

Comparing pristine and depleted ecosystems : the Sør fjord, Norway vs the Gulf of St. Lawrence, Canada. Effects of intense fisheries on marine ecosystems.

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Abstract

The Sør fjord, Norway, and the Gulf of St. Lawrence, Canada, are two sub-arctic ecosystems with similar trophic structure. However, in the Gulf of St. Lawrence, severe exploitation of groundfish stocks has led to important shifts in the trophic structure. In the Sør fjord, the situation is different: fishing pressure is much lighter. Our hypothesis is that overexploitation leads to changes in the trophic structure and severely alters the resilience of ecosystems. Based on the same modelling approach (*Ecopath with Ecosim*) the food web structure was compared, using different ecosystem indicators. Patterns of food web structure and trophodynamics were contrasted. The keystone species in both ecosystems is cod. In both ecosystems, forage fish are also important. Even after similar environmental changes in both ecosystems, and after a reduction of fishing pressure in the Gulf of St. Lawrence, there is no recovery of cod stocks in this ecosystem. In the Sør fjord, after different perturbations (but not from the fishery), the ecosystem seems to return to his equilibrium.

Keywords

Sør fjord, Gulf of St. Lawrence, *Ecopath with Ecosim*, Fisheries, Ecosystem approach, cod

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Introduction

High latitude ecosystems have historically hosted the largest then densest cod (*Gadus morhua*) stocks (Brander 1995; Myers *et al.* 2001). Nevertheless, in recent years, most cod stocks have steeply declined because of heavy exploitation (Garrod and Schumacher 1994; Christensen *et al.* 2003). In the Northern Gulf of St. Lawrence (NGSL), for example, fishing moratoria were imposed in 1994 by the Canadian government to promote the recovery of these depleted fish populations (Anonymous 1994). Ended in May 1997, this moratorium resulted in a modest improvement in the abundance of mature cod in the Northern Gulf of St. Lawrence, and since the re-opening of directed cod fisheries in this ecosystem, mature cod biomass has remained roughly constant (Fréchet *et al.* 2005) (Figure 1).

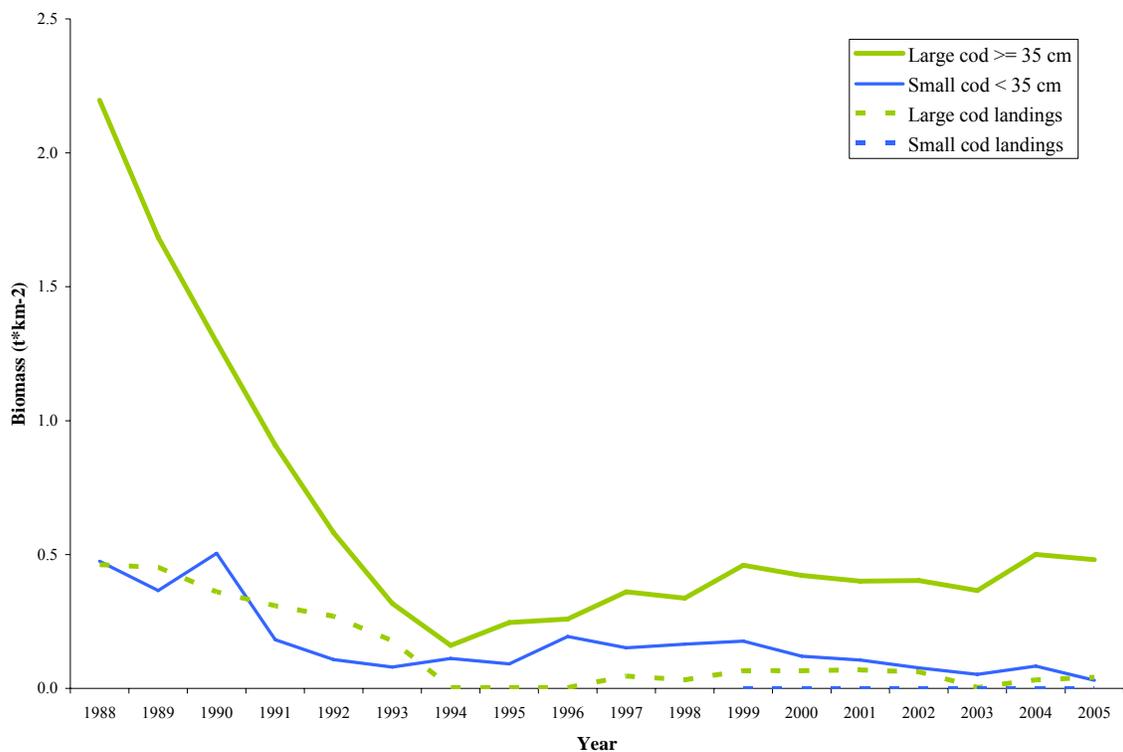


Figure 1. Collapse of cod biomass (wet weight) in the Northern Gulf of St. Lawrence.

Many studies have tried to address this issue in the North Atlantic; first by using single-species approach (Nakken 1994; Lambert and Dutil 1997), then via ecosystem

approach (Christensen 1995; Bundy 2005; Frank *et al.* 2005), always with the aim of trying to explain what really happens in the food-web that would explain this important collapse of groundfish stocks.

In contrast, few quantitative studies have investigated food-web structure in lightly exploited ecosystems of high latitude. One of the few ecosystems studied in that sense would be Sør fjord, which can be considered as a lightly exploited food-web of high latitude ecosystem (Pedersen *et al.*, submitted). Indeed, in this ecosystem, the cod stock have returned to a relatively stable state after being pertubated (Pedersen and Pope 2003a,b). During 1986-1988, large numbers of harp seals from the Barents Sea migrated south along the Norwegian coast and also invaded the Sør fjord where they mainly fed on fish including cod (Nilssen *et al.* 1992). In 1989 after the harp seal had left the Sør fjord system, the cod stock in Sør fjord was very low, but high cod recruitment and low fishing mortality contributed to a rapid recovery of the stock during the early 1990'ies (Pedersen and Pope 2003a,b).

Heavy exploitation of top predators and commercial fish species may induce trophic cascades effects leading to deteriorating effects on the fishery itself and possibly on other components of the ecosystem (Pauly *et al.* 1998; Worm and Myers 2003; Frank *et al.* 2005).

In this study, the software *Ecopath with Ecosim (EwE)* was used to develop models for NGSL and Sør fjord ecosystems, for the period 1994-1996 after the collapse of demersal fish stocks in the NGSL, and the analogous period (1993-1996) in Sør fjord. The objective was to use modeling as a common and central approach to determine if the intensity of fishing exploitation could lead to significant variations in the patterns of food web structure and thus explain why cod stocks and ecosystems have different dynamics and structure in a heavy *versus* light exploitation context.

