20th anniversary of the PINRO-IMR cooperation in the investigations of fish feeding in the Barents Sea – results and perspectives

Andrey V. Dolgov[1], Natalia A. Yaragina[1], Emma L. Orlova[1]

Bjarte Bogstad[2], Edda Johannesen[2] and Sigbjørn Mehl[2]

[1] PINRO
[2]Institute of Marine Research

Abstract

Since 1986 the Institute of Marine Research, (IMR), Norway and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia, have carried out a joint research program on the trophic relationships in the Barents Sea. As part of this program, the two institutions have exchanged quantitative diet data from fish in the Barents Sea, mainly cod. Diet data can give information about important trophic links in the ecosystem and the strength of those links. Therefore, diet data is important for quantifying interactions between fish stocks, e.g. by calculating how natural mortality due to predation influences their dynamics. In this paper we give an overview of diet data collected by IMR and PINRO during the last 20 years, and present some results and perspectives for future work.

Background

Trophic investigations using quantitative diet data started in the Barents Sea in the 1920s-1930s (e.g. Idelson, 1929; Zenkevich and Brotskaya, 1931; Zatsepin and Petrova, 1939; Zatsepin, 1939; Brown and Cheng, 1946) and continued during the 1950-1960s (e.g. Grinkevich, 1957; Sysoeva, 1958; Ponomarenko, 1958). After this period, studies on fish feeding in the Barents Sea were not so intensive and used mainly qualitative diet analyses (e.g. Ponomarenko et al., 1978; Ponomarenko and Yaragina, 1985, 1990a,b).

In the mid-1980s a new joint project was initiated by the Institute of Marine Research (IMR, Bergen, Norway) and Knipovich Polar Institute of Marine Fisheries and Oceanography (PINRO, Murmansk, Russia) to study diet and food consumption of the Barents Sea fish. The motivation for the project was to develop multispecies models for the Barents Sea fish stocks. To be able to quantify stock interactions, detailed quantitative diet data were needed together with a model of stomach evacuation rate.

In the mid-1980s, IMR together with “Fiskeriforsking“ in Tromsø got funding by the Norwegian Research Council for an initial project, where IMR sampled and analyzed diet data (Mehl 1986a), whereas Fiskeriforskning conducted laboratory experiments on stomach evacuation for cod by keeping cod in temperatures similar to what is experienced in the Barents Sea and feeding cod prey typical of the Barents Sea. Similar investigations were conducted in Murman Marine Biological Institute (MMBI) in Russia during 1984-1990 (Orlova, 1991; Orlova et al., 1989c, Orlova and Antonov, 1991). Based on their experiments dos Santos and Jobling (1992, 1995) developed stomach evacuation models that have been fundamental for the project by allowing calculation of consumption of cod using input data from the Barents Sea (Bogstad and Mehl 1992,1997, Dolgov, 1995b).

The joint project was started in 1987 by Alexander Glukhov and Natalia Yaragina from PINRO and Sigurd Tjelmeland and Sigbjørn Mehl from IMR. They initiated and developed the project, the methods for sampling, for analyzing the stomach content in the laboratory and for storing, processing and exchange of data.

The main objectives of the project were to:

- Organize the long-term sampling and quantitative analysis of demersal fish stomachs (mainly cod)
- Calculate the consumption by cod of the commercially important prey species
- Create the basis for the development of multispecies models for the Barents Sea

Methods used

Target species

Cod is the main fish predator in the Barents Sea (Zatsepin and Petrova 1939; Bogstad et al. 2000), and the main focus in the joint project has been on cod. From the start of the project until 1991, both IMR and PINRO collected and exchanged stomach content data on cod and haddock, but because haddock consume only small amounts of commercially important prey species (Burgos and Mehl 1987), IMR stopped sampling stomach content of haddock in 1991, while PINRO continued such sampling. Haddock stomach sampling and analysis of stomach content has followed the same procedures as for cod. Scattered information on stomach content of pelagic fish species (capelin, herring, polar cod, blue whiting) from 1980s was also included in the joint data base.

Since the mid-1990s PINRO started to regularly collect data on diet of other abundant fish species including non-target fishes in the Barents Sea – Greenland halibut, saithe, long rough dab, skates, blue whiting and some others. IMR has since the mid-1990s had some collection of data for saithe, Greenland halibut and blue whiting. These data have not been exchanged so far. At present, both institutes collect diet data from capelin and polar cod, and the exchange of such data is in process.

Data on the diet of marine mammals and seabirds have also been collected, and consumption estimates have been made also for these predators (e.g. Nilssen et al. 2000; Folkow et al. 2000; Bogstad et al. 2000; Barrett et al. 2002, and references therein). We will not go into detail on the work done on these species, as it has not been carried out within the framework of the PINRO-IMR cooperation on investigation on fish feeding. It should be noted, however, that harp seals and minke whales are very important predators on Barents Sea fish – only cod is more important as a fish consumer than these two marine mammal species.

Sampling

Cod stomachs have been sampled on Russian and Norwegian surveys as part of the regular sampling procedures (Mehl and Yaragina 1992). Cod stomachs have also been sampled on Russian commercial vessels with PINRO observers onboard. The sampling procedures have changed over time, including the number of stations sampled, spatial coverage of the sampled stations and the number of stomachs per station. In general, the spatial coverage of the cruises has increased, the number of stations for which stomachs samples have been taken has increased, whereas the number of stomach per stations has decreased (Jakobsen et al. 1997). This change have been motivated by work by Bogstad et al. (1995c) who found that the variation in diet between stations was much larger than the variation in diet within stations, and that is there is strong correlation between stomach samples from the same station. Thus, the effective sample size increases when few stomachs are taken from many stations compared with many stomachs from few stations, even though the total number of stomachs is the same. Currently, 1 stomach per 5 cm length group of cod is taken per station for both Norwegian and joint Russian-Norwegian surveys. The sampling procedures on Russian commercial vessels and Russian national research surveys is different, usually 25 stomachs are analysed from each trawl station using random sampling. Spatial coverage of stations with stomach samples by year and quarter is shown in Appendix 1. Samples taken outside the Barents Sea itself have been included (cod in the Lofoten area, saithe along the Norwegian coast).

Laboratory analysis

The methods used for the quantitative laboratory analysis of stomach content in this project is mainly the same as standard methods used in Russia (Anon., 1974) and for the North Sea stomach sampling project developed in the early 1980s where stomach data was collected and applied in multispecies VPA models (Anon. 1981).

Stomachs are analyzed individually. The total content of sampled stomachs is weighed and the content of the stomachs are divided according to prey species when identifiable. The total weight and the degree of digestion (from 1: newly eaten to 5: digested not identifiable) of the different prey items are recorded. Length measures are taken of prey species that can be identified and when the length is unaltered because of digestion. Finally, the number of identifiable prey individuals per stomach is recorded. From 1984-1992 the resolution of the length measurement in the Norwegian and Russian data varied by the size of the prey (Mehl and Yaragina 1992), but from 1993 on, all the prey items were measured to the nearest cm (or to a finer scale for very small prey).

