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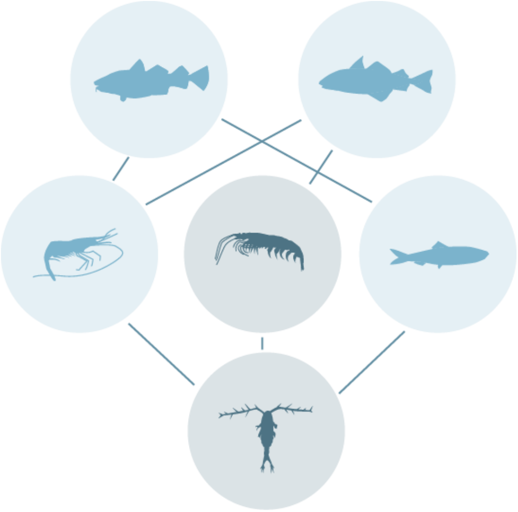
FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Investigating coastal ecosystem structure and dynamics using Ecopath mass-balance modelling and stable isotope data



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A dissertation for the degree of Philosophiae Doctor
June 2013

Acknowledgements

First I would like to thank my main supervisor Torstein Pedersen for being supportive, helpful and to always have time to discuss, read manuscripts and to be able to answer questions I would never expect you to. Your efforts as a supervisor are really beyond what can be expected. This thesis would never have been finished had it not been for you.

Thank you to Trond Ivarjord for helping so much with all the work in the field and the lab. I was truly impressed by all you practical skills. My field work would have been a lot less smooth without you. I also want thank our master students Ina Kolsum and Håvard Fause for work in the field and for contributing with samples. You all contributed to lots of fun times onboard R/V Johan Ruud, along with the outstanding crew who are always helpful and cheerful. I always looked forward to going on the boat. Thank you to the rest of the people on the "Ullsfjord-project", Marianne, Lyne and Einar.

Thank you to the Norwegian Research Council, Oceans and Coastal Areas (Hav og Kyst) for financing this project and following me through my progress, and to the University of Tromsø for supplying a work environment.

Mona, Nina, Arve, Emma and other colleagues at the University; I appreciate every one of you and all the time we have spent together, discussing everything from statistics to skiing via politics over lunch in "Kaffekroken" and having fun off campus. I hope we can continue with lots of dinners, hytteturer and nights out in the future. Thank you, Vibeke for designing the excellent graphical abstract. Thank you, Ellen Kathrine, for being my "roommate" the last year and switching between helping me procrastinate and looking over my shoulder whenever I was doing anything non-work-related.

My dear Ole; I am so happy I have you in my life. I couldn't be luckier than to have you as my boyfriend. You support me, encourage me and give good advice on my research and I could never have found a better marine biologist to share my life with. To our biggest adventure so far, Eira Helene, you are not yet born as I write this, but you really contributed to me speeding up and delivering. All misspellings and "slurvefeil" I will accredit to you. You made me realize that this isn't that important in the big picture, and I guess my science may be outdated by the time you are able to read it.

Contents

Abstract

Ecosystem modelling and stable isotope analysis are both widely applied in marine ecology. Both methods have been used to study food web structure and predator prey interactions. Stable isotopes have also been used to compare the trophic level from the Ecopath model with the trophic level from the nitrogen isotope as a validation of the Ecopath model, and the main aim of this PhD thesis was to investigate whether we can use stable isotope analysis to depict diet data to use as input to an Ecopath mass balance ecosystem model.

The study area has been Ullsfjord-Sørfjord, a northern fjord ecosystem at 70° N. Ullsfjord is the outer part of the system and is larger, more open towards the western Barents Sea and therefore highly influenced by Atlantic water. Sørfjord is the inner part of the system and is smaller, shallower, colder in winter and has lower species diversity of birds, fish and semi-pelagic crustaceans. The impact of fishing is very low in Sørfjord. We wanted to use as much local data as possible in the Ecopath model, and conducted extensive field work, sampling and collecting data on biomass and diet for as many of the groups in our model as possible.

We show that stable isotopes can be used to detect niche shifts. In this case for haddock in Ullsfjord we showed how haddock feeding habits at a young stage (10 to 25 cm in length) differed from those of larger haddock and from small and large cod. Haddock had a pelagic feeding isotope signature and more pelagic than what has been reported in literature. We also showed that several of the most common fish species in Ullsfjord had overlapping carbon isotope signature at sizes between 25 and 45 cm, indicating they may be feeding on similar prey and suggest trophic redundancy.

We investigated structure and flow in the two ecosystems Ullsfjord and Sørfjord, using data from 1993 – 96 and Ecopath models of the two fjords. We found that while Sørfjord was dominated by cod as a top predator and keystone species, Ullsfjord, with its higher species diversity, showed a more web-like structure and several lower trophic level groups were keystone groups from the Ecopath model.

For the final part and main objective of this project we used a MixSIR mixing model to estimate possible prey contributions from the stable isotope signatures. This was used to change the diet matrix of an Ecopath model from 2010 based on gut content analysis (GCA) data. Then the two models (GCA and stable isotope) were compared. Graphical abstract of main objective of this thesis is shown in fig. 1. We conclude that stable isotopes and mixing models show good promise for being both an alternative way of getting diet information, especially on lower trophic levels, and an addition to GCA on higher trophic levels to reduce uncertainty and increase robustness in the model.

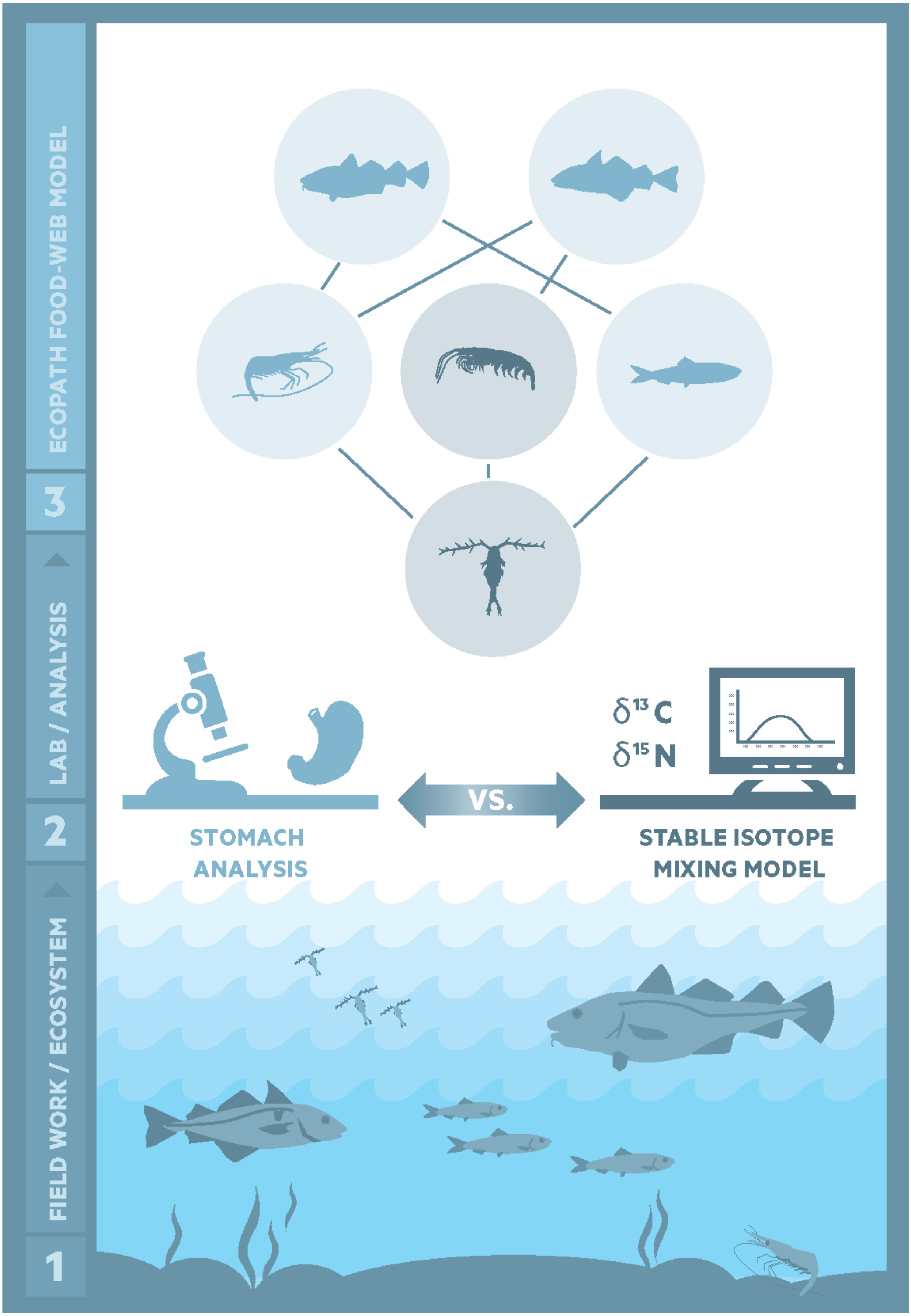

Fig. 1. Graphical abstract of main objective in thesis: “Can stable isotopes be used as input to an Ecopath food-web model?”