The use of a common modeling approach represents an asset to this research, allowing an assessment of the two ecosystems' ecology as well as their differences and similarities. Since *EwE* is a widely used approach, it is also possible to compare the following results with other published models from different ecosystems.

Material and methods

Study areas

Sørfjord (69°35'N, 19°45'E) is situated in Tromsø County, northern Norway, and is the inner part of the Ullsfjord-Sørfjord system (Figure 2). A 300 m wide and 8 m deep sill separates Sørfjord and Ullsfjord (Figure 2), and the average tidal amplitude is about 1.60 m. The fjord has three basins and a total area of 55.2 km². The outer basin with a maximum depth of 125 m is subject to extensive vertical mixing due to the strong tidal currents over the sill. The midfjord basin has a maximum depth of 65 m, and the inner basin has a maximum depth of 130 m (Figure 2). The extent of the vertical mixing decreases with the distance from the sill. Freshwater runoff and surface warming during summer create a vertically stratified water column in the inner deep basin with colder water (< 3°C) below 50 m depth, and temperatures of 9-13°C in the upper 20 m (Sælen, 1950; Heimdal, 1974). During the period 1990-96, average water column temperature was about 2.5°C with an yearly amplitude of ca 2.5°C. More details on the hydrography are given by (Soot-Ryen, 1934; Sælen, 1950; Heimdal, 1974). For a more detailed description of the investigation area and the sampling of fish, see Kanapathippillai *et al.*, (1994), Berg and Pedersen, (2001) and Pedersen and Pope (2003).

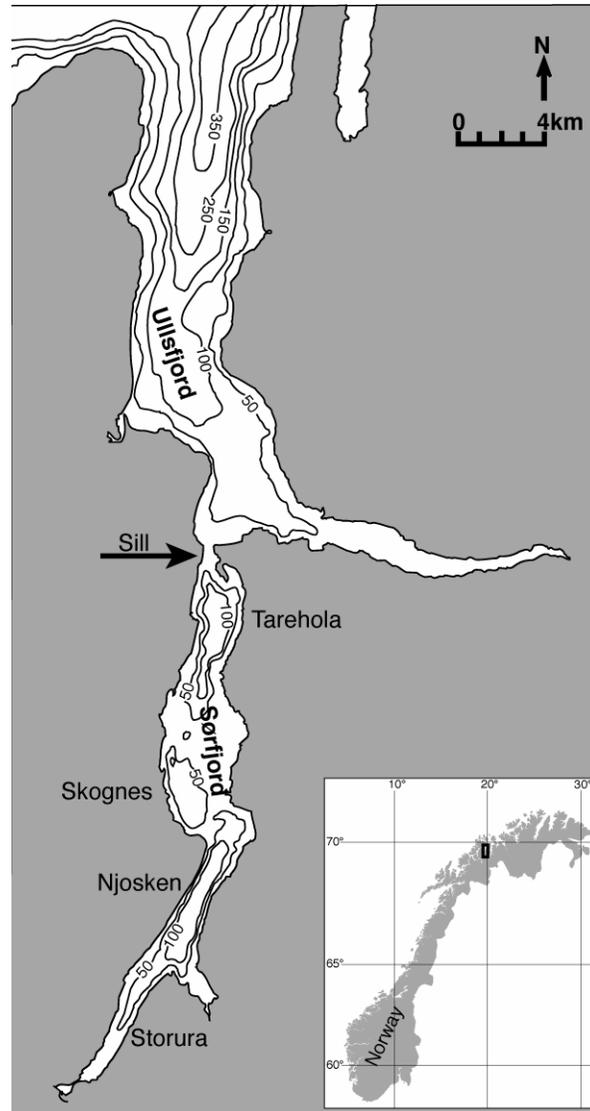


Figure 2. Map of the Ullsfjord/Sørfjord area.

The Gulf of St. Lawrence forms one of the most important estuarine shelves in the world (Therriault 1991). It is the outlet of the St. Lawrence River into the Atlantic Ocean via the Strait of Belle Isle, in the north between Newfoundland and Labrador, and Cabot Strait in the south (Figure 3). At its widest, the Gulf extends roughly 500 km from north to south. The northern and southern parts have very different bathymetric characteristics and, to some degree, different faunas. The Southern Gulf of St. Lawrence (SGSL) (Northwest Atlantic Fishery Organization [NAFO] division 4T) is a relatively shallow shelf (generally < 60 m deep; maximum depth 130 m), with a total area of 64,075 km², and a permanent cold water layer that is in contact with the sediments in water 35 to 100 m deep (Gilbert and Pettigrew 1997) (Figure 3). In contrast, the Northern Gulf of St.

Lawrence (NGSL) (NAFO divisions 4RS) is characterized by channels as deep as 500 m: the Laurentian Channel, which extends nearly 1,000 km from the St. Lawrence Estuary to the Atlantic Ocean, in addition to the Esquiman Channel and the Anticosti Channel (Figure 3). In the NGSL, the study area covered 103,812 km². Depths shallower than 37 m were not included in the NGSL model. The nearshore region was not included in the models because exchanges between infra-littoral and pelagic zones are not well sampled by government scientific survey trawlers; consequently, the community structure of the shallow depth zones is poorly understood.

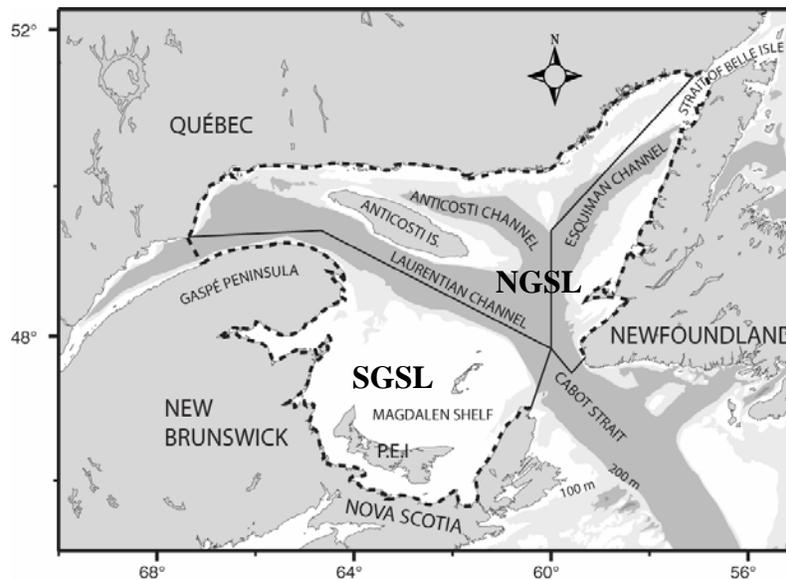


Figure 3. Map of the Northern Gulf of St. Lawrence (NGSL, NAFO zone 4RS).