In the 1990s IMR also did some of the stomach content analysis on board the cruises, but this approach was abandoned because it reduced the quality of the data. Since 1995, PINRO has in addition to the standard methods used a simplified version of the quantitative method, which is conducted onboard at the sea conditions. Total weight of stomach content, visually estimated proportion of prey species and in some cases length and number of commercially important species are determined onboard (Dolgov, 1996).

Software

The program 'MAGE' ('stomach' in Norwegian) was developed in the beginning of the project for storage and exchange of data and for simple diet calculations (Westgård 1982, Mehl 1986b). When the project was initiated, stomach content data could not be included in the data bases of the two institutions, and thus a 'stand-alone' stomach content data base was created. MAGE is still used for converting data into a joint format, and for doing diet analysis, but both institutions now have their own data base systems (IMR: STUVW (Mjanger et al. 2006), PINRO: BIOFOX (Anon., 2001)) where stomach data are stored together with the relevant data on the predator (age, length, weight etc.) and station (time, date, position, catch etc.).

Data gathered

The number of cod stomachs analyzed in the joint project by nation and year is shown in Figure 1. Exchange of haddock data was discontinued in 1991 after approximately 12 000 haddock stomachs had been analyzed. The number of cod stomachs analyzed is now (on the 1st January of 2007) approximately 244000.

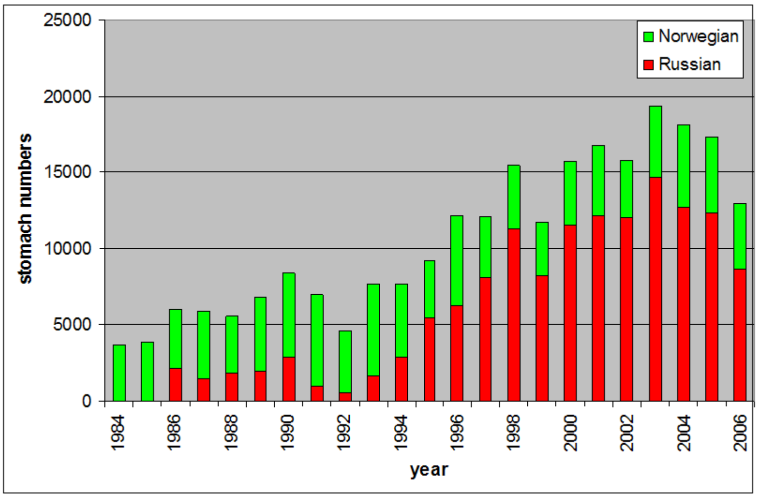

Figure 1. Total number of cod stomachs collected by Norway and Russia during 1984-2006.

From 1984-1995 between 5-10 thousand stomachs were analyzed per year (Figure 2). Since 1996 when new methods of stomach content analysis were applied in PINRO, stomach numbers increased up to 15-20 thousand and then to 35 thousand stomachs per year. This was mainly because PINRO increased the number of species for which stomach were sampled. Total stomach numbers analyzed by PINRO and IMR was approximately 380 thousand by the end of 2006. It should be noted that the joint IMR-PINRO data includes mainly cod after 1991.

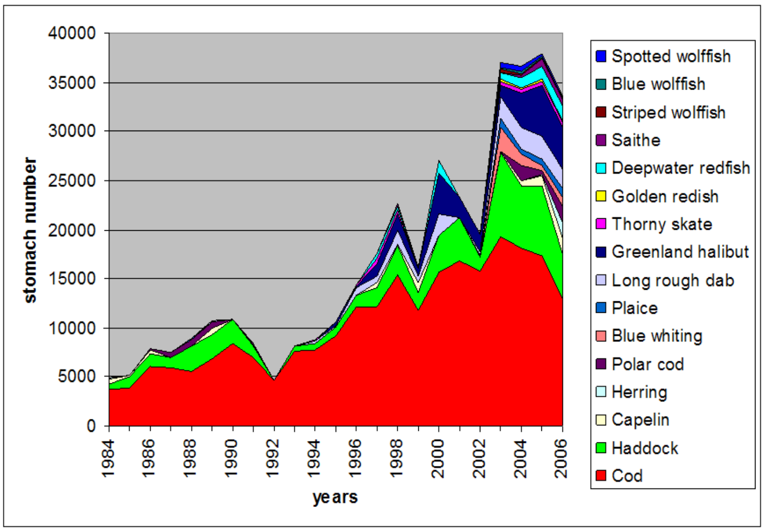

Figure 2. The number of fish stomachs (all species) analyzed by IMR and PINRO by species and year. The joint data consists mainly of cod after 1991.

Since 1999 PINRO started to collect data on energy content of the most important prey species of cod (capelin, euphausids, shrimp etc.). This allowed for calculation of food rations of cod in energy units (kcal). Bogstad and Mehl (1997) also carried out such calculations, based on energy content data from the literature

Results and applications

There have been extensive publications from the joint feeding investigations, both refereed papers, institutes publications, ICES papers and working documents, popular science publications, master theses, posters and presentations on symposia and conferences. The publications can be grouped into two main categories; publications on diet, feeding and biology and publications on models.

Results: feeding, diet and biology

The large body of studies in this category can be grouped in the following way:

- Papers describing the diet of a given species (including consumption calculations)
- Papers on the effect of predation on a given prey species
- Papers on the effect of prey abundance on predator population dynamics

Papers describing the diet of a given species (including consumption calculations)

A summary of some key references for the diet of each predator is given in Table 1. Data on total diet composition of the most abundant demersal fishes of the Barents Sea is shown in Figure 3.

Table 1. Papers on the diet of each predator

Predator	Reference
Cod	Zatsepin and Petrova 1939, Mehl 1986a, 1989, Orlova and Matishov 1993; Ponomarenko and Yaragina 1996; Bogstad and Mehl 1997, Dolgov 1999, Dalpadado and Bogstad 2004
Haddock	Zatsepin 1939, Tseeb 1964; Sonina 1969; Antipova et al. 1990; Burgos and Mehl 1987; Jiang and Jørgensen 1991, Dolgov 1989b
Redfish	Boldovsky 1944; Dolgov and Drevetnyak 1990, 1993a, 1995
Greenland halibut	Shvagzhdis 1990, Michalsen and Nedreaas 1998; Dolgov 2000, Hovde et al. 2002; Vollen et al. 2004
Skates	Berestovsky 1989; Dolgov 2005a
Blue whiting	Zilanov 1984; Belikov et al. 2004; Beck et al. 2006
Long rough dab	Komarova 1939; Simacheva and Glukhov 1990; Berestovsky 1995; Dolgova and Dolgov 1997
Capelin	Prokhorov 1965; Panasenko 1989; Ajiad and Pushaeva 1991, Orlova et al. 2004
Herring	Boldovsky 1941; Manteifel 1941; Orlova et al. 2000c, 2006f
Polar cod	Belova and Tarverdieva 1964; Pechenik et al. 1973; Tarverdieva et al. 1996; Ajiad and Gjøsæter 1990; Orlova et al., 2005f
Saithe	Dolgov 2000, 2002a, Mehl 2005

Some trophic groups of the Barents Sea fishes have been identified (Dolgov, 1992). Planktivorous fishes include herring, capelin, polar cod and blue whiting. Haddock, wolffishes, plaice and dab are benthivorous species. Cod, Greenland halibut, larger thorny skate and long rough dab could be considered as piscivorous fishes. Many species have a mixed diet and can relatively easy switch to feed on other more available prey organisms. Regular sampling of fish feeding allowed for new information on species where abundance sharply increased in the Barents Sea – blue whiting (Belikov et al., 2004) and saithe (Dolgov, 2000) and to evaluate the possible effect on trophic relationships in the ecosystem.