1. Introduction

1.1 Ecosystem modelling

An ecosystem with all its living organisms (biotic factors) as well as its physical environment (abiotic factors) and the interactions between them, is overwhelmingly complex, and therefore we need models. A model is a simple representation of a complex phenomenon. It does not contain all the details of the real system, but the overall structure and the main interactions should be included. Food web modelling has become a vital tool in ecology. It helps us communicate structure and functioning of an ecosystem and is essential for understanding the interactions that take place. A food web model can be a conceptual model drawing of boxes with arrows between them (Fig. 2a), an Ecopath food web model (Fig. 2b) or it can be an advanced dynamic model where ecological equations regulate the dynamics of the components through time or space. Ecopath with Ecosim is a trophic mass-balance modelling software for building ecosystem models, originally developed by Polovina (1984) for the French Frigate Shoals in Hawaii. It has later been improved and made more user friendly for ecologists. The software is developed primarily for fisheries research and includes a suite of tools for this purpose. Ecopath is an end-to-end model, meaning we try to represent the whole ecosystem (Fulton 2010) and this separates it from the single species- and multispecies models that are used in management today.

Any model is a simplification of the real world and it is impossible to model an ecosystem with all its complexities. A model is therefore constructed for specific questions or problems and the level of detail in the model depends on the research question. For example; a model developed for fisheries is usually not suitable for investigating variations in phytoplankton abundance. Increasing the level of detail in a model will not always improve the model as it may just introduce larger uncertainties (Fulton et al. 2003). It is important to keep in mind that an ecosystem model is only as good as the data we have. How we choose to organize our model and the number of species we include is to some extent based on our pre-understanding on how the components interact and what our research questions are. Knowledge on ontogenetic shifts or migrations can be important when we choose the detailing of our model and whether we need multi-stanza groups. Multi-stanza groups represent life history stages or stanzas for species that have complex trophic ontogeny (Christensen & Walters 2004).

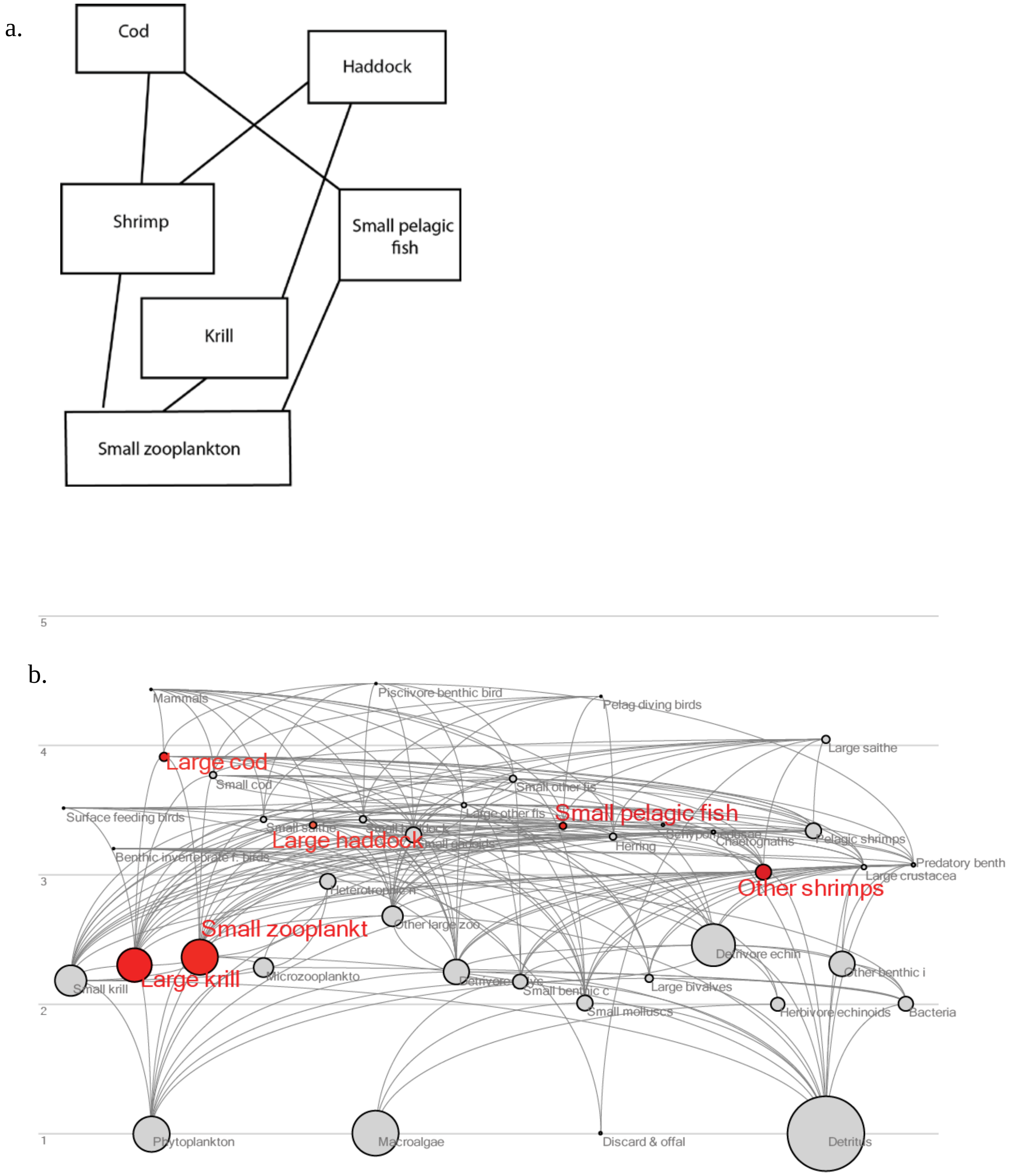

Fig. 2, a) Conceptual ecosystem model and b) Ecopath model of Ullsfjord based on GCA with the species represented in the conceptual model in red. Circles represent groups in the model scaled to biomass, lines represent predation, and y-axis is the trophic levels.

Comparing ecosystems is a way of understanding how structure, diversity and other ecological parameters influence the functioning of an ecosystem. Using a standardized method or model for comparative studies is essential or biological differences cannot be separated from modelling artefacts (Coll et al. 2006, Coll & Libralato 2012). Ecopath with Ecosim has been widely applied in comparative studies, using the ecological indicators supplied directly from this modelling approach, often with respect to fisheries and its ecosystem effects (e.g., Moloney et al. 2005, Coll et al. 2006, Morissette et al. 2009, Tomczak et al. 2009).

1.2 Who eats whom?

Common to all food-web models is the need for knowledge on predator-prey interactions. One needs to know who eats whom, and preferably also how much a predator consumes of any prey. This is necessary to say anything about the links in the food web, interaction strengths and trophic levels.

No ecosystem is the same and variations in species composition, production rates, biomasses and diet can be very different even for seemingly similar ecosystems as we show through this work in Ullsfjord and Sørfjord. Therefore we need local data, and as most marine research, this is time consuming and expensive to obtain. Any method that can reduce this should be welcome. Gut Content Analysis (GCA) is the classical way of obtaining diet data, and this may be the best method for getting taxonomically detailed data. There are however some problems with GCA. With fish, the method may seem straight forward, but there are pitfalls. There is a risk of overestimating the significance of large prey such as fish as they are easy to see and relatively slow to digest. Large crustaceans can easily be overestimated as the hard exoskeleton is slowly digested since most fish swallow their prey whole and the remains of the exoskeleton will be identifiable for a long time compared to the actual energy content of the animal. Conversely, small animals, especially those without exoskeleton may be overlooked or digested quickly and therefore underestimated. “Mush” or “unidentified” are often large prey categories in data from stomach investigations. At lower trophic levels (TL), identification of prey in stomachs of invertebrates such as shrimp, krill, polychates or even copepods is close to impossible with conventional methods especially as they tear the prey apart before they consume it. Literature data from other areas or even different species is often used to construct food webs. This will not always be representative of what they feed on in this particular ecosystem as some species feed opportunistically and will easily shift to feeding on high availability prey. Omnivores shift between feeding on different trophic levels; e.g., large krill (*Meganyctiphanes norvegica*) can shift between feeding on phytoplankton and copepods (Båmstedt & Karlson 1998), and such shifts can have a major influence on the food web model as these low trophic level species usually have very high biomasses and may also be keystone species, as we will show in this study.