Additional details of how the original parameters and input variables were estimated are given in the original paper describing the models.

Ecopath modelling

Ecopath is a modelling approach that creates a simple static model to describe the average interactions of the populations within an ecosystem during a certain period. The model assumes mass-balance, i.e., that we account for all flows in a food web. Hence, its parameters can change. Such an approach is much simpler than other attempts to model multispecies interactions such as MSVPA (Sparre 1991) for which an enormous quantity of catch-at-age data and stomach contents analyses is required (Morissette 2001). The

principal advantage with *Ecopath* is that the input values (mainly total mortality, consumption and diet composition) are often already available for several species or groups in the ecosystem, and that they can easily be placed in an ecological model (Christensen and Pauly 1992). *Ecopath* is thus an approach allowing the construction and the rapid evaluation of balanced ecosystem models (Christensen and Pauly 1992).

During the last decades, *Ecopath* models were constructed for more than 270 ecosystems, and more than 55 others are presently under development (Morissette, in prep.). Models were published for ecosystems as diverse as the Peruvian upwelling system (Jarre *et al.* 1991), coral reefs in the Philippines (Aliño *et al.* 1993), the Southern Gulf of Mexico (Arreguín-Sánchez *et al.* 1993), Antarctica (Schalk *et al.* 1993), and Lake Victoria (Moreau *et al.* 1993). This type of modelling was also applied to various uses (comparison of the structure of estuaries (Monaco and Ulanowicz 1997), estimate of the trophic levels (Pauly *et al.* 1995) or the modelling of inundated rice fields in the Philippines (Lightfoot *et al.* 1993).

Because many ecosystems of the world are represented through an *Ecopath* model, it is now possible to carry out comparative analyses between ecosystems modeled with a common approach. In our case, the two *Ecopath* models available allow a comparison of heavy *versus* light exploitation in similar Nordic ecosystems.

Each *Ecopath* model was based on mass balance principles, assuming that production of a given prey group (i) was equal to the biomass lost to fishing or export, predation, and natural mortality other than predation (other mortality). This mass balance can be expressed as:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (1)$$

and

$$\text{Production} = \text{predation} + \text{fishing mortality} + \text{other mortality} \quad (2)$$

where consumption is composed of consumption within the system and consumption of imports (i.e., consumption “outside the system”), and production may be

consumed by predators, be exported from the system or contribute to the detritus (Jarre-Teichmann 1998).

The terms of these equations may be replaced by:

$$\text{Production by } i = B_i * P_i/B_i, \quad (3)$$

$$\text{Predatory losses of } i = \sum_j (B_j * Q_j/B_j * DC_{ij}), \text{ and} \quad (4)$$

$$\text{Other losses of } i = (1-EE_i) * B_i * P_i/B_i \quad (5)$$

For any species or group of species of the system, this leads to the linear equation:

$$B_i * P_i/B_i * EE_i - (\sum_j B_j * Q_j/B_j * DC_{ij}) - Ex_i = 0 \quad (6)$$

where:

i indicates a component (stock, species, group of species) of the model,

j indicates any of the predators of i ,

B_i indicates the biomass of i ,

P_i/B_i indicates the production/biomass ratio, which is equivalent to total mortality (Z) under the most circumstances (Allen 1971),

Q_i/B_i indicates the food consumption per unit biomass of i ,

DC_{ij} indicates the contribution of i to the diet of j (in terms of mass),

EE_i indicates the ecotrophic efficiency of i , or the fraction of production that is consumed or caught within the system,

Ex_i indicates the export of i from the system (by emigration or fisheries catch).

Each group in the model is represented by one balanced equation and requires six input parameters: biomass (B_i), production to biomass ratio (P_i/B_i), consumption to biomass ratio (Q_i/B_i), ecotrophic efficiency (EE_i), diet composition ($\sum DC_{ij}$) and catch by the fisheries. Algorithms included in the model also allow for the estimation of one missing parameter in each group (B_i , Q_i/B_i , P_i/B_i , or EE_i) (Christensen and Pauly 1992).

In the present study, all mass units are given as wet weight (WW, in tonnes per kilometre square), when other units are not provided.

Trophic level decomposition and flows between trophic levels

Both food-web models were depicted by a number of trophic groups, representing the main pelagic, demersal, and benthic species present, which are interconnected by mass flows of matter. The number of compartments was based on data availability and the ecological and commercial significance of species. The NGSL model was divided into 32 ecological groups, while Sørffjord had 27 groups (Table 1). Some groups, such as large pelagic feeders and large demersal feeders in NGSL are composite groups, of similar size and presumed ecological role. On the other hand, species such cod (and Greenland halibut in NGSL only) were each separated into two groups based on diet, age/size at first capture, and age/size at maturity. Finally microbial loop was considered as an important component of the food web. The Sørffjord model treated it as a separate trophic group, while in the NGSL, bacteria was considered part of the detritus compartment, and respiration parameters were included to represent bacteria.

Table 1. Trophic groups used in modeling the NGSJ and Sørkjord ecosystems. Our analysis was based on models constructed by Morissette *et al.* (submitted) for NGSJ and Pedersen *et al.* (submitted) for Sørkjord.

Northern Gulf of St. Lawrence (Morissette <i>et al.</i> submitted)	Sørkjord (Pedersen <i>et al.</i> submitted)
1 Cetacea	1 Mammals
2 Harp seals	2 Cormorants
3 Hooded seals	3 Large cod
4 Grey seals	4 Small cod
5 Harbour seals	5 Large other fish
6 Seabirds	6 Small other fish
7 Large cod	7 Herring
8 Small cod	8 Krill
9 Large Greenland Halibut	9 Small zooplankton
10 Small Greenland Halibut	10 Microzooplankton
11 American Plaice	11 Heterotrophic nano-flagellates
12 Flounders	12 Scyphomedusae
13 Skates	13 Chaetognaths
14 Redfish	14 Shrimps
15 Large demersals	15 Other large zooplankton
16 Small demersals	16 Large crustacea
17 Capelin	17 Predatory benthos
18 Sandlance	18 Detritivore polychaetes
19 Arctic Cod	19 Small benthic crustaceans
20 Large pelagics	20 Small molluscs
21 Pisciv. Small pelagics	21 Large bivalves
22 Plank. Small pelagics	22 Detritivore echinoderms
23 Shrimp	23 Other benthic invertebrates
24 Large crustaceans	24 Bacteria
25 Echinoderms	25 Phytoplankton
26 Molluscs	26 Macroalgae
27 Polychaetes	27 Detritus
28 Other benthic invertebrates (OBI)	
29 Large zooplankton	
30 Small zooplankton	
31 Phytoplankton	
32 Detritus	