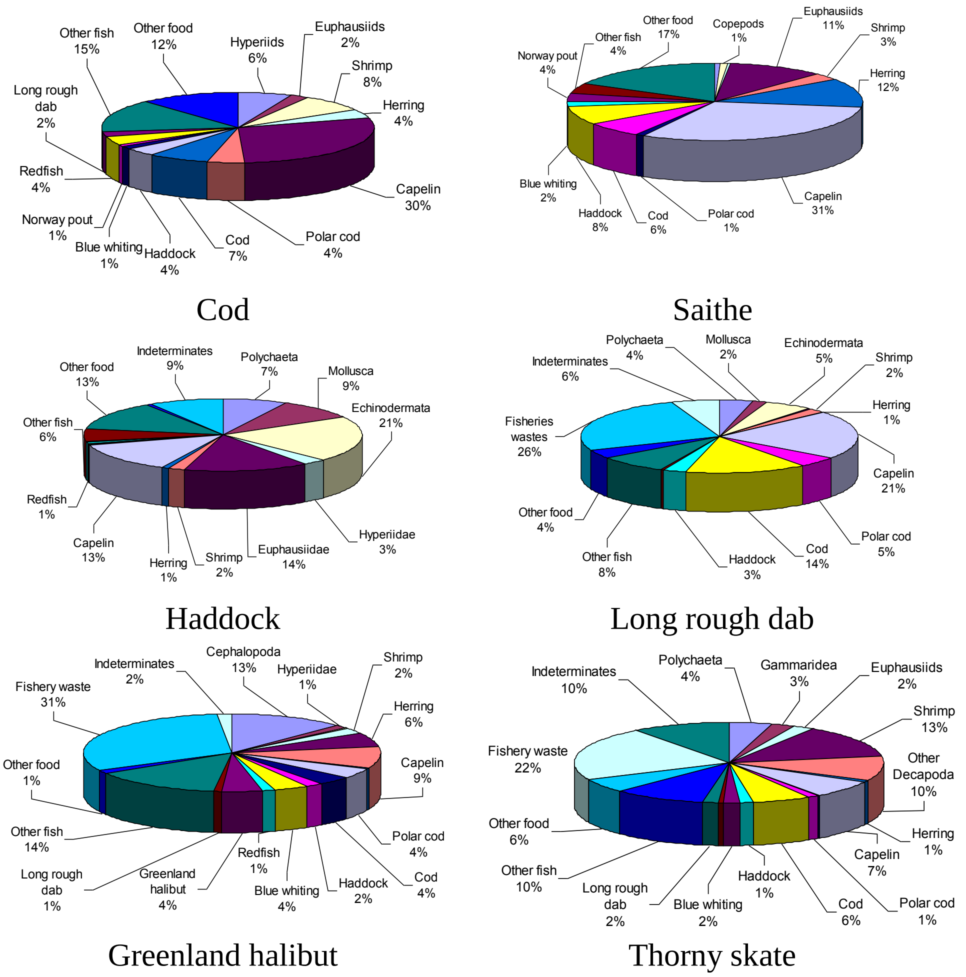

Figure 3. Diet composition of the most abundant fishes in the Barents Sea (combined data for all periods), % by weight.

Juveniles and adult fishes of some species usually belong to different trophic groups. Cod juveniles feed mainly on plankton organisms while fishes with lengths above 25-30 cm prey on larger crustaceans (shrimps) and fish. For some fish where rather high numbers of stomachs was sampled length/age changes in its diet were recognized (Figure 4). Such changes were most clearly observed in cod (e.g.; Orlova et al., 1994; 1995a; Dalpadado and Bogstad, 2004). The main tendency was a dominance of small plankton organisms or benthos in the diet of juveniles, appearance of larger crustaceans and small fishes in the diet of medium sized fishes and prevalence of larger fish species in the diet of the largest individuals.

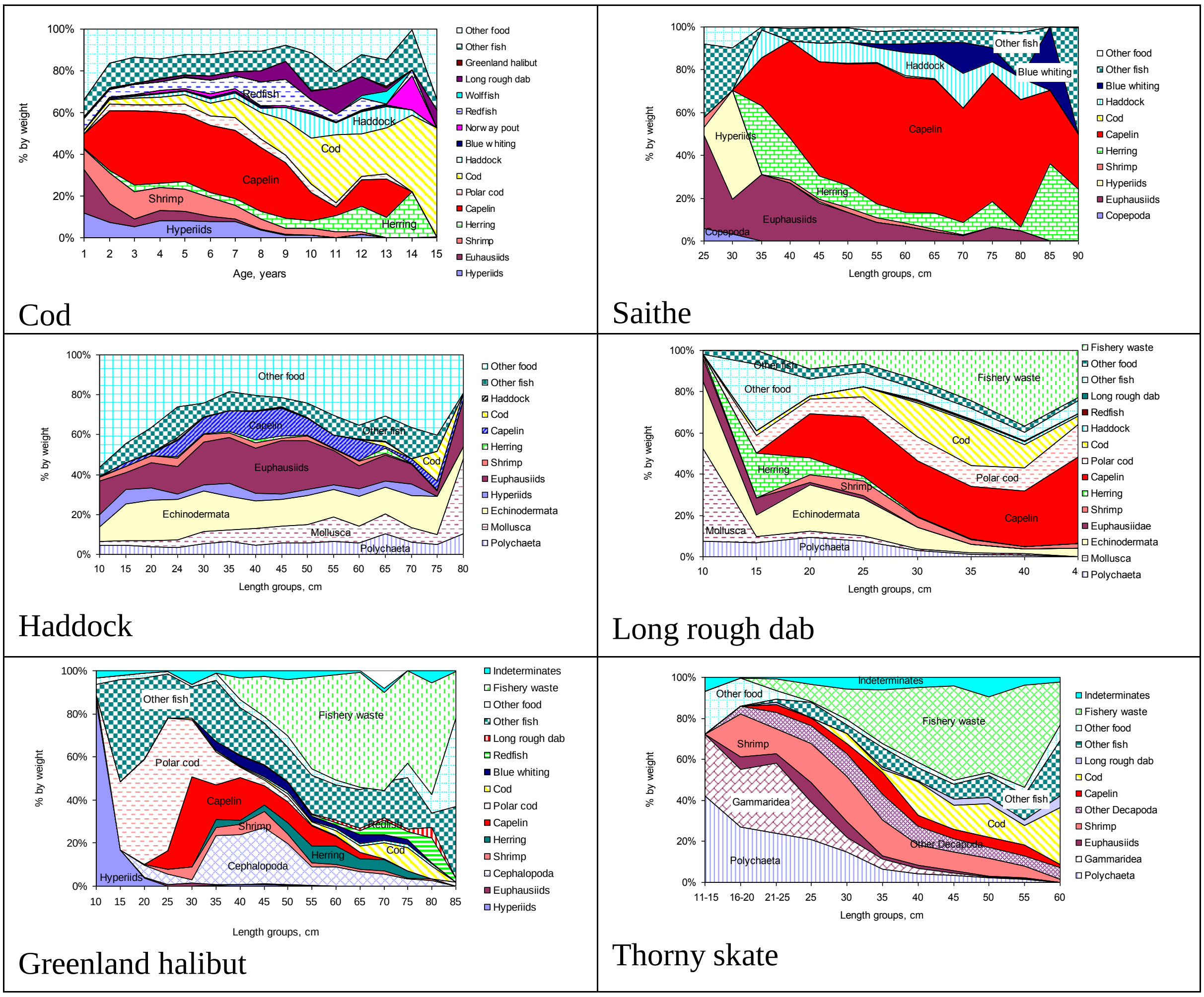

Figure 4. Diet composition of different age/length groups of the most abundant fishes in the Barents Sea (combined data for all periods), % by weight.