1.3 You are what you eat

Stable isotope analysis has emerged as one of the primary means of investigating the structure of food webs. This application takes advantage of the natural variation of isotopes in the environment and the enrichment of the heavier isotope across trophic levels. Stable isotopes and Ecopath modelling have separately been widely applied to analyse food webs in marine ecology. Isotopes have also been used to validate the model by comparing the TL from Ecopath with the TL calculated from the δ^{15}N (Nilsen et al. 2008, Milessi et al. 2010) and to compare measures of trophic diversity from stable isotopes with ecosystem indicators from Ecopath (Navarro et al. 2011). These approaches have shown both methods to be useful and comparable and the main aim of this project was to see if the stable isotope signatures can be used as input to the Ecopath model and thereby reduce the need for time-consuming diet investigations. A major advantage of stable isotopes is that they provide a time-integrated average of what the animal has been consuming. For food-web models like Ecopath this is an advantage as the parameters are averaged over a longer time period, usually a year, so time-integrated diet representation means that the sample size per species can be lower than with GCA. Therefore stable isotopes could be a way of getting more local data in a less time consuming way as stable isotope samples are relatively easy to collect and analyse. The sampling can also be non-invasive, as feathers, fur or a biopsy sample can be used on animals where there might be ethical concerns in killing.

1.4 Objectives

1. To investigate multi-stanza structure and ontogenetic shifts in major fish species in Ullsfjord

2. Investigate food-web structure and trophic flows by a comparative ecosystem study. How does species diversity affect ecosystem properties and are we able to represent this in Ecopath?
3. To investigate if we can use stable isotopes as input to an Ecopath mass-balance model.

2. Material and methods

2.1 Study area

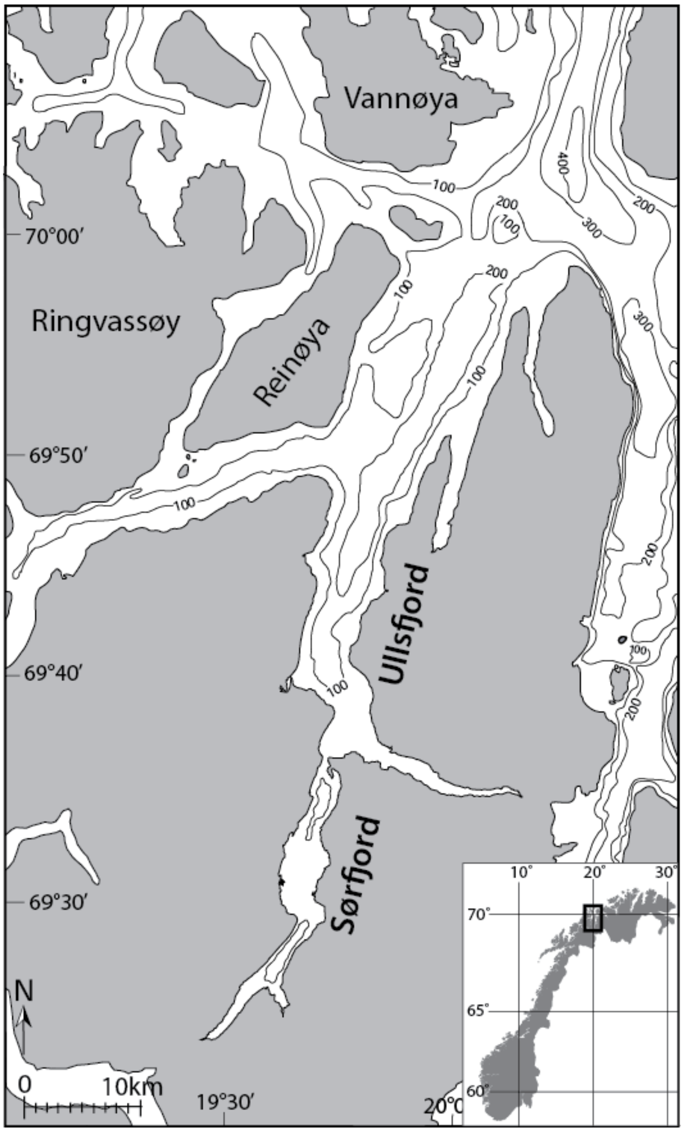

Fig. 3, Map of the study area, Ullsfjord and Sørfjord in Northern Norway.

Ullsfjord

The study area is shown in fig. 3. Ullsfjord is a high latitude fjord ecosystem at 70°N that supports small scale fisheries for Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens* and other large fish species as well as a commercially important shrimp fishery. The fjord was chosen as study area because several studies have previously been conducted there so a lot was already known about the ecosystem, and data were available from the 1990-ies. The total area of the fjord is 412 km^2 and the total coastline is 175 km. A deep trench runs from the south to the north with depths of about 275 m. The outer part is open towards the western Barents Sea, and the fjord is therefore highly influenced by Atlantic water. In the inner part, Ullsfjord is separated from Sørfjord by a shallow sill, only 8 meters deep and 300 m wide. Occasionally, we have observed marine mammals in the fjord, mainly white beaked dolphin *Lagenorhyncus albirostris* and harbour porpoises *Phocoena phocoena* and there were invasions of harp seals *Phagophilus groenlandicus* in 1986 to 88 (Haug et al. 1991) and a smaller invasion of young animals in 1995 (Haug & Nilssen 1995). However they are not normally present in large numbers.

Sørfjord

Sørfjord is the inner part of the Ullsfjord-Sørfjord fjord system, and is smaller and shallower than Ullsfjord. The fjord is 27 km long and has a total area of about 55 km^2. Sørfjord is less influenced by Atlantic water, has higher influence of fresh-water run-off from the surrounding mountains and glaciers, and is colder in the winter than Ullsfjord. Sørfjord has a lower diversity of fish and pelagic crustaceans than Ullsfjord and can be seen as a representation of a typical Arctic marine ecosystem, expected to be top-down controlled by large top-predators (Frank et al. 2007). There is a very small commercial fishery in Sørfjord, mainly targeting cod with hand-, long line and gill nets, while bottom trawling is prohibited.

2.2 Ecopath mass balance modelling

The Ecopath modelling approach is to develop a static model that describes the average interactions within a food-web over a certain period. Mass-balance means we assume all flows are accounted for; “Mortality of a prey is consumption of a predator”. However it allows for biomass accumulation or reduction during the averaged time period and does not assume steady-state. There are two master equations. The first describes how the production term for each group can be split into components.

Production = catches + predation mortality + biomass accumulation + net migration + other mortality

The second describes the energy balance of each group in the model through consumption

Consumption= production + respiration + unassimilated food

The balanced Ecopath model is used to calculate trophic level (TL) of all the groups, keystoneness, omnivory index and many other ecosystem indicators. These indicators can then be used to compare ecosystems, as we do in MS2.

One of the biggest advantages of Ecopath, and also one of the reasons the software has been continuously developed for more than 15 years is that it makes modelling available to biologist, who are often not “modellers”. It is not made to replace single-species stock assessment, but to be a strategic tool that can be used to investigate and explore possible outcomes of harvesting strategies, to test different policy management plans and to identify where more research or data is needed. The data required to make a model can often be found in existing stock assessment data.

During this project we made several Ecopath models. For Ullsfjord we constructed one model for the period 1993 to 1996 to compare to an existing model for Sørfjord for the same time period (Pedersen et al. 2008). We prepared another model for Ullsfjord for 2010 with data collected during late 2009 and 2010 and we then made a second version of this Ullsfjord 2010 model updated with data on diet from stable isotope analysis calculated using a mixing model. The Ecopath models consisted of 40 groups including mammals, birds, fish, pelagic and benthic invertebrates, primary producers and detritus. Detailed information on how all parameters were calculated is given in the appendix to MS2 and MS3. The model for Sørfjord for 1993-96 was updated to have the same 40 groups as the Ullsfjord model to make them more comparable (see Appendix to MS2).

Birds

We chose to include 4 groups of birds in our model. They were separated by their foraging behaviour into surface feeding birds, pelagic diving birds, piscivore benthic feeding birds and benthic invertebrate feeding birds. In general birds are often overlooked in fisheries modelling or only represented by one group (e.g., Dommasnes et al. 2002, Harvey et al. 2003). In many marine ecosystems however, seabirds have high food consumption, biomasses and may be important predators on pelagic fish and fish juveniles. Outside Ullsfjord, there is a large breeding population of puffins at Nord-Fugløy, a bird-island outside the fjord. These birds have been observed to forage in Ullsfjord, and in summer there are abundances of up to 50 puffins per km^2. A number of species of gulls are present throughout the year, and there is a small breeding colony of black legged kittiwakes *Rissa tridactyla* and numerous eiders *Somateria mollissima* that breed by the fjord. It seems obvious that the feeding from these birds will have an effect on the marine ecosystem. Therefore, large efforts were made to estimate the abundance of seabirds in Ullsfjord.