Mixed Trophic Impact

The mixed trophic impact (MTI) routine of the *Ecopath* program assesses the direct and indirect interactions between species in the ecosystem and gives an ecosystem overview of the trophic interactions. It synthesizes all the effects that a small change in the biomass of a group will have on the biomass of other groups in a system (Ulanowicz and Puccia 1990). This routine is derived from Leontief economic input-output analysis, and quantifies all the direct and indirect trophic impacts of all groups in the system based

on the assumption that the direct impact between group i and group j can be estimated from the difference between the proportion that group i contributes to the diet of group j , and the proportion that group i takes from the production of group j (Christensen 1995). The MTI for living groups is calculated by constructing a matrix, where the i,j^{th} element representing the interaction between the impacting group i and the impacted group j is:

$$MTI_{ij} = DC_{ij} - FC_{j,i} \quad (7)$$

where DC_{ij} is the diet composition term expressing how much j contributes to the diet of i , and $FC_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i as a predator. When calculating the host compositions, the fishing fleets are included as "predators".

The mixed trophic impact routine was used to evaluate positive or negative impacts that one group might have on another, as well as the magnitude of estimated direct and indirect impacts. This also estimated the relative impact of a change in the biomass of one group on other components of the ecosystem, under the assumption that the diet composition remains constant (Ulanowicz and Puccia 1990).

Ecosystem Properties

Ecopath methods also allow the calculation of many indices that can describe the complexity in the community structure (Christensen 1995). Attributes were selected according to a previous study by Vasconcellos *et al.* (1997), who identified ascendancy, connectance index, and system omnivory index as representative of Odum's attributes of ecosystem complexity (Odum 1971).

The Ascendency of a food web is an index developed from Ulanowicz and Norden's (1990) interpretation of ecosystem structure and dynamics, and gives a good description of a community overall homeostasis. This is computed by *Ecopath* and corresponds to the percentage of possible throughputs that is used for trophic interactions in the ecosystem.

Connectance index (CI) represents the ratio of the number of actual trophic links in the food web to the number of possible links. Consider a contingency table showing all possible trophic interactions in an ecosystem, with r rows (e.g., prey species) and c columns (e.g., predators). Connectance is calculated as

$$C = \frac{I}{r * c}$$

where I is the total number of non-zero elements in the matrix (i.e. real trophic links).

However, it does not use the strength of the flows in its calculation, but is only based on the presence or absence of trophic links. Pimm (1982) defined an omnivore as a 'species which feeds on more than one trophic level'. In *Ecopath*, an index called system omnivory index (SOI) is computed based on the average omnivory index (OI) of all consumers weighted by the logarithm of each consumer's food (Christensen and Pauly 1992). In other words, SOI is a measure of how the feeding interactions are distributed between trophic levels. This was inspired by perceived drawbacks of the connectance index. Indeed, the connectance index is strongly dependent on how the groups of the system are defined: (1) as this is quite arbitrary in aquatic systems, where interactions of nearly all groups are possible at some development stage, connectance would be close to 1 in most systems described. Moreover (2), a prey would have the same 'score' in the connectance index whether it contributes 1, 10 or 100% of its predators' diet. Both of these drawbacks are overcome by the system omnivory index, which is computed as the variance of the trophs of a consumer's food groups. According to Christensen *et al.* (2000), the use of this index is recommended to characterize the extent to which a system displays web-like features. The omnivory index can be calculated as:

$$OI = \sum_{j=1}^n (TL_j - TL_{prey})^2 * DC_{ij} \quad \text{Eq. 3.2}$$

where i is the predator, j the n^{th} prey, TL_j is the trophic level of a predator, TL_{prey} is the average trophic level of n prey species of i and DC_{ij} is the diet composition, expressing the fractions of each i in the diet of i .

Assuming an equilibrium or steady state, model estimates of biomass, production, catch in fisheries and consumption by predators were used to derive estimates of total

mortality (Z), and its components (fishing mortality F , predation mortality $M2$, and other mortality $M0$). Note that, in contrast to the usual notation in fisheries science (e.g., Ricker 1975), we use these symbols to refer to annual rates rather than instantaneous rates. These indices were compared for some important groups, and between similar trophic groups of each ecosystem. The systems' emergent properties were also compared using emergent properties estimates and network analysis indices of the two models calculated by the *Ecopath with Ecosim* software (Christensen *et al.* 2000). The indices used include the sum of all consumption, exports, respiration, production, and flow to detritus (reported as $t \cdot km^{-2} \cdot year^{-1}$), the mean trophic level of the catch, gross efficiency of the catch (the catch divided by the net primary production; dimensionless), and the net system production (see Christensen [1995] and Christensen *et al.* [2000] for a description of the emergent properties indices). Network analysis indices were also analysed in terms of ascendancy (A), which is the product of the total systems throughput and the average mutual information of the flow structure (Ulanowicz and Puccia 1990), development capacity (C), which is a measure of the network's potential for competitive advantage over other real or presumed network configurations and is the upper bound to the ascendancy (Ulanowicz and Puccia 1990), and overhead (O), which is complementary to ascendancy and indicates the inefficiency and redundant degrees of freedom in the system (Ulanowicz 2000).

Results

Ecosystem structure and trophic transfers

Table 2 2 and 3 show the basic model outputs of Sør fjord and NGSL ecosystems. Both models are balanced scenarios (i.e. their EE are all below 1.0), and are identical to their original versions fully described in Pedersen *et al.* (submitted) and Morissette *et al.* (submitted).

Table 2. Trophic composition and basic statistics for the Sør fjord *Ecopath* model. Note that the biomass was first calculated in carbon mass (g C m^{-2}) in the model. Conversions to wet weight were based on Pedersen *et al.* (submitted).

