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Species diversity affects ecosystem structure and mass flows in fjords

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ABSTRACT

Latitude and temperature have been hypothesized to influence species richness, diversity and trophic control (top-down vs. bottom-up) in marine ecosystems. Ecosystem structures and mass flows of two moderately exploited fjord ecosystems with different temperatures and species diversity were compared. The Ullsfjord and Sørfjord systems (69°–70° N) are located between the relatively simple, low-diversity arctic Barents Sea in the north (71°–80° N) and the more species-rich and temperate North Sea (51°–62° N) in the south. Ullsfjord is the outer part of the fjord system and is deeper, warmer and more diverse than Sørfjord. Ecopath mass-balance models containing 40 ecological groups were developed for Ullsfjord and Sørfjord for the time period 1993–96. To obtain input data, abundance and diet of top-predators, fish, pelagic and benthic invertebrates were investigated. In the more diverse Ullsfjord system, large krill and pelagic shrimps were abundant and lower trophic level groups (TL < 3) had the highest keystoneness, suggesting importance of bottom-up control. In contrast, large cod had the highest keystoneness and a large top-down effect as predator on small fishes and the larger crustacean groups in Sørfjord. For the diverse benthic invertebrates, the warmer and faster system (Ullsfjord) had higher mortality rates, shorter life spans and lower biomass (6.3 vs. 9.2 g C m^{-2}) than the colder system (Sørfjord), but production (3.2 vs. 3.6 g C m^{-2} $year^{-1}$) was similar in the two systems suggesting bottom-up control of benthic invertebrates.

1. Introduction

Biodiversity have been thought to affect ecosystem functioning (Raffaelli, 2006), and knowledge about the relationship between diversity and food-web structure is important to understand ecosystem dynamics (Rooney and McCann, 2012). Latitude and temperature have influence on species richness, diversity and trophic control (top-down vs. bottom-up) in marine ecosystems (Frank et al., 2006, 2007). Warmer and lower latitude ecosystems generally have higher fish species richness and diversity (Macpherson and Duarte, 1994; Macpherson, 2002), and this has been suggested to favour bottom-up control, while top-down control may be more common in less diverse and colder ecosystems at higher latitudes (Frank et al., 2006, 2007). Atlantic cod (*Gadus morhua* L.) has been an important fish predator and commercial species in Atlantic temperate and high-latitude ecosystems, but many cod stocks have decreased due to overexploitation (Savenkoff et al., 2007; Link et al., 2009; Brander, 2010). The role of cod as top-predator and how cod interact with prey resources is much debated (Van Leeuwen et al., 2008). In cold marine ecosystems, intermediate-sized fish species tend to be scarce and the systems are dominated by small and large fish species such as capelin *(Mallotus villosus)* and cod (Pope et al., 2009). Small and intermediate sized gadoids like Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*) and whiting (*Merlangius merlangius*) have been very common in the more temperate North Sea (Bergstad, 1990; Daan et al., 1990), but have been less abundant in the colder Barents Sea (Bergstad et al., 1987; Fossheim et al., 2006; Byrkjedal and Høines, 2007; Johannesen et al., 2012a).

The Ullsfjord–Sørfjord (69–70°N) area is located between the arctic Barents Sea in the north and the temperate North Sea in the south (Daan et al., 1990; Fossheim et al., 2006), at the coast of northern Norway and may be expected to possess characteristics

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intermediate to the Barents and the North Sea, and also to be influenced by the coastal environment. Sørfjord is the inner, shallower and colder part of the fjord system, and a mass-balance ecosystem model of this lightly exploited fjord shows that Atlantic cod (*Gadus morhua* L.) is the main keystone and the major consumer of other fish species (Pedersen et al., 2008). Ullsfjord is the outer coastal connected, warmer and deeper fjord (Zhou et al., 2005), and has a larger number of fish species than in the inner Sørfjord (Nøstvik and Pedersen, 1999a). The cod stocks of Sørfjord and Ullsfjord are relatively stationary within their fjord and differ with regard to growth rate, size at maturity and year class variability (Nøstvik and Pedersen, 1999b; Berg and Pedersen, 2001). Spatial integrity of the two fjord systems is also indicated by the difference in species composition of euphausiids; while the smaller species *Thyssanoessa* sp. are common in both systems, the larger *Meganyctiphanes norvegica* is only common in Ullsfjord (Zhou et al., 2005).

In addition to fishes, a number of other marine taxa including both benthic and pelagic invertebrates show a decrease in species richness towards high latitudes (Macpherson, 2002; Willig et al., 2003). Latitudinal gradients in zooplankton diversity have been suggested to affect fish abundance (Beaugrand et al., 2010), but there is little knowledge of effects of differences between ecosystems in species diversity on structure and mass flow patterns in the systems. The comparative ecosystem approach has been applied to investigate the relative influences of human-induced, environmental and climatic effects on marine ecosystems (Coll et al., 2008; Megrey and Aydin, 2009; Morissette et al., 2009). Comparison of large marine ecosystems have given insight into factors affecting ecosystem structure (Lasalle et al., 2013; Whitehouse et al., 2014).