The diet of 0-group cod in the Barents Sea in the 1970s was studied by Ponomarenko (1958, 1973, 1983, 1984). Survival rates of bottom-dwelling cod until recruitment at age 3 years were found to be connected, in particular, with abundance of euphausiids - the primary food of 0-group cod. The University of Tromsø has recently completed a research program titled 'Capelin and Herring in the Barents Sea - coexistence or exclusion (Basecoex)'. Within this program, stomach samples were taken, mainly from herring (0-group and older) and 0-group cod. A few stomachs of young haddock, sandeel and saithe were also sampled. The results from this research program are under publication, many of them were presented at the ECONORTH symposium in Tromsø in March 2007.

Large differences were revealed in the diets of some species in the different areas of the Barents Sea, an example of geographic variation in cod diet is shown in Figure 5. Cod diet reflects the geographical distribution of main prey species which again is determined by their seasonal migrations and water masses distribution

Some studies on diurnal variations in diet and variation in diet between fishes distributed at different depths have also been carried out (e.g. Dolgov and Yaragina 1990, Yaragina 1988, Tarverdieva and Yaragina 1989, Ajiad 1990, Michalsen 1993).

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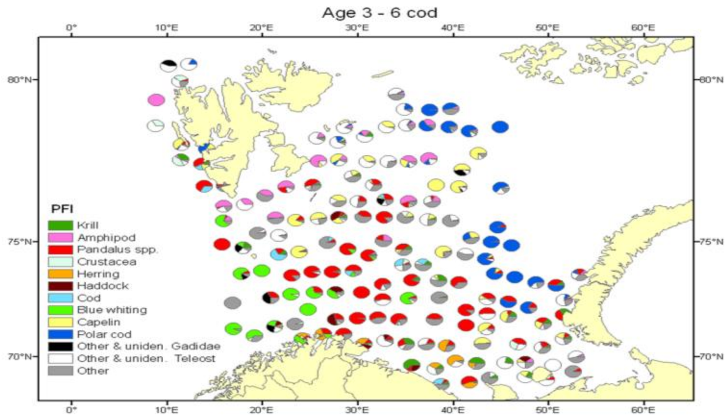

Figure 5. Geographical variation of diet composition of age 3-6 cod during the ecosystem survey August-September 2005.

Tjelmeland and Alvarez (1994) compared real stomach content data with simulated distributions of stomach content based on a feeding model, and estimated some parameters in the feeding model. This approach was developed further by Magnússon and Aspelund (1997). Comparison of food energetic rations of cod in different areas of the Barents Sea has also been conducted. The important role of capelin and herring in the energetic rations was revealed, as well as higher energetic rations in the Northern Barents Sea (Yaragina et al., 2003; Orlova et al., 2003).

Papers on the effect of predation on a prey species

Cod is a generalist predator so changes in cod diet and consumption reflects changes at lower trophic levels in the ecosystem. For instance, we can see how the fluctuations in capelin abundance influence yearly consumption (Figure 6). We also can see how the increase in blue whiting abundance and the decline in redfish abundance are reflected in cod consumption. The fluctuations of the Barents Sea capelin stock have had strong effects on the population dynamics of its main predators, such as cod and harp seal. For cod, effects were observed on growth, maturation, fecundity and cannibalism, while for harp seal, effects on condition, reproduction, mortality and migration have been seen. The overall picture is that the first capelin collapse in the late 1980s affected the predators to a much larger extent than the second and third collapse (Gjøsæter et al. 2007). One important reason for this is probably that more alternative fish prey was available to the predators during the second and third capelin collapses.

Diet data allowed the calculation of food consumption by some fishes of the Barents Sea. The highest food consumption was observed in cod and can reach 6 million tons (Mehl 1989, Bogstad and Mehl 1992, 1997). Other predators consume less biomass. Biomass consumed by haddock did not exceed 1 mill. tonnes, other predators (Greenland halibut, long rough dab and thorny skate) – 200-250 thousand tons. Biomass of prey consumed by cod is rather variable (Figure 6) and reflect both changes in prey abundance and distribution and cod abundance and distribution as well as oceanographic conditions.

Unfortunately, there is still some discrepancy between the results from Norwegian and Russian consumption calculations (see e.g. ICES 2007a). This is due to use of different spatial and temporal aggregation when the consumption is calculated. Data on diets was used to estimate importance of the most commercially important prey species of cod (shrimp, capelin, herring etc).

Table 2. Papers on predation by prey species

Prey	Reference
Cod	Korzhev and Tretyak 1992, Bogstad et al. 1994, Dolgov et al. 1995, Dolgov 1999, Bogstad 2002, Yaragina et al. 2007
Haddock	No papers
Redfish	Dolgaya and Tretyak 1992; Øvstetun 2006
Shrimp	Berenboim et al. 1987, 1992, 2001, Ponomarenko and Yaragina 1990ab, Korsbrekke et al. 1991, Aschan 2000, Johannesen and Aschan 2005, Aschan et al. 2006, Johannesen et al. 2007
Zooplankton	Hassel et al. 1991, Dalpadado et al. 2001, 2002;Orlova et al. 2001b
Long rough dab	Dolgova and Dolgov 1997
Capelin	Ponomarenko and Yaragina 1990b, Ushakov et al. 1992, Huse and Toresen 2000, Dolgov 2002b, Bogstad and Gjøsæter 1994, 2001; Johannesen et al. 2006
Herring	Johansen 2002, 2003, Johansen et al. 2004, Orlova et al. 1995, 1996, 2001d, 2006c, Mehl et al. 2006a
Polar cod	Orlova et al. 2001c

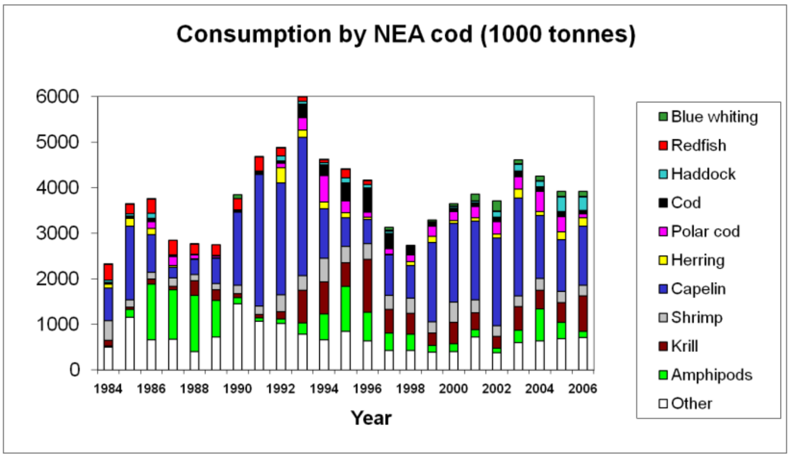

Figure 6. Annual consumption of major prey species by cod 1984-2006.