Trophic group	TL	B (g C m²)	B (t*km⁻²)	P/B	Q/B	EE	P/Q
Mammals	4.41	0.001	0.01	0.102	35.300	0.533	0.003
Cormorants	4.52	0.0001	0.001	0.110	37.100	0.595	0.003
Large cod	3.55	0.217	1.81	0.360	3.000	0.774	0.120
Small cod	3.58	0.017	0.14	1.200	6.000	0.662	0.200
Large other fish	3.20	0.094	0.78	0.360	3.000	0.882	0.120
Small other fish	3.27	0.134	1.12	1.200	6.700	0.900	0.179
Herring	3.36	0.026	0.22	1.000	6.000	0.917	0.167
Krill	2.18	2.230	25.06	2.500	16.700	0.428	0.150
Small zooplankton	2.37	2.000	20.00	6.500	26.000	0.960	0.250
Microzooplankton	2.28	0.400	4.00	36.500	121.700	0.994	0.300
Heterotr. Nano-flagellates	2.95	0.250	2.50	36.500	121.670	0.925	0.300
Schypomedusae	3.39	0.011	3.24	6.500	17.330	0.133	0.375
Chaetognaths	3.33	0.590	10.00	3.800	19.000	0.006	0.200
Shrimps	2.94	0.034	0.37	2.000	13.300	0.900	0.150
Other large zooplankton	2.69	0.066	0.85	2.000	13.300	0.900	0.150
Large crustacea	3.04	0.056	0.59	0.500	3.330	0.900	0.150
Predatory benthos	3.05	0.221	2.33	0.500	3.330	0.900	0.150
Detrivore polychaetes	2.25	2.494	43.00	0.750	5.000	0.382	0.150
Small benthic crustaceans	2.17	0.304	4.00	0.450	3.000	0.915	0.150
Small molluscs	2.01	0.754	26.00	0.350	2.330	0.914	0.150
Large bivalves	2.20	2.618	187.00	0.190	2.375	0.343	0.080
Detrivore echinoderms	2.36	2.214	41.00	0.200	2.500	0.903	0.080
Other benthic ivertebrates	2.31	0.096	2.00	0.500	3.330	0.934	0.150
Bacteria	2.00	0.290	2.90	143.000	340.500	0.900	0.420
Phytoplankton	1.00	2.000	20.00	65.000	-	0.803	-
Macroalgae	1.00	20.250	173.08	0.450	-	0.155	-
Detritus	1.00	67.000	670.00	-	-	0.977	-

Table 3. Trophic composition and basic statistics for the NGSL *Ecopath* model.

Trophic group	TL	B (t*km⁻²)	P/B	Q/B	EE	P/Q
Cetacea	4.13	0.230	0.064	6.580	0.027	0.010
Harp seals	4.15	0.244	0.039	4.290	0.830	0.009
Hooded seals	4.71	0.005	0.091	10.980	0.000	0.008
Grey seals	4.52	0.040	0.045	4.620	0.000	0.010
Harbour seals	4.35	0.004	0.050	5.380	0.000	0.009
Seabirds	4.20	0.003	0.379	48.350	0.176	0.008
Large cod	4.06	0.153	0.497	2.480	0.728	0.200
Small cod	3.82	0.077	0.768	3.090	0.939	0.249
Large Greenland Halibut	4.16	0.204	0.173	1.140	0.859	0.152
Small Greenland Halibut	4.04	0.140	0.685	2.960	0.831	0.231
American Plaice	3.11	0.689	0.319	1.540	0.892	0.207
Flounders	3.11	0.064	0.308	1.300	0.834	0.237
Skates	3.99	0.139	0.278	1.420	0.882	0.196
Redfish	3.64	1.054	0.237	1.410	0.876	0.168
Large demersals	3.29	0.217	0.184	1.180	0.963	0.156
Small demersals	3.31	0.316	0.293	1.270	0.923	0.231
Capelin	3.32	2.916	1.053	5.310	0.889	0.198
Sandlance	3.20	0.201	0.617	2.590	0.930	0.238
Arctic Cod	3.24	0.019	0.720	3.450	0.864	0.209
Large pelagics	3.67	0.033	0.255	1.260	0.910	0.202
Pisciv. Small pelagics	3.42	0.498	0.394	1.570	0.947	0.251
Plank. Small pelagics	3.27	1.025	0.483	2.240	0.947	0.216
Shrimp	2.57	0.703	0.815	3.900	0.930	0.209
Large crustaceans	2.99	0.829	0.282	1.640	0.916	0.172
Echinoderms	2.00	82.582	0.399	1.450	0.008	0.275
Moluscs	2.00	93.548	0.738	2.540	0.011	0.291
Polychaetes	2.10	11.761	2.031	8.280	0.406	0.245
OBI	2.00	6.040	1.281	7.740	0.143	0.166
Large zooplankton	2.48	6.580	3.587	18.000	0.655	0.199
Small zooplankton	2.13	53.491	5.289	17.230	0.568	0.307
Phytoplankton	1.00	12.094	93.352	-	0.644	-
Detritus	1.00	132.608	-	-	1.000	-

To characterize the structure of Sør fjord *versus* the NGSL, we compared their biomass structure (Figure 4). In both ecosystems, benthic invertebrates are the predominant trophic group, followed by zooplankton in the NGSL but by primary producers in Sør fjord. There is a larger proportion of fish in the NGSL than is Sør fjord, but overall, the total biomass is higher in Sør fjord than in the NGSL.

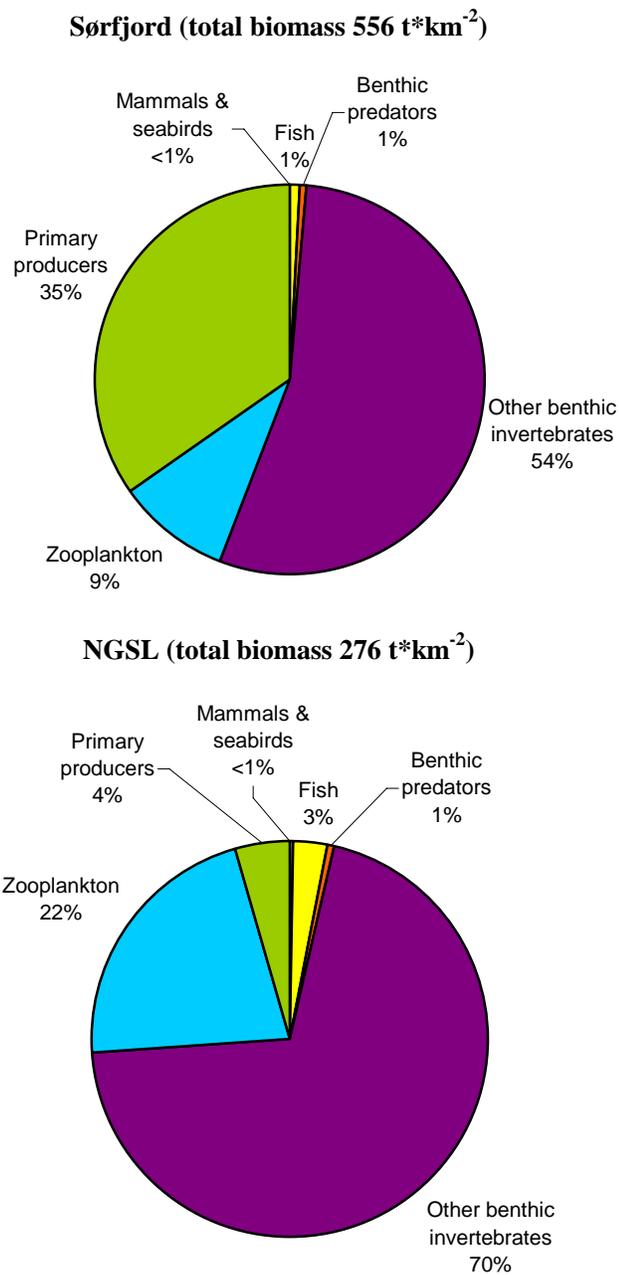


Figure 4. Biomass composition of the major ecological groups (excluding detritus and bacteria) in the Sørfjord and NGSL ecosystems.