2.3 Stable isotopes

When measuring isotopes, greek delta (δ) in parts per thousand (‰) is used to note the difference between the sample and a standard material:

$$\delta X = [(R_{sample}/R_{standard})-1]*10^3$$

For the carbon isotope, $\delta^{13}C$ refers the ratio of ^{13}C to ^{12}C relative to Pee Dee belemnite limestone. The carbon isotope at the base of the littoral food-web is generally enriched in ^{13}C compared to the base of the pelagic food web, and because the enrichment of ^{13}C is low per trophic level (0 to 1‰), $\delta^{13}C$ can be used to determine the primary source of carbon leading up the food chain to the animal in question (e.g., Peterson & Fry 1987). For nitrogen the $\delta^{15}N$ refers to the ratio of the heavier isotope, ^{15}N to the lighter isotope ^{14}N relative to atmospheric nitrogen. The nitrogen isotope ratio is enriched in a stepwise of about 3.4‰ per trophic level (Post 2002) referred to as the trophic fractionation ($\Delta\delta^{15}N$). This is caused by the retention of the heavier isotope ^{15}N relative to the diet. $\delta^{15}N$ is therefore used to calculate the trophic level of an animal.

2.3.1 Calculating trophic level (TL)

The relative trophic position of animals within the food web can be calculated easily within one food web from the nitrogen isotope ratio. However to calculate absolute TL in order to compare across food webs one needs a base-line; the nitrogen isotope signature, N_{base}, of a species we already know the trophic level of (TL_{base}), because there can be high variations between ecosystems both in $\delta^{15}N$ and $\delta^{13}C$. Ideally we would sample a primary producer (TL 1), however the primary producers may display larger temporal variations in $\delta^{15}N$ than its consumers, and therefore be unsuited to find N_{base} (Vander Zanden & Rasmussen 2001). Also sampling pure phytoplankton is difficult and the samples will often contain pelagic detritus as well as phytoplankton (Fredriksen 2003). Going one trophic level up we would try to sample an obligate primary consumer (TL 2). For example mussels and gastropods have been found to give good baseline estimates for the pelagic and the littoral food-webs respectively (Post 2002). We chose to use *Calanus finmarchicus*, a very abundant pelagic herbivorous copepod and an important source of food in the ecosystem. However it is not obligate herbivorous (Saage et al. 2008), and this is discussed in MS1. In MS3 we appointed TL 2.3 to this species as this was calculated from the GCA Ecopath model. The trophic level is then calculated as

(1) $TL = (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / \Delta\delta^{15}N + TL_{base}$

2.3.2 Lipids

Lipids are depleted in ^{13}C compared to proteins. This can cause bias (highly negative $\delta^{13}C$) in the stable isotope signature for lipid rich animals such as calanoid copepods, and the pelagic fish capelin *Mallotus villous* and herring *Clupea harengus*. Lipids may be chemically removed before isotope analysis; however the lipids may provide valuable information, such as condition, about the animal (Abrantes et al. 2011). The chemical lipid removal may also influence the nitrogen isotope ratio (Sweeting et al. 2006) and it is an additional cost. For gadoids such as haddock and Atlantic cod, lipids do not pose a problem because their per cent of lipids in the muscle is low (below 5%). There is no general consensus on what method should be used although literature on the subject is plentiful (e.g., DeNiro & Epstein 1977, Sotiropoulos et al. 2004, Sweeting et al. 2006, Post et al. 2007, Soreide & Nygard 2012). One solution to this is a quantitative method for normalizing for the effect of lipids. The ratio of carbon to nitrogen (C:N) in the tissue is highly correlated to the amount of lipids in the sample (Post et al. 2007), and this C:N ratio is measured during spectrometry analysis an can be used to calculate the amount of lipid as well as normalizing the $\delta^{13}C$ value in the sample. We chose to use a normalization regression suggested by Post et al. (2007) on all samples.

(2) $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N$

2.3.3 Mixing models

In MS3 we use a stable isotope mixing model to estimate the contributions of several sources (prey) to a mix (consumer) (Fig. 4). A mass balance mixing model assumes that for a given isotope the isotopic signature of the mixture (δ_M) is defined as:

$$\delta_M = f_1 * (\delta_1 + \gamma_1) + \ f_2 * (\delta_2 + \gamma_2) + \ldots f_n * (\delta_n + \gamma_n)$$

where f_i is the proportional contribution of the ith source to the mixture. δ_i is the isotopic signature of the ith prey source and γ_i is the isotope-specific fractionation of the ith source. Using n isotopes, one can only find one unique solution for n + 1 prey. However, mathematical approaches can be used to solve underconstrained models. We used MixSIR mixing model (Moore & Semmens 2008, Semmens & Moore 2008) to calculate possible contributions of various prey groups for each predator species and then balanced the diet matrix in the Ecopath model for Ullsfjord 2010, using the output from the mixing model.

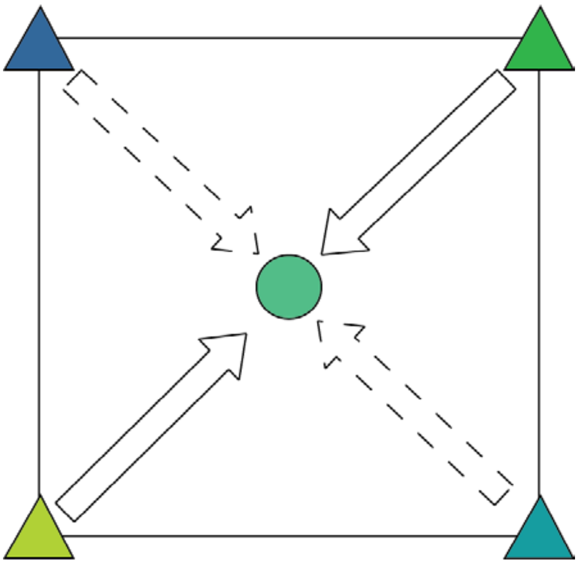

Fig. 4, a conceptual drawing of a mixing model problem. The triangles represent the different sources (prey) and the circle represents the mix (consumer). The colour represents the isotope signature. Adopted from Fry (2013).

MixSIR is a Bayesian mixing models and employs a Hilborn sampling-importance-resampling approach to determine the likelihood of potential source contributions (prey) to the mix (consumer). So for each source, a random proportional contribution vector is proposed and the mean and standard deviations of the proposed mixture based on randomly drawn proportional contributions are calculated and the likelihood of the mixture, given these parameters, is determined from the isotopic signature of the mix (a vector of the isotope signatures of the consumer). An unnormalized posterior probability is calculated and accepted if it is higher than the previous unnormalized posterior probability. The MixSIR model gives us a range of possible source contributions with explicit probability distributions (Moore & Semmens 2008) while for linear mixing models, each probability distribution has the same probability (uniform distribution) (Newsome et al. 2012). We used the median value as input to the Ecopath diet matrix where possible, but supply the range from minimum to maximum values in MS3. The value we used as the diet proportion for each prey group also had to fit with available biomass and production of the prey species (groups) in the Ecopath model and of course to be likely from a biological point of view. To limit the number of possible sources included in the mixing model, only prey species present from GCA or literature references was used and functionally similar species with similar isotope signatures were grouped. These methods were in accordance with the recommendations by Moore and Semmens (2008) as well as a later review on mixing models and quantitative stable isotope analysis by Layman et al. (2011). MixSIR incorporates uncertainty in the model, unlike earlier stable isotope mixing models and allows the use of prior information in the form of informative priors that can be used to limit the range of the proportional contributions. We chose not to use the GCA as informative priors as it can bias the mixing model in the same way as GCAs can be biased (see introduction and MS3), as every possible draw of source contribution is multiplied by the expected source contribution from the informative priors (Moore & Semmens 2008).

3. Main findings

3.1 MS1

Ramsvatn, S., Pedersen, T. (2012)

Ontogenetic niche shifts in haddock *Melanogrammus aeglefinus* reflected by stable isotope signatures, δ^{13}C and δ^{15}N, Mar Ecol Prog Ser 451:175-185

Manuscript 1 showed that stable isotopes can be used to detect niche shifts. In this case for haddock in Ullsfjord we showed how haddock feeding habits at a young stage (10 to 25 cm in length) differed from those of larger haddock and small and large cod. Haddock had a pelagic feeding isotope signature and more pelagic than what has been reported in literature. We also showed that several of the most common fish species in Ullsfjord had overlapping carbon isotope signature at sizes between 25 and 45 cm, indicating they may be feeding on similar prey. We proposed that the large biomasses of semi-pelagic crustaceans in the fjord are attractive as prey for several of the predatory fish species, but because of the high availability of prey, they are not necessarily competing. However, their stable isotope signatures suggest trophic redundancy.