Use of feeding data for some investigations of other aspects of biology of fishes of the Barents Sea

Data obtained during the project were used for the investigations of the cod growth (Ozhigin et al., 1994, 1995, 1996, Mehl and Sunnanå 1991), as well as reproductive potential of cod (Marshall et al., 2000, 2002; Yaragina and Marshall, 2000; Yaragina et al., 2003). Influence of feeding conditions on biological parameters and fatness dynamics of capelin was studied by Orlova et al., (2006a, 2006b), and bioenergetics models for cod have also been developed (Ajiad 1996).

Results: Models

The joint stomach content data base has been the basis for a variety of multispecies and ecosystem models developed for the Barents Sea. Unfortunately, no ‘truly’ joint Russian-Norwegian models have so far developed, although there are models which have got some input from both parties.

In the first years of the project, model development was done at IMR, while model development at PINRO started in the mid-1990s. The model development at IMR and their Norwegian cooperation partners until 1997 is summarized by Tjelmeland and Bogstad (1998). We have adapted slightly the model classification given by Plagányi (2007), to group the models applied for the Barents Sea. Most of the models applied have been 'minimum realistic' multispecies models, while also some whole ecosystem models (Ecopath with Ecosim) have been applied.

Multispecies models

All the models in this category can be considered as minimum realistic models, they are restricted to represent a limited number of species most likely to have interactions with the target species. The actual implementation of results has been done through extended single-species assessment models; these are described in Section 4.3

Age-length-area-structured models (MULTSPEC, Gadget, others)

Several models with age-length and area structure have been set up for the Barents Sea. The first one was MULTSPEC (Bogstad et al. 1997a), which contained the species cod, capelin, herring, harp seal and minke whale. MULTSPEC was a predecessor of the Gadget modelling framework (www.hafro.is/gadget, Begley and Howell 2004), for which model development is continuing (Lindstrøm et al. 2008, Howell and Bogstad 2007). The present Gadget model for the Barents Sea includes cod, capelin, herring and minke whale, with plans for also including harp seal. Krill abundance is included as an exogenous prey for whales. The model is age-length structured, with a monthly time step and four spatial areas (the Barents Sea and three subsidiary regions), with hindcast and forecast components. Currently, cod and capelin are modeled as having a fully closed life-cycle, while whales and herring have simpler recruitment functions. Predation by whales on cod, capelin and herring, and by cod on cod and capelin is included within the model, although the effects of prey availability on predator condition/growth are not currently modeled. Prey selection for each fish species is according to the length of the predator and prey, and conditioned to the stomach content data. Work is underway to include uncertainty in the forecast part of the model.

Models of this kind for which model development has been discontinued are, in addition to MULTSPEC, the 'Scenario' models (Schweder et al. 1998; 2000) and Systmod (Hamre 2003). Also, Bormicon, a predecessor of Gadget, was applied by PINRO in the late 1990s to study cod-capelin interactions.

MSVPA

MSVPA models have been adapted for the Barents Sea (Bulgakova et al., 1995d; Korzhev et al., 1995; Tretyak et al., 1999; Korzhev and Dolgov, 1999) but this approach has now been abandoned. Up to 7 prey species were included (cod, haddock, capelin, shrimp, polar cod, herring, redfish), with cod the only predator. Harp seal and minke whale were considered as external predators. A major problem when using MSVPA for the Barents Sea is that capelin, which is a key species, has almost total spawning mortality and thus is not suitable for use of VPA-type approaches.

Other age-structured models

The Bifrost model (Tjelmeland 2005, www.assessment.imr.no) include the species cod, capelin, harp seals and herring, and is a forward simulation model which is fitted to the observations (survey data, catch data, stomach content data) and which accounts for the uncertainty in the observations. It is an age-structured model, and for capelin length structure is also included, although in a non-dynamic way.

Stocobar (Filin 2005b) is an age-structured forward simulation model with growth depending on consumption. Feeding, growth, fishery, migration distance and maturity are included. Stocobar has cod as the only predator, and cod, haddock, capelin, shrimp, polar cod, herring, redfish and krill as prey species. STOCOBAR is a further development of the model CONCOD, which was developed to estimation of feeding intensity and yearly rations as well as growth rate of cod (Filin and Gavrilik, 2001). Cod was considered as predator and 6 species (shrimp, capelin, polar cod, herring, juvenile cod and haddock) as prey. The model STRAFICOD was based on CONCOD and developed for analysis of effectiveness of different strategies of cod fisheries management taking into account its trophic relations with capelin. Only two species (cod as predator and capelin as prey) were included in this model.

The Norwegian models AGGMULT and ECONMULT, described by Tjelmeland and Bogstad (1998), but no longer in use, also belong to this category.

Ecosystem models

As part of the collaboration between the Sea Around Us project at the University of British Columbia and the 'Ecosystem Norwegian Sea' program of the Institute of Marine Research, Dommasnes et al. (2001) constructed an Ecopath with Ecosim (EwE) model for the Norwegian Sea and Barents Sea. The model covers 3,116,000 km^2 of Atlantic, Arctic and shelf waters. Thirty functional groups were included, ranging from marine mammals to phytoplankton and detritus. Partly based on the model from 2001, Skaret and Pitcher (2007) constructed a model for the Barents Sea and Norwegian Sea mass balanced for the years 1950 and 2000. They included 58 functional groups including 12 juvenile fish groups. They used Ecosim to simulate the period 1950 to 2000 based on the 1950-model. Catch data on all targeted functional groups were used as forcing functions and the simulated abundance was fitted to 15 abundance time series from VPA, acoustic abundance estimates or CPUE-estimates. A primary production forcing function was added to investigate bottom-up effects in the ecosystem and significantly improved the fit, in particular for the variable capelin abundance. This suggests that bottom-up effects are important in this ecosystem. The model was partly validated using 15 independent time series and time series on stomach data from cod and haddock.

Blanchard et al. (2002) also developed an EwE model of the Barents Sea. The model has been used to investigate the consequences of alternative functional response formulations on the predictions of responses by marine mammals (Mackinson et al. 2003) and to examine effects of model structure on the robustness of outputs (Pinnegar et al. 2005). A model for the Barents Sea by Falk-Petersen et al. (in prep.) to investigate effects of different management regimes on benthos is under construction.