Connectance flow diagrams in *Ecopath* provide a visual depiction of the food webs organization by easily showing the differences in the structure of the two ecosystems.

Trophic level

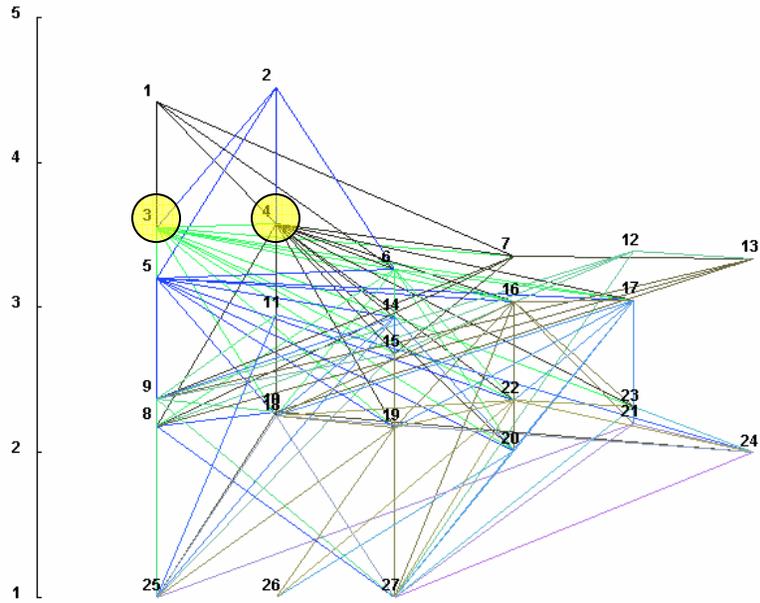


Figure 5. Sør fjord food web showing trophic levels and how groups are connected. Large cod (group #3) and small cod (group #4) are highlighted in yellow.

Trophic level

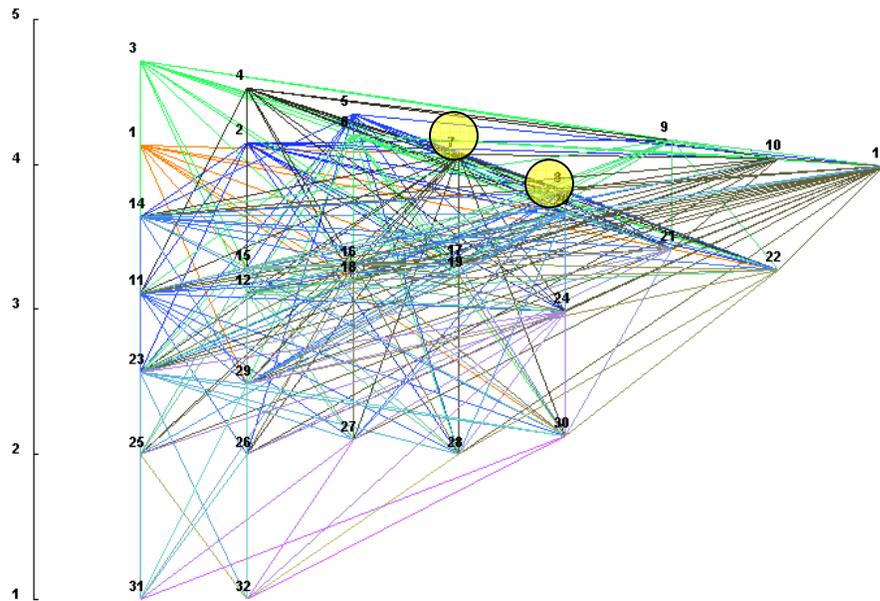


Figure 6. NGSL food web showing trophic levels and how groups are connected. Large cod (group #7) and small cod (group #8) are highlighted in yellow.

Compared to the NGSL, the Sør fjord ecosystem is broader at the base and at the intermediate trophic levels.

Ecosystem Properties

To characterize the structure of the northern Gulf and Sør fjord ecosystems, we compared different key indices (Table 4). The total biomass density (excluding detritus biomass) estimate for the northern Gulf of St. Lawrence ($276 \text{ t}\cdot\text{km}^{-2}$) is half of that in Sør fjord ($572 \text{ t}\cdot\text{km}^{-2}$). The total production is higher in Sør fjord than in the NGSL ($2375 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ versus $1574 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, respectively), so is the primary production ($1391 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ versus $1129 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, respectively). Along with a lower total biomass in the NGSL ecosystem, the fishery is more intensive, catching a total of 0.47 tons of fish per km^2 per year at an average trophic level of 3.05. In Sør fjord ecosystem, the exploitation level is lighter, with a total 0.36 tons of fish per km^2 per year at an average

trophic level of 3.41 (Table 4). In Sørffjord, however, there relatively more cod caught by the fishery.

The total system throughput represents the sum of all flows into and from the boxes in an ecosystem, including imports, exports of usable materials or energy (e.g., fisheries catches, or emigration), respiration, and flows to and from the detritus box. When expressed per area, this value summarizes the relative size of an ecosystem better than the sum of the biomass (Ulanowicz 1986). In terms of total system throughput, the Sørffjord ecosystem is higher than the northern Gulf of St. Lawrence (Table 4).