For the main research question in my thesis, this paper showed that stable isotopes can be used to detect niche shifts, and thereby giving detailed information on feeding. The paper also explored some of the variation found within the commercial species in our model area (Ullsfjord), and highlights the importance of using local data, as haddock stable isotope signatures differed between Ullsfjord and Sørfjord.

3.2 MS2

Pedersen, T., Ramsvatn, S., Nilssen, E.M., Nilsen, M., Morissette, L., Ivarjord, T., Systad, G., Kolsum, I., Fause, H.

Species diversity affects marine ecosystem structure and mass flows
Submitted to Ecosystems

In manuscript 2 we compared Ullsfjord and Sørfjord using two Ecopath models with data from 1993 to 1996. We explored how diversity in fish and crustacean species influence the functioning of the fjord ecosystems by comparing ecosystem traits like: biomasses, keystoneness, trophic levels and flow of carbon. There was some top-down control by several commercial fish species in Ullsfjord, while the high biomass of krill in the system contributed with bottom-up control. The total biomass of seabirds was much higher in Ullsfjord than in Sørfjord and their predation on small pelagic fish was high. Sørfjord was dominated by cod as a predator, while in Ullsfjord, we suggest that the predatory fish display trophic redundancy as there was no clear top predator among the larger fish species and their diets seem to be overlapping. Ullsfjord had a higher connectance- and system omnivory index, indicating a more web-like structure than Sørfjord and we discuss how this may contribute to higher stability in Ullsfjord.

3.3 MS3

Ramsvatn, S., Pedersen, T., Nilsen, M., Nilssen, E. M.

Can stable isotopes be used to parameterize a marine food-web model in Ecopath?
In submission to Ecological Modelling

In manuscript 3 we explored the main objective of my PhD. We show that stable isotope (SI) analysis and mixing models can be used as input to a food-web model. The stable isotopes provided information that we did not get from gut content analysis (GCA) and the two methods used together may be a good way of getting diet information on all trophic levels. Stable isotopes are faster to collect and analyse than gut content and one needs fewer samples. However, there are uncertainties on the taxonomic resolution of the output from the mixing model, and the model is very sensitive to small variations in the input values (mean and standard deviation of the prey as well as the vector of signatures for the predator) and therefore lipid-rich tissues would possibly influence the output if not taken into consideration. The results showed that it’s necessary with some previous knowledge of what are potential prey species to use a mixing model, especially for generalist predators like cod. When using SI analysis and the mixing model we found higher predation on small fish by cod and haddock than what GCA reflected. It might be that the large fish are feeding on krill and shrimp at the time when they are in the areas when they are possible to catch by trawl as these areas are typical shrimp trawling grounds, while they may feed on fish at other times. We propose that SI analysis can uncover bias in sampling. For lower trophic levels the SI analysis provided information on diet where we would otherwise have used literature data. Uncertainty in modelling is reduced by using several approaches to data collection and SI analysis may therefore be a way of reducing model uncertainty.

4. General discussion

4.1 Stable isotope mixing models and ecosystem modelling

The term isotopic niche (Newsome et al. 2007) or niche space is used to refer to the area in the carbon-nitrogen-bi-plot "covered" by one species. One can get qualitative information about an animals', species' or populations' position in a food web in relation to the other species, its potential prey and predators and even possible habitat use just from plotting the isotope signature. On the other hand, quantitative estimates on resource use and realized niche space are only available through the use of mixing models. Stable isotope mixing models are developed to estimate source contributions. However, a major challenge in only using carbon and nitrogen is that we cannot find a unique solution for more than three sources, so the model is underconstrained. Stable isotope analysis and mixing models are not a solution to replace poor sampling, and we need a priori knowledge of what possible prey species to sample when we go into the field. However stable isotopes provide valuable information from a relatively low sampling effort, and are an easy way of reducing uncertainty by having multiple sources of data on diet. In summary, using a stable isotope mixing model proved to supply data we would not have otherwise.

The ontogenetic niche shift described for haddock (MS1) had implications for the Ecopath model configuration, and was the reason we decided to have multi-stanza groups for haddock. Haddock seemed to feed on pelagic prey when they were at sizes of 10 to 25 cm, while cod at the same size seemed to have shifted their diet towards a more demersal diet. At the time of writing the first manuscript we did not have stable isotope data on possible prey species, and assumed krill to be the main prey. From GCA analysis for MS3, krill was the main prey item for small haddock (80%), but from the mixing model output small zooplankton, mainly consisting of *Calanus finmarchicus*, was the main prey composing 83 to 98% of the diet. However, small zooplankton and small krill have similar isotope signatures and several times when running the mixing model we detected that a small change in any of the values, the mean or standard deviation (SD) of the prey or fractionation factors, or what prey groups were used, would dramatically change the output of the mixing model, as it did with capelin (see discussion in MS3). Therefore we chose to split the prey contribution to small haddock between small zooplankton and small krill so that we used 40 and 43% as the diet proportions respectively. There is the possibility that haddock prey on something we have missed in our sampling, such as small or soft prey that will be digested fast, however from the available data this seems to be the most likely solution. In MS1 we also noted that large haddock (> 35 cm) had relatively pelagic isotope signature and we could not see that their diet could be mainly invertebrate benthos as often reported in literature (Demain et al. 2011). Also here we assumed krill to be the prey of preference as this was found in GCA from haddock in Ullsfjord (Kolsum 2011), however from the mixing model, pelagic fish and small gadoids came out as the main prey. This would also explain the pelagic signature even if there are some claiming this to be highly unlikely prey for haddock (e.g., Mattson 1992). They could also prey on capelin eggs and dead capelin, as capelin has been observed to spawn in Ullsfjord (unpubl. data), and this type of feeding has been reported from the Barents Sea (Bogetveit et al. 2008).

Small cod (< 35cm) from the sub-littoral zone of Ullsfjord, had significantly different stable isotope signatures than the small cod caught in the deeper demersal zone by bottom trawl. This is briefly described in MS3. Cod from the two habitats got different results from the mixing model, where small krill was the main prey for the demersal cod, while large crustaceans such as the crab *Hyas* sp. were the most important for the sub-littoral cod (Fig. 5). For the understanding of the ecology of cod this is of course very interesting. Unfortunately we did not have estimates of biomass for the sub-littoral cod, and therefore calculating how large a proportion of the population the sub-littoral cod represents was impossible. Thus we only included the results from the demersally caught cod in the Ecopath model assuming these to be representative of a larger proportion of the total population. Knowing how large a proportion of the total population inhabits the sub-littoral zone, and at what size they migrate to the deeper areas, assuming they do, would be interesting, and could have been included in the Ecopath models for Ullsfjord and Sørfjord.

For lower trophic level groups like krill, the mixing model gave us information on diet proportions where we did not have GCA data and thereby increasing the use of local data. Unfortunately we did not have local samples of all possible prey species, and this would have improved the robustness of the calculations.

The group called small gadoids included the species Norway pout, silvery pout, whiting and blue whiting. Whiting and blue whiting grow larger than Norway pout and silvery pout, and are more picivorous. According to the mixing model results, whiting had a diet proportion of

0.15 on the other small gadoids. Still, Norway pout and silvery pout have much higher biomasses than the two other species, so when weighting the diet by the biomasses in the trawl the whiting and blue whiting became relatively unimportant compared to Norway pout and silvery pout. One could argue that it would have been better to split these species into two groups in the Ecopath model; (1) piscivorous gadoids: whiting and blue whiting, and (2) planktivorous gadoids: Norway pout and silvery pout, to better represent the different species and possible predator-prey interactions. However, there is the question of available data and added uncertainty by including more groups.