Application in assessment and management

- Important milestones:
- 1987- first calculation of total prey consumption by cod (IMR)
- 1990- stomach data used in joint capelin assessment
- 1991- 5th joint symposium: Interrelationships between fish populations in the Barents Sea (Murmansk, Russia)

- 1995- stomach data used in cod and haddock assessment (ICES Arctic Fisheries Working Group)
- 2000 – calculations of energetic food rations of cod (PINRO)
- 2003- calculation of food consumption by other predators (PINRO)

Interrelations between cod, haddock and capelin were considered by the ICES North-East Arctic Fisheries Working Group as early as 1975 (ICES 1975), but such interrelations were then not taken into account in the assessment.

Since the start of the project application of results to the assessment of commercially important fish stocks and fisheries management was a goal. Consumption estimations of various prey species by different predators is needed to achieve these goals. The most direct application of results from the feeding investigations for management has been the inclusion of cod consumption into fish stock assessment, of commercially important prey species. This has been done using extended single-species assessment models.

Cod consumption was used in capelin assessment for the first time in 1990, to account for natural mortality due to cod predation (Bogstad and Gjøsæter 1994). This methodology has been developed further using the Bifrost and CapTool models (Gjøsæter et al. 2002, Tjelmeland 2005). These models include predation by cod in a single-species, age-length structured capelin model.

Predation by cod on cod and haddock has since 1995 been included in the assessment of these two species in a MSVPA-like way by assuming that M=M1+M2, where M2 is the predation mortality induced by cod. The amount of cod and haddock eaten is taken from calculations of the cod stock's total consumption by predator age groups and prey species and length/age groups (Bogstad and Mehl 1997, updated calculations given in ICES 2007a). For cod, an iterative procedure is needed to carry out the calculations.

An extended single-species cod Gadget-type model (Frøysa et al. 2002) is used as an additional assessment model for assessing Northeast Arctic cod. The model includes cod cannibalism, and uses capelin abundance as an exogenous alternate prey for cod.

SeaStar (Tjelmeland and Lindstrøm 2005) should also be mentioned, although it at present utilises data from a predator species not considered here (minke whale). It allows for including predation by minke whale on herring in the herring assessment, although SeaStar is at present used only as single-species model in assessment of Norwegian Spring-spawning herring. Cod and harp seals could be included in addition to minke whale as predators on herring.

Shrimp is also a commercially important prey species of cod, and natural mortality of shrimp due to cod predations is probably large. Some attempts were made to estimate shrimp mortality due to cod predation (Berenboim et al., 1992, 2001). However, there is no agreed upon assessment of shrimp, and including cod predation into shrimp assessment have proved to be problematic (Hvingel 2006).

Dolgov (2005b) calculated the amount of commercially important prey consumed by other fish predators (haddock, Greenland halibut, long rough dab and thorny skate), but these consumption estimates are not used in assessment yet.

The Joint Norwegian-Russian Fisheries Commission (JRNC) has initiated a project to make a scientific assessment of optimal harvest (maximum sustainable yield) for the most important species in the Barents Sea, taking into account existing knowledge. This work should be based on an analysis of the population dynamics of Northeast Arctic cod and take into account this species' interaction with other species than cod. The project started in 2005, and will last until 2014. The first phase of the project ends in 2007. Data on fish feeding will be crucial for this project. More information about the project can be found at:
http://www.assessment.imr.no/Request/index.html.

Work by ICES and in EU projects

Species interactions in the Barents Sea have also been addressed by other parties than Russia and Norway. The ICES Multispecies Assessment Working Group considered multispecies modeling of the Barents Sea at several of its meetings, in particular the 1990 and 1995 meetings (ICES 1990, 1996). The new ICES Working Group on Multispecies Assessment Methods summarized multispecies modeling work in all areas, including the Barents Sea, at its 2007 meeting (ICES, 2007b).
Also, the EU projects dst^2 (2000-2003) and BECAUSE (2004-2007) helped advance multispecies modeling of the Barents Sea at IMR, particularly with the development of the Gadget modeling framework. Multispecies modeling, with focus on recruitment processes and stock recovery, will continue further during the new EU project UNCOVER (2006-2010), in which both IMR and PINRO take part.

Perspectives and conclusions

The cooperation of IMR and PINRO has been productive and fruitful. The most important result is a creation of extensive data base on long term time series (more than 20 years) of cod stomach content. It is one of the most extensive and long time series of this kind in the North Atlantic. Joint efforts of both institutes allowed reducing the cost of trophic investigations and simultaneously improving temporal and spatial coverage of sampled data. Stomach data analysis is relatively labour intensive, so careful thinking is needed before stomach sampling effort in the Barents Sea is increased or altered.
The ecosystem approach to management avowed by the ICES requires use of compound multispecies models. Extensive stomach content data such as those available in the Joint stomach data base are necessary for model verification. Further studies are needed to investigate North Atlantic marine ecosystems taking into account climatic changes and impacts of intensive fisheries as well as species interactions.