Table 4. Summary statistics referring to system size of the Sørffjord and the Northern Gulf of St. Lawrence ecosystems. The percentage contribution of the microbial loop groups; Microzooplankton, Heterotrophic nano-flagellates and Bacteria, to the values are given in brackets for the Sørffjord model

Ecosystem properties	Sørffjord Carbon	Sørffjord Wet weight	Gulf of St. Lawrence	Units
Sum of all consumption	310.085	3131(19.3)	1573	t/km ² /year
Sum of all exports	3.003	30.0 ¹	0.716	t/km ² /year
Sum of all respiratory flows	136.134	1582(48.7)	1128	t/km ² /year
Sum of all flows into detritus	129.858	1782(13.1)	1214	t/km ² /year
Total system throughput	579	6525	3916	t/km ² /year
Sum of all production	227	2375(27.4)	1574	t/km ² /year
Mean trophic level of the catch	3.41	3.41	3.05	
Gross efficiency (catch/net p.p.)	0.000314	0.0026	0.000417	
Calculated total net primary production	139.113	1391	1129	t/km ² /year
Total primary production/total respiration	1.022	0.88	1.001	
Total primary production/total biomass	3.723	2.43	4.092	
Total biomass/total throughput	0.065	0.088	0.07	
Total biomass (excluding detritus)	37.367	572	276	t/km ²
Total catches	0.044	0.364	0.471	t/km ² /year
Ascendency (%)	23.9	23.9	16.3	
Overhead (%)	68.7	68.7	83.7	
Capacity	1642	1642	15973	
Connectance Index	0.198	0.198	0.293	
System Omnivory Index	0.194	0.194	0.128	
% of PPR for marine mammals consumption	36	36	22	
% of PPR for fisheries catches	2	2	4	

¹ Assumed Carbon/wet weight ratio equal to 0.10

According to these comparisons, we can thus say that the Sørffjord is similar to other inland sea ecosystems (Morissette *et al.* 2006) such as the North Sea (Christensen 1995), while the NGSL is more similar to coastal regions such as the west coast of Greenland (Pedersen and Zeller 2001), and the Hecate Strait (Beattie 2001). NGSL is also a less productive ecosystem than the Sørffjord.

Major sources of mortality

Three sources of mortality are distinguished by the *Ecopath* models: predation mortality ($M2$), fishing mortality (F), and other mortality (disease, other natural causes of death, and unexplained mortality, $M0$). At equilibrium, total mortality (Z) should be equivalent to the production to biomass ratio of each group.

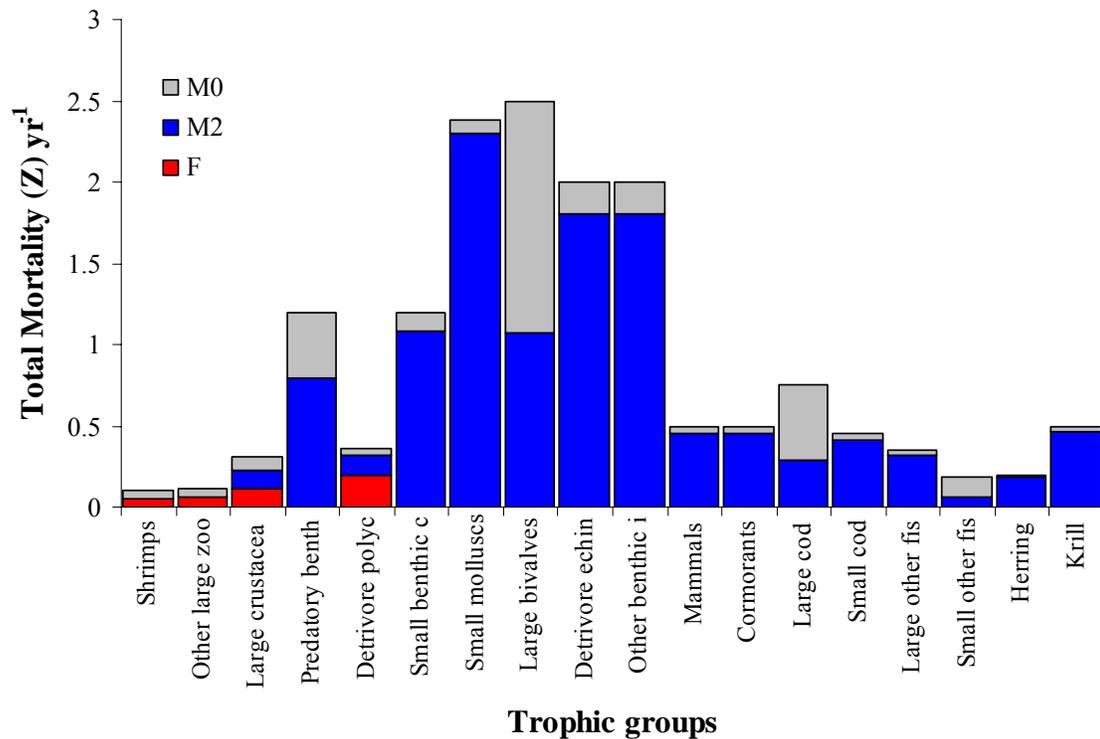


Figure 7. Breakdown of total mortality (Z) into predation ($M2$), fishing (F) and other mortality ($M0$) for trophic groups of the Sør fjord ecosystem.

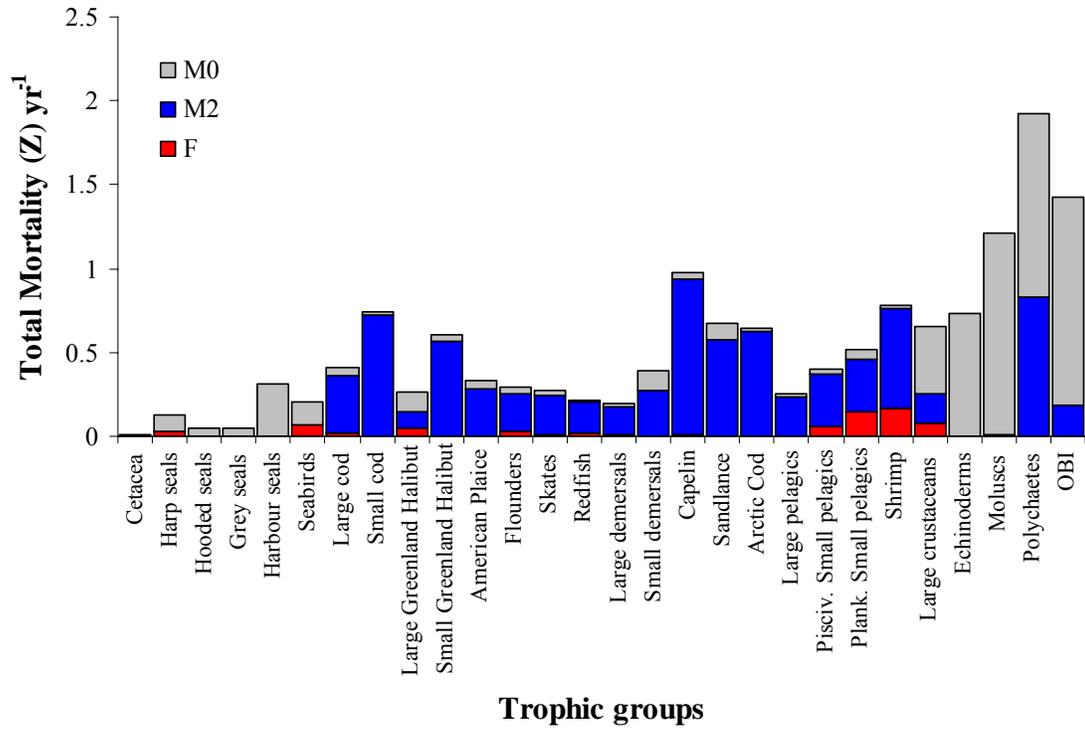


Figure 8. Breakdown of total mortality (Z) into predation (M2), fishing (F) and other mortality (M0) for trophic groups of the NGSLEcosystem.