The main objectives of this study were to investigate and compare ecosystem structure, mass-flow patterns and keystoneness patterns in two closely situated fjord ecosystems with different species diversity, with emphasis on fish, invertebrate benthos and crustaceans. Our main hypotheses were that; (1) diversity differences affect ecosystem structure, (2) cod have lower keystoneness in the more diverse ecosystem, (3) production of fish, crustaceans and invertebrate benthos will be equal in the two systems. The approach adopted in this study was to develop an Ecopath model for Ullsfjord for the time period 1993–96 and compare this model to an updated published model with the same group configuration for the lightly exploited and cod-dominated Sørfjord system for the same time period (Pedersen et al., 2008). To obtain input data for the Ullsfjord model, data on top-predators, fish, pelagic and benthic invertebrates were sampled, and trophic interactions and population dynamics were investigated.

2. Materials and methods

2.1. Study sites and fishery exploitation

The Ullsfjord and Sørfjord (69°N, 19°E) area is located in Troms County, northern Norway (Fig. 1). The average tidal amplitude in the area is 1.60 m and a 300 m wide and 8 m deep sill separates Ullsfjord and Sørfjord (Fig. 1). Ullsfjord has an area of 412 km^2 compared to 55 km^2 for Sørfjord. In Ullsfjord, which has a maximum depth of 270 m, the bottom water have temperatures >5.5 °C and salinity higher than 34.0 (Zhou et al., 2005). Sørfjord has a maximum depth of 130 m and during winter the water column is vertically mixed and the water temperature and salinity in winter may range from 0 to 3 °C and 33 to 34, respectively (Zhou et al., 2005; Pedersen et al., 2008). During 1990–96, annual average water column temperature in Sørfjord was 4.1 °C with 2.5 °C amplitude (Pedersen et al., 2008). During spring and summer surface water becomes stratified due to river run-off and heating

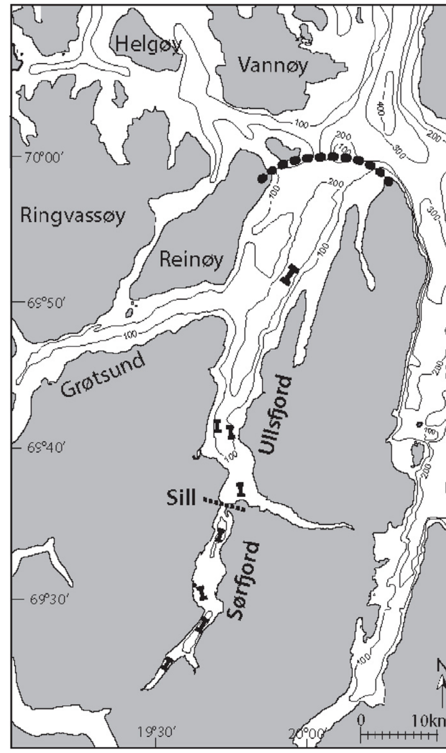

Fig. 1. Overview of the Ullsfjord and Sørfjord systems. Thick stippled lines show outer boundaries for the area for the Ullsfjord 40 group model for 1993–96. Bars show locations for bottom trawl hauls. Shallow sill between Ullsfjord and Sørfjord is shown by thin stippled line.

and in summer and autumn, the surface temperatures in Ullsfjord and Sørfjord are similar in the upper 30 m (Zhou et al., 2005).

During 1993–96, the large gadoids Atlantic cod, haddock and saithe were the main targets for exploitation. Small boats (<11 m length) exploited fish using gill-nets, long-line and hand-line. Groundfish commercial trawling was prohibited, but shrimp trawling aimed at deep-water shrimp (*Pandalus borealis*) using trawls equipped with sorting grids to avoid fish capture was allowed in Ullsfjord, but not in Sørfjord.

2.2. The Ecopath model

The Ecopath model approach assumes mass balance and uses a set of linear equations for all compartments *i* in the ecosystem and estimates trophic flows among the compartments (Christensen et al., 2005). It is expressed by a mass-balance equation:

$$B_i \left(\frac{P}{B}\right)_i = \sum_j B_j \left(\frac{Q}{B}\right)_j DC_{ji} + Y_i + E_i + BA_i + B_i \left(\frac{P}{B}\right)_i (1 - EE_i) \quad (1)$$

where B_i is the biomass of group *i* in g C m^{-2} year^{-1}, $(P/B)_i$ is the production/biomass ratio of group *i*, B_j is biomass predator *j* in g C m^{-2}, $(Q/B)_j$ is the consumption/biomass ratio of the predator *j*, DC_{ji} is the fraction of prey *i* in the diet of predator *j*, Y_i is the catch of group *i*, E_i is the export of group *i*, BA_i is the biomass accumulation of group *i*, and *EE* is the ecotrophic efficiency which is the proportion of production of group *i* that is consumed by compartments within the model, caught by fisheries or exported from the system. For each group, energy balance is ensured when consumption by group *i* equals production, respiration and unassimilated food of *i* (Winberg, 1956). Diet compositions,