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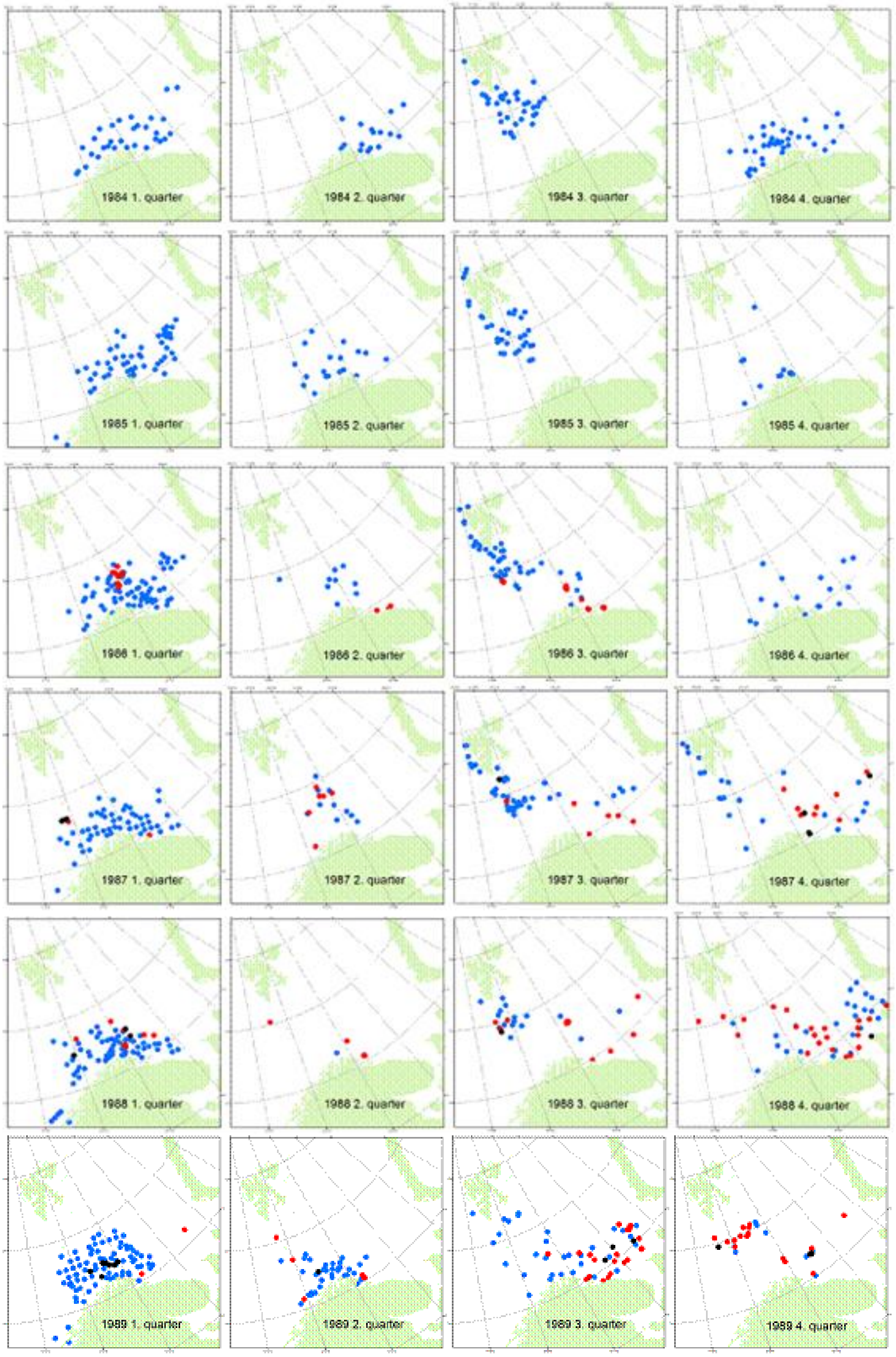
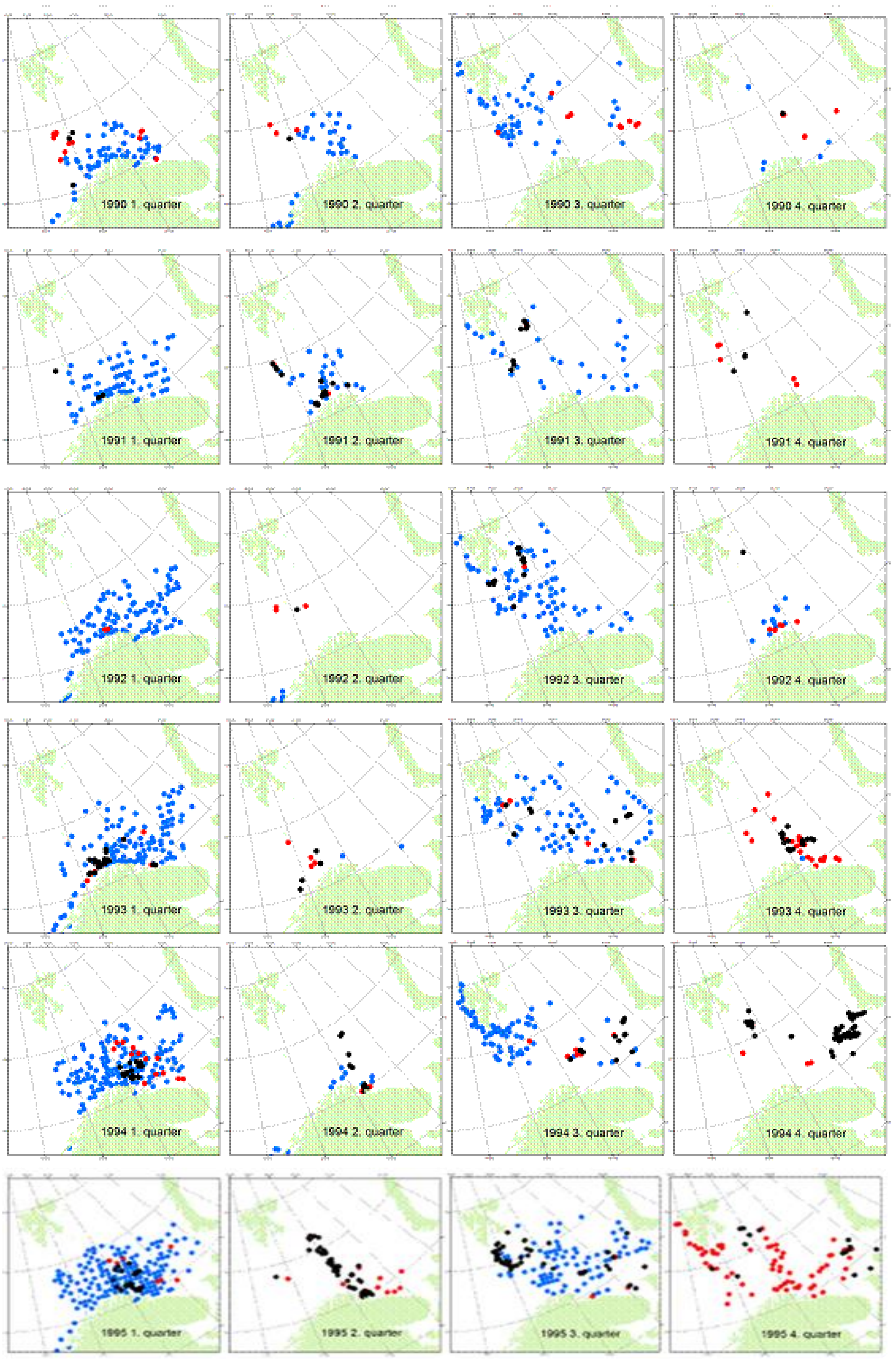
Appendix 1.

Stations with stomach samples by year and quarter 1984-2006. Blue represent Norwegian stations, red Russian stations with trawling time less than 1.5 h, and black Russian stations with trawling time more than 1.5 h.