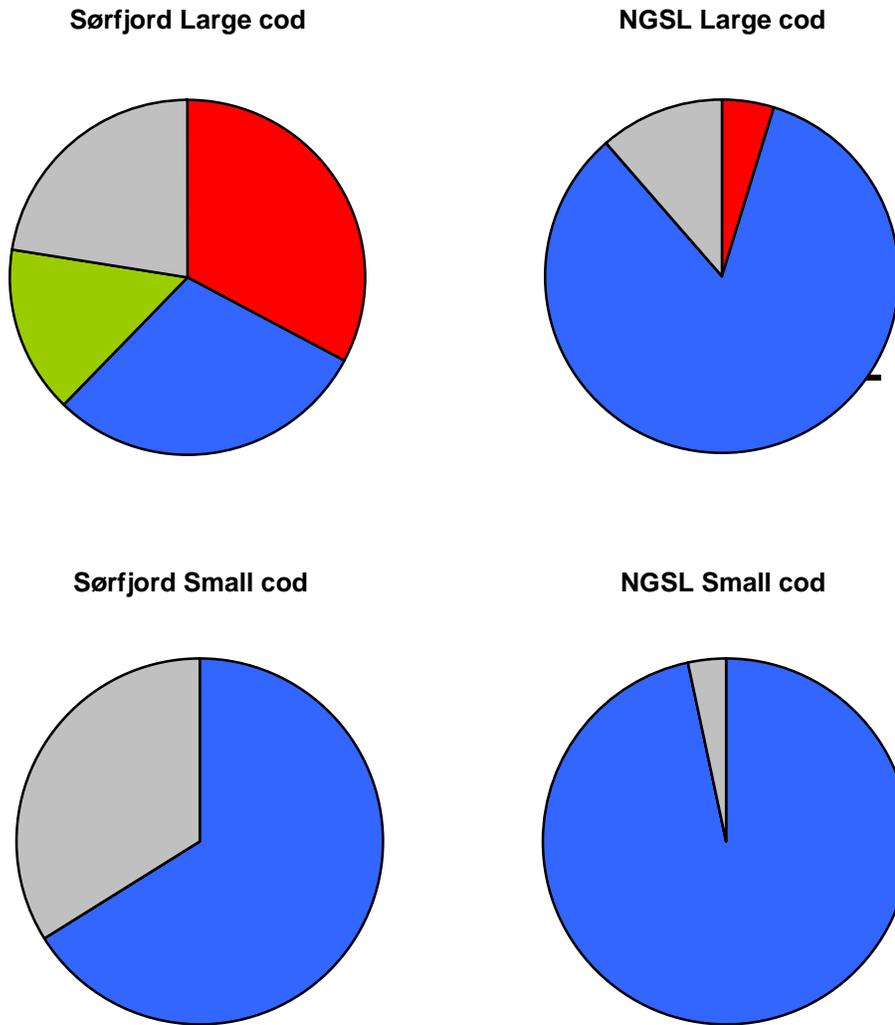


Figure 9. Breakdown of total mortality (Z) into fishing (F, in red), predation (M2, in blue) and unexplained (M0, in grey) mortalities, and biomass accumulation (BA, in green), in annual rate (year^{-1}), for large and small cod of the Sør fjord and NGSL ecosystems.

Proportion of total mortality due to predation

The main predators of fish species in Sør fjord were large cod, small cod, and chaetognaths. These predators accounted for more than three quarters of total predation mortality in the ecosystem. In the northern Gulf of St. Lawrence, more than 75% of predation mortality by all predators on fish prey was attributed to marine mammals, large

cod, and seabirds. The commercial fisheries accounted for than 7% of this mortality in the NGSL, while it accounted for only 1% in Sørffjord.

Finally, the average trophic level of predation (M2) in Sørffjord is 2.01, while it is 2.30 in NGSL.

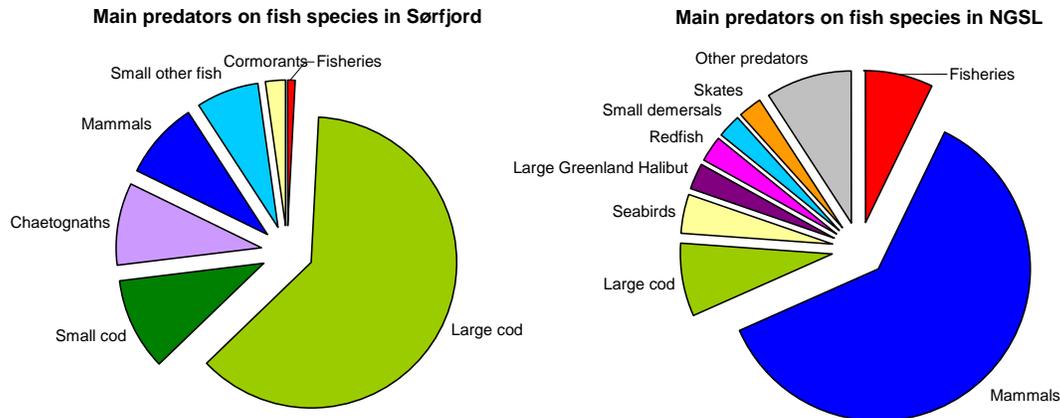


Figure 10. Main predators (including the fisheries) of fish species in the Sørffjord and NGSL ecosystems.

Impact of fisheries

Even if reduced from its 1980s level, commercial fisheries was still a significant source of mortality in the northern Gulf of St. Lawrence ecosystem, while it is unimportant in Sørffjord. The gross efficiency of the fishery (catch / primary productivity) was estimated to be 0.03% in Sørffjord and 0.04% in NGSL, which means that this part of the system's production is harvested and thus not available to sustain the system as a whole. Overall, the primary production required to sustain the catches from all fisheries in Sørffjord represented 50.5% of the total primary production, while it was 12.4% of the NGSL's total primary production. Fishing mortality had its greatest impact on large fish and seabirds in Sørffjord, while it affected more shrimp, planktivorous small pelagics, large crustaceans and seabirds in the NGSL.