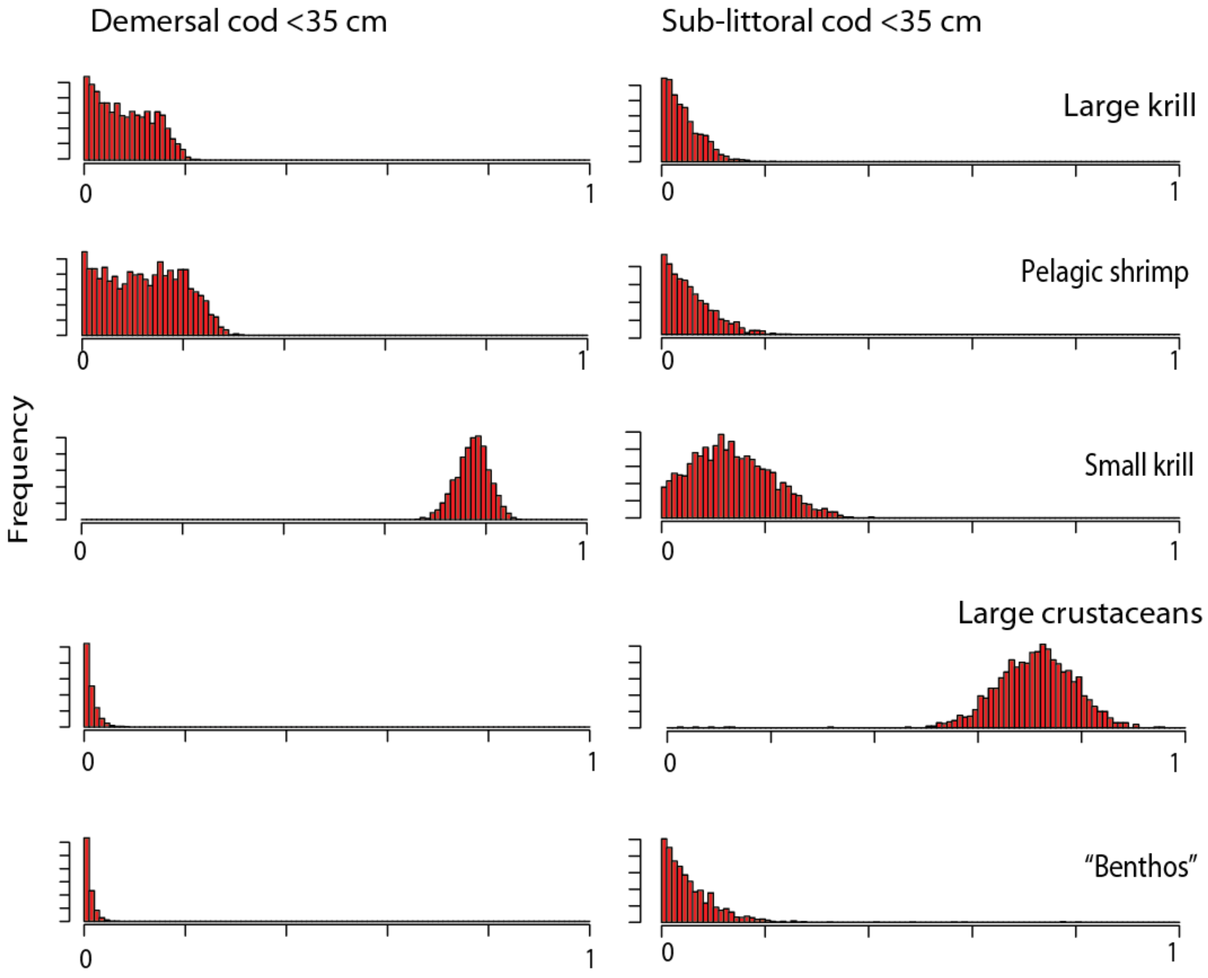

Fig 5, MixSIR output small cod (< 35cm) from Ullsfjord, cod caught in the demersal zone by trawl (> 125 m) on the left and by fishing rod or net in the sub-littoral zone (< 50m) on the right. “Benthos” includes mussels, ophiurids, and polycheates.

4.2 Comparative ecosystem analysis

4.2.1 Community measures reflecting trophic stucture from SI and Ecopath

In the comparative study (MS2) of two adjacent fjord systems using Ecopath, ecosystem indicators were calculated from the model and used as measures of trophic structure. We used for example **connectance index**: defined for a given food web as the ratio of the number of actual links to the number of possible links (Christensen & Walters 2004), **system omnivory index**: a measure of how the feeding interactions are distributed between trophic levels. An omnivory index is also calculated for each consumer group and is a measure of the variance of the trophic level estimate for the group (Christensen & Walters 2004). From stable isotope signatures there are also available a number of community-wide measures of trophic structure. Layman et al. (2007) suggested several measures, described in Box 1.

Navarro et al. (2011) used some of these SI-based measures to compare with the output of Ecopath models. When comparing the total isotopic area (TA) for each Ecopath group with the omnivory index calculated by Ecopath, they found no correlation between the two metrics of trophic diversity. We did the same comparison, and did not find any significant (5% level) correlation either (Spearman's rank correlation: p = 0.16, rho = -0.30) (Fig. 6). However it was not necessarily expected that TA and omnivory index should be correlated. The omnivory index in Ecopath is a measure of how generalist or specialist a species is (Christensen & Walters 2004), and provided the data comes from gut content analysis, this is true if we have many samples. The isotopic TA of a generalist species will not necessarily increase if all the sampled individuals have diverse but similar diets. They may have similar SI signatures and therefore a small TA but a high Ecopath omnivory index. While if a group is composed of many individual specialists feeding on different trophic levels and on prey with different carbon signatures, the TA will be large, as will the omnivory index in Ecopath. Several of the Ecopath groups in our analyses are functional groups with several species and I expect this will influence the omnivory index and the TA in the same way if species have different diets.

The TA of a species or model group could however be very useful as a description of the data before using a mixing model. A high TA means we have high variation in diet and this needs to be considered before applying a mixing model. The benthic invertebrate groups proved difficult to use MixSIR on, and the TA of some of these groups is very high (Fig. 6). In MS3 we discuss the challenges in using the mixing model on the benthic invertebrate groups, and the main reason this did not work was because of very large variation in the stable isotope signatures of benthic invertebrates. In Ecopath all detritus, including discard from fishing vessels is assigned to TL1, however the stable isotopes will not necessarily reflect TL1. The group detrivore echinodermata (#33) has the highest isotopic TA, and this could be because of differences in feeding mode, as well as enrichment in the signature of detritus by bacterial degradation (Macko & Estep 1984). Also, it is not so easy to make uniform groups of species, so it could be debated whether all the species in this group are in fact detritus feeders. Large cod (#6) also had a relatively high TA, and this can have been influenced by individual specialists and a high sample number spanning many length groups and therefore be expected to have different diet composition giving a high TA.

By calculating community-wide measures the trophic complexity of an ecosystem can be characterized by continuous variables that can be used to compare ecosystems between time periods or across systems. Of course, they depend on the ecosystems being structured and sampled in comparable manners (Layman et al. 2007); to be able to compare ecosystems quantitatively it is necessary to have a common structure, or differences in ecosystem indicators cannot be separated from model differences (Coll et al. 2006). Sørfjord and Ullsfjord have been sampled in similar ways as this project has been conducted with several of the same scientists and the aim of making it possible to compare the two systems. Nilsen et al. (2008) analysed stable isotope samples from Sørfjord to compare with the trophic level calculated from the Ecopath model, and these values can be used to compare with Ullsfjord (Table 1). The nitrogen range is slightly higher in Ullsfjord, indicating a longer food chain with more trophic levels; however we did not have stable isotope data on the top predators birds and mammals in either ecosystem, and these are the groups with the highest TL in the Ecopath model. In MS2 we suggest that Ullsfjord has higher trophic redundancy than Sørfjord and this is supported by the stable isotope data with Ullsfjord having a slightly lower distance to centroid and mean nearest neighbour. Especially the fish groups have similar isotope signature in Ullsfjord, and this is also discussed in MS1, and Ullsfjord has a slightly lower standard deviation of mean nearest neighbour indicating a less even species packing. This could be attributed to the fish groups being close together in the isotope bi-plot (Fig. 6) while the benthic invertebrate groups are very spread out.

Table 1, different metrics proposed by Layman et al. (2007) as measures of diversity and structure from isotope signatures and some measures related to diversity from Ecopath (EwE) from Ullsfjord and Sørfjord.

Metrics/Location	*Sørfjord*	*Ullsfjord*
Nitrogen range, NR	9.36	10.24
Carbon range, CR	6.67	7.55
Total isotopic area, TA	46.12	50.96
Mean distance to centroid, DC	2.48	2.39
Mean nearest neighbour, MNN	0.60	0.56
Standard deviation of MNN, SDMNN	0.59	0.71
Centroid, ($\delta^{13}C$, $\delta^{15}N$)	-18.28, 11.14	-19.11, 11.13
TL range (EwE)	4.54	4.51
Omnivory index (EwE)	0.178	0.183
Connectance index (EwE)	0.154	0.168

Box 1

Nitrogen range (NR): Distance between the most enriched and the most depleted $\delta^{15}N$ values (maximum $\delta^{15}N$ – minimum $\delta^{15}N$). A larger range in $\delta^{15}N$ suggests more trophic levels.

Carbon range (CR): The distance between the most enriched and the most depleted $\delta^{13}C$ values (maximum $\delta^{13}C$ – minimum $\delta^{13}C$). A large CR would suggest an ecosystem with multiple sources of primary production and varying $\delta^{13}C$ at the base of the food web. This will then give room for niche diversification.