1990 1. quarter
1990 2. quarter
1990 3. quarter
1990 4. quarter
1991 1. quarter
1991 2. quarter
1991 3. quarter
1991 4. quarter
1992 1. quarter
1992 2. quarter
1992 3. quarter
1992 4. quarter
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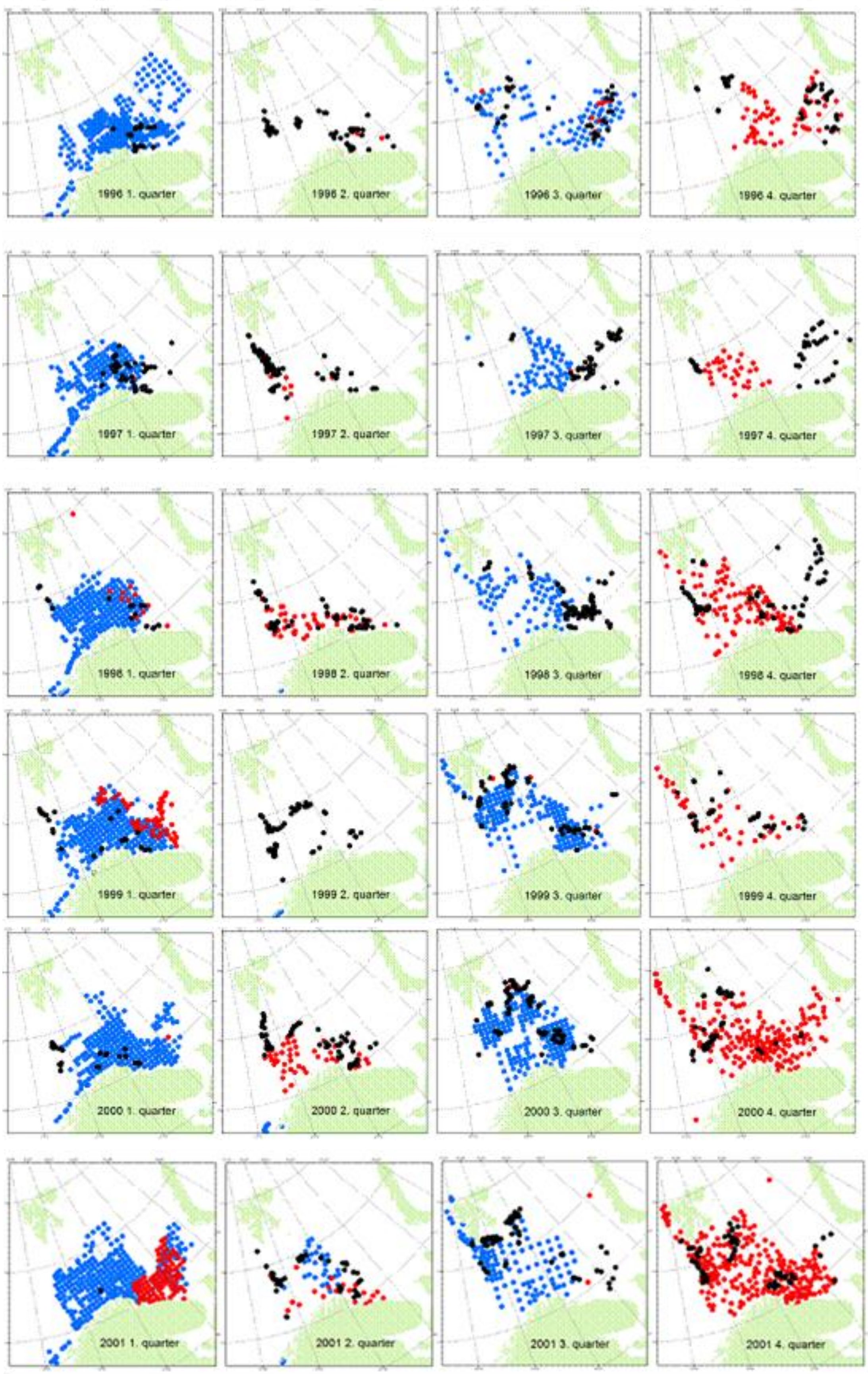
1995 4. quarter


1996 1. quarter
1996 2. quarter
1996 3. quarter
1996 4. quarter
1997 1. quarter
1997 2. quarter
1997 3. quarter
1997 4. quarter
1998 1. quarter
1998 2. quarter
1998 3. quarter
1998 4. quarter
1999 1. quarter
1999 2. quarter
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1999 4. quarter
2000 1. quarter
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2000 4. quarter
2001 1. quarter
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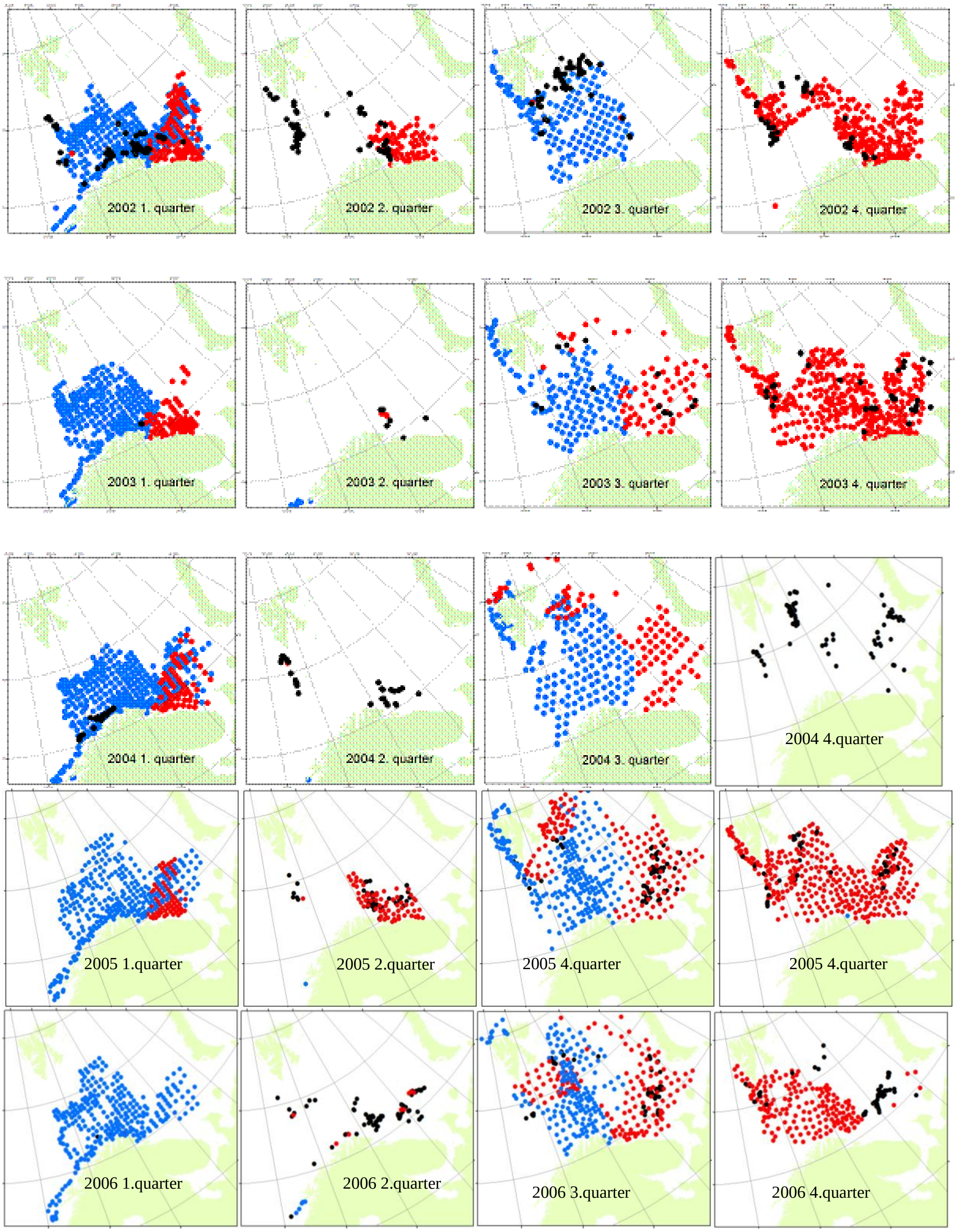
2002 1. quarter
2002 2. quarter
2002 3. quarter
2002 4. quarter
2003 1. quarter
2003 2. quarter
2003 3. quarter
2003 4. quarter
2004 1. quarter
2004 2. quarter
2004 3. quarter
2004 4.quarter
2005 1.quarter
2005 2.quarter
2005 4.quarter
2005 4.quarter
2006 1.quarter
2006 2.quarter
2006 3.quarter
2006 4.quarter