiksen 2010), and nursery area (Holst & Slotte 1998), among other factors, there are clear signs of intra- and interspecific competition in the pelagic complex. The planktivorous fishes also feed on krill, amphipods and mesopelagic fish, which also are predators on *Calanus*. It is a bit paradoxical that in spite of the observed reduction in zooplankton biomass, an increased abundance of planktivorous fish may have decreased the *Calanus* predation by macroplankton and mesopelagic fish and thus increased the carrying capacity for planktivorous fish (Skjoldal et al. 2004b).

In order to address how local depletion of zooplankton due to fish predation might be dispersed over the winter (Olsen et al. 2007), the drift patterns of RAHFOS floats drifting at 800 m in the Norwegian Sea over the winter were studied (Søiland & Huse 2012). This depth is representative of the depth where the *C. finmarchicus* drift passively in diapause during winter. The drift trajectories of the RAHFOS floats varied substantially in displacement direction and magnitude. The results show that the transport of overwintering *C. finmarchicus* is likely to
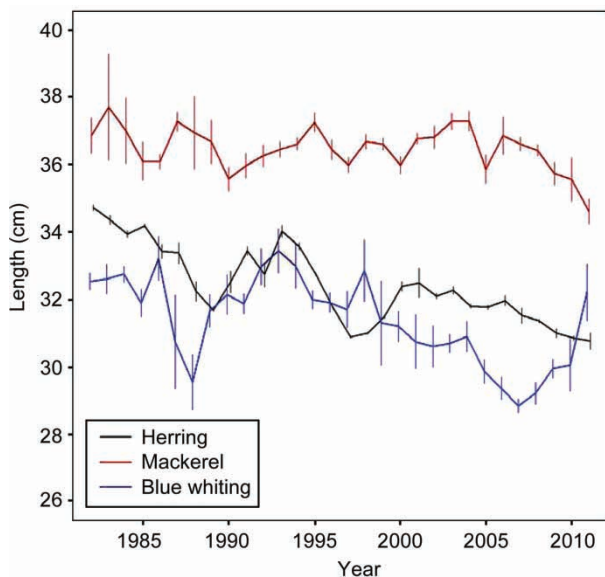

Figure 3. Average length at age 6 (± 95% confidence intervals) for NSS herring, blue whiting and NA mackerel.

disperse the distribution and substantially diminish 'traces' of feeding by planktivorous fish.

In conclusion, there are rather strong overall spatial interactions within the pelagic complex during the feeding season in the NS, with considerable potential for exploitative competition for common zooplankton resources due to the large overlap in diet. During the study period there has been a strong build up of biomass of planktivorous fish in the Norwegian Sea. The negative relationships between length at age and stock biomass, the pronounced reduction in zooplankton abundance witnessed in the Norwegian Sea in recent years, and expansion in spatial distribution of fish indicate that the biomass of planktivorous fish in the area has been above the carrying capacity. All the stocks showed signs of density-dependent length growth, whereas for herring and blue whiting there were also significant effects of interspecific competition (Table I). The results of the INFERNO project and associated research activities therefore support the original hypothesis that the planktivorous fish populations feeding in the NS have interactions that negatively affect individual growth, mediated through depletion of their common zooplankton resource. It will be important to include these findings in the future ecosystem based management of the Norwegian Sea.

With this current issue, *Marine Biology Research* adds an increasingly important research field to the foregoing three Thematic Issues which focused primarily on purely empirical topics. Individual-based ecosystem modelling tries to thoroughly integrate differences among species, populations, size/year classes, and habitats in temporally and spatially dynamic algorithms aiming at generating predictions on larger-scale ecological processes and changes. While certainly not intended to provide the 'golden key to omniscience', this theoretical approach rests on a firm foundation, as it relies on a large data set gathered in the Norwegian Sea over a rather long time period and has been additionally supported by enhanced sampling, *in-situ* observation, and experimentation efforts in distinct areas, using technologically advanced methods. Although both the data and the modelling approach refer to the Norwegian Sea, we hope to reach out to a much wider range with this issue, because we firmly believe that this research may represent a very valuable example of what could be applied in many other marine ecosystems (see also Huse 2012).

Because the present modelling approach is rather new, relies partly on freshly collected data, and still awaits full implementation, and as the INFERNO project ended only recently, it was certainly a challenge for the four journal editors involved to have the nine original articles of this issue properly reviewed and revised, and to remain within a reasonable time frame until the issue could be finalized. We want to express our sincere gratitude to the 18 anonymous referees for their readiness to critically scrutinize each of the submissions and provide so many helpful and stimulating comments! All manuscripts profited from this reviewing process. Finally, we would like to thank the Norwegian Research Council for financial support of the INFERNO project.

In order to keep track of changes on our Editorial Board, the editors would like to welcome our new subject editors Heino Fock and Kathrine Michalsen (Fisheries Biology), Alf Josefson (Quantitative Benthos Ecology), Tina Molodtsova (Actiniaria and Octocorallia), Stefania Puce (Hydroida), Eric Thompson (Developmental Biology and Physiology), and Christiane Todt (Mollusca)!

At the end of this issue we include – for actual reasons – a short obituary combined with the bibliography of Christoffer Schander, Professor of Marine Biodiversity, University of Bergen, also in acknowledgement of his contributions to our journal as a former subject editor, reviewer and author.

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