Total isotopic area (TA) is the convex hull area from the $\delta^{13}C$ - $\delta^{15}N$ bi-plot of all the species. This is a representation of the total niche space occupied and can be used as a "proxy for the total extent of trophic diversity within the food-web". The TA is highly influenced by outliers as it only uses "the extremes" of the data.

Mean distance to centroid (DC) is the average Euclidean distance of each species to the $\delta^{13}C$ - $\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and $\delta^{15}N$ value for all the species in the food web. This provides the average degree of trophic diversity within the food web and is less influenced by outliers as it includes all data in the dataset, and not only the periphery.

Mean nearest neighbour distance (NND) is the mean Euclidean distance between each species and its nearest neighbour in the bi-plot space. A food web with many species occupying similar niches will have a small NND and so this can be used as a measure of high trophic redundancy.

Standard deviation of nearest neighbour distance (SDNND) is a measure of the evenness of species packing in the bi-plot space. The SDNND is less influenced than NND by sample size. A low SDNND value suggests more even distribution of trophic niches.

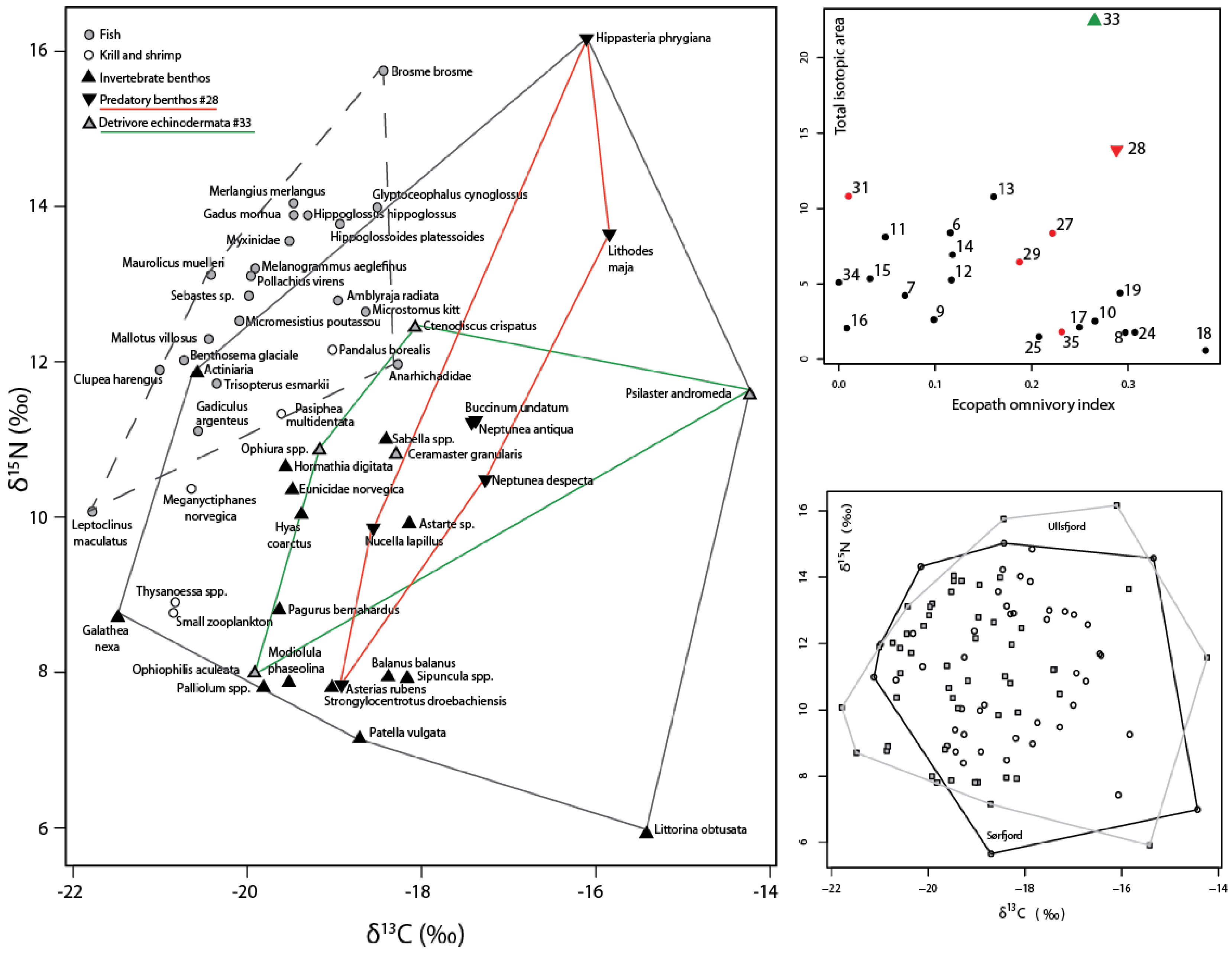
Fish
Krill and shrimp
Invertebrate benthos
Predatory benthos #28
Detrivore echinodermata #33
δ15N (‰)
δ13C (‰)
16
14
12
10
8
6
-22
-20
-18
-16
-14
Hippasteria phrygiana
Brosme brosme
Merlangius merlangus
Glyptocephalus cynoglossus
Gadus morhua
Hippoglossus hippoglossus
Myxinidae
Hippoglossoides platessoides
Lithodes maja
Maurolicus muelleri
Melanogrammus aeglefinus
Pollachius virens
Sebastes sp.
Amblyraja radiata
Microstomus kitt
Micromesistius poutassou
Ctenodiscus crispatus
Mallotus villosus
Pandalus borealis
Benthosema glaciale
Actiniaria
Anarhichadidae
Clupea harengus
Trisopterus esmarkii
Psilaster andromeda
Gadiculus argenteus
Pasiphea multidentata
Buccinum undatum
Neptunea antiqua
Sabella spp.
Ophiura spp.
Ceramaster granularis
Hormathia digitata
Neptunea despecta
Eunicidae norvegica
Meganyctiphanes norvegica
Leptoclinus maculatus
Hyas coarctus
Astarte sp.
Nucella lapillus
Thysanoessa spp.
Pagurus bernahardus
Small zooplankton
Galathea nexa
Modiolula phaseolina
Balanus balanus
Ophiophilis aculeata
Sipuncula spp.
Palliolum spp.
Asterias rubens
Strongylocentrotus droebachiensis
Patella vulgata
Littorina obtusata
Total isotopic area
Ecopath omnivory index
0
5
10
15
20
0.0
0.1
0.2
0.3
33
28
31
13
11
6
27
14
29
34
15
12
7
19
9
17
10
16
8
24
18
25
35
δ15N (‰)
δ13C (‰)
Ullsfjord
Sørfjord

Fig. 6, Large fig: Stable isotope signatures (mean) of all species in Ullsfjord, total area of the groups Predatory benthos (#28, in red) and Detrivore echinoderms (#33, green), added to compare with total area of all fish (stippled line) as well as all invertebrate benthos (black line). Upper right: Total isotopic area for each Ecopath group where we had SI data, plotted against omnivory index calculated by Ecopath, benthic invertebrate groups are displayed in red or equivalent to the large figure on the left. Lower right: The total isotopic area of Sørfjord and Ullsfjord, the points are species, and values are corrected according to lipid normalisation equation (eq. 2) by Post et al. (2007).

4.2.2 Diversity, structure and stability

An important discussion in ecology is how diversity and structure influences stability of an ecosystem. It has for long been assumed that diversity increases stability (Elton 1927) and that “stability increases as the number of links increase” (MacArthur 1955). In more recent years, the mechanisms behind this have been debated (e.g., Yodzis 1981, Neutel et al. 2002). Trophic redundancy is expected to increase stability; if one species disappears another will be able to fill its niche (Andersen & Pedersen 2010). Top predators couple fast (pelagic) and slow (detrital) energy channels in food webs and this has been shown to improve stability (Rooney et al. 2006, McCann & Rooney 2009, Rooney & McCann 2012). The fast phytoplankton channel is more productive than the slow detrital channel (Rooney & McCann 2012) and the linking of the two channels provides stability. Another explanation for increased stability is that the benthic compartments have more complex habitats than the homogenous pelagic zone, and supports niche diversification, and that this increases stability of an ecosystem (Rooney & McCann 2012). Plotting trophic level against proportion of detritus flow to each group in Ecopath creates an overarching structure for Ullsfjord and Sørfjord (Fig. 7) where the top predators, seabirds, mammals and some of the large fish groups, couple the pelagic- and the benthic channel together. The top predators may also “switch” between the two channels (McCann et al. 2005, Rooney et al. 2006) and haddock may be an example of this. All manuscripts showed how haddock preys on pelagic prey in Ullsfjord, while in Sørfjord, haddock were preying mostly on benthic invertebrates (MS2 and Pedersen et al. (2008)). In fig. 7 haddock is displayed in red and shifts from the detrital channel in Sørfjord (a) to the pelagic channel in Ullsfjord (b). Ullsfjord is overall more dependent on the pelagic than Sørfjord, as expected from the topography as well as the species composition. There are some analogies between this “channel theory” and the isotopic carbon range as an increasing carbon range means there are several sources of primary production to the system, macroalgae, phytoplankton and terrestrial sources, and this can give room for niche diversification (Layman et al. 2007). Ullsfjord has a slightly higher isotopic carbon range, and this could indicate a more stable ecosystem than Sørfjord. In MS2 we argue that increased web like structure and higher species diversity gives Ullsfjord a higher stability than Sørfjord. One could test the stability of the ecosystem models using the dynamic component of Ecopath, Ecosim, by modelling a perturbation in both ecosystems, and observing the recovery rate. This would be a task for future investigations.

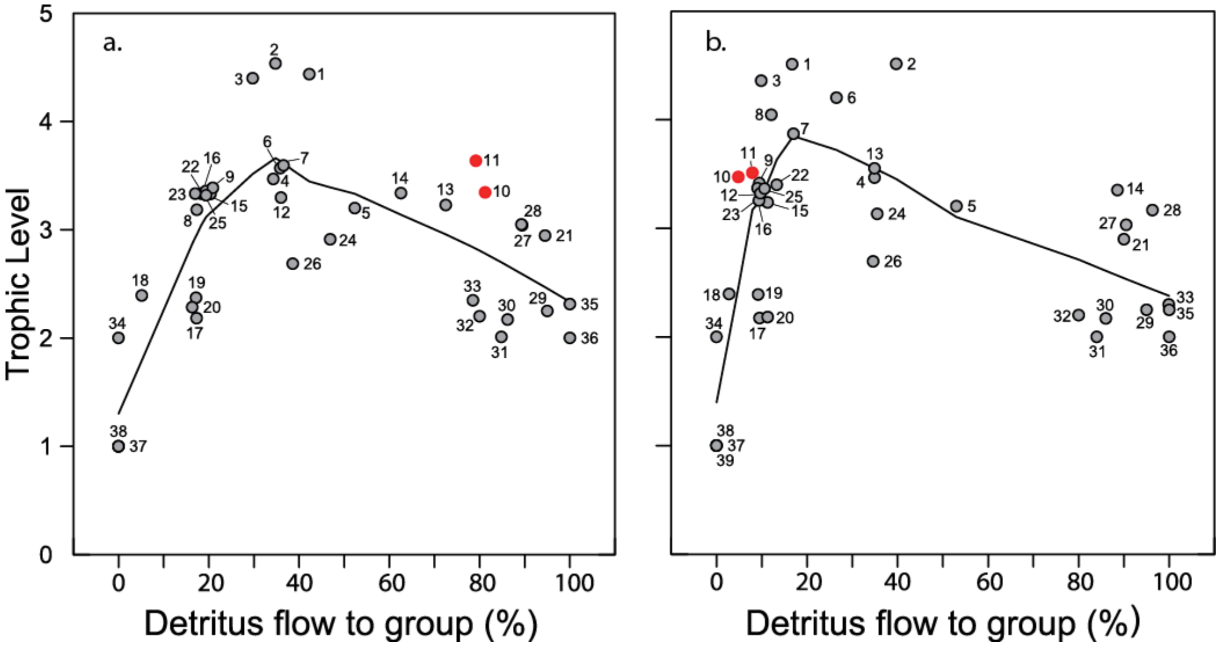

Fig. 7, Proportion of detrital flow to each Ecopath group versus trophic level and the line is a lowess smoother. Haddock is shown in red to display how predators can shift between the detrital and the pelagic channel. a. Sørfjord and b. Ullsfjord. Group numbers as in Table 1 in MS3.

4.3 Uncertainty in ecological modelling

Article 10, National research ethical committee for natural sciences and technology (NENT), Guidelines:

> "The researcher should clearly communicate what certainty and precision is connected with his or her research results. The scientist should especially be thorough in describing the findings' relative area of safety and validity and he or she should strive to point out any potential risk or uncertainty that may be of significance for the use of the results" (National research ethical committee for natural sciences and technology 2007)

All models are simplifications of the real world and we cannot model everything. This is referred to as reductionism. To cite Ivanovic and Freer (2009) "the only way … to understand and represent all processes absolutely, would be to run the universe at the universe scale!". We have to ask ourselves: What is the objective of the model? What data are available? Does increasing the number of groups increase model performance or just add uncertainty? Model complexity is a compromise between model resolution and data requirements.

In MS2 we estimated confidence intervals for estimates of biomass from trawl catches and from bird-counting transects (input data) and used these estimates of uncertainty as input to an Ecoranger routine (from the 5.0 version of Ecopath) to estimate how uncertainty affects the output from the model. This showed that uncertainty in the output from the model was similar to the uncertainty in the input, in accordance with what has been reported by Essington (2007). Morissette (2005) evaluated the Ecopath modelling software and examined the uncertainty issue in ecological modelling by looking at sensitivity analysis and other tools that have been suggested as a standard approach to hopefully detect large sources of uncertainty. She concluded that "uncertainty and variability are inherent in the very nature of ecosystem modelling", and suggests that the only way to gain more robustness is to combine several approaches. Using both stable isotopes and gut content analysis should reduce uncertainty on the diet of the animals. Ecopath has a built in possibility to evaluate all the parameters in the model and assign an uncertainty to every estimate of biomass, production and other measures. Then an overall pedigree index is calculated. For the 2010 model for Ullsfjord, this was 0.521 for the GCA model and 0.557 for the SI-based Ecopath model. This slight increase in pedigree index was lower than expected; however, what uncertainty to assign to each parameter is somewhat subjective. For example, two of the categories to assign for biomass estimates are “sampling based, high precision” and “sampling based, low precision”. The difference could just depend on how certain the scientist is of his or her sampling routine. The overall pedigree index may be helpful and informative for a fellow Ecopath-user; however it will not be very useful to anyone else, especially not a non-scientist.

Article 11 in the NENT guidelines (2007) states that scientists should strive to contribute with knowledge relevant for the use of a precautionary approach. I think it is safe to say that even if we make large efforts on communicating the uncertainties in our results and models, we also have a responsibility to communicate what our findings mean and to make sure they are not misunderstood, misinterpreted or misused.

In summary

This discussion has hopefully shown how using stable isotopes in combination with gut content analysis and ecological modelling is a way of improving our knowledge base. On every level from individual to species to ecosystem, the stable isotopes can provide information. We have shown how we can detect an ontogenetic niche shift, or detect possible niche overlaps. We can calculate trophic level from the nitrogen isotope and what a species preys on by using a mixing model. We can use the stable isotopes to calculate community wide measures of trophic diversity and structure of a food web, and for all of these measures we have presented alternative methods to use to compare and thereby increase robustness of our conclusions.

4.4 Future research

Cod and haddock, as well as all other fish that grow to a large size, feed on different prey as young-of-the-year (YOY) than they do later in life. They also have different predators at this stage and are an important source of food for fish and seabirds. The habitats may also be different from when they reach larger sizes. However including this in a realistic way in an Ecopath model is a major challenge. This would first of all require data on different life stages, and it seems to be difficult to represent the rapid growth. This is a challenge for future work. As discussed earlier we don't have good methods for estimating biomass of fish in the sub-littoral zone. This zone is somewhat "left out" of the ecosystem model even if we know there are species of fish, crustaceans, gastropods and echinoderms there that in addition to being interesting from an ecological point of view, many of them may be important for the early life stages of the commercial species as well. We did video transects for estimating sea urchin abundance and this is a good method for surveying the sub-littoral zone. However, we are not able to estimate biomasses of these species without a larger effort in field surveys.

Ecosystem models like Ecopath show great potential in being used for a more Ecosystem based Management. The models are relatively easy to develop for areas where large scale commercial fishing takes place, as most of the data will be available from the fishing fleet. The models can be used to evaluate management strategies, to look at temporal variations of several stocks (predator prey fluctuations), to compare areas, etc. The models do not replace the single-stock or multispecies models that are used for stock estimates but can be used for more strategic purposes.

I also hope that collecting stable isotope samples will become routine on ecosystem surveys where stomach data is already being collected as this will supply more information. The samples are easy to collect and can be stored frozen so there is little effort required in the field. Potentially this could be used to gain more insight in the diet of for example early life stages of commercial fish species, small prey such as zooplankton and any other species that is not routinely sampled for gut content analysis.

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Paper 1

Paper 2

Paper 3

ISBN xxx-xx-xxxx-xxx-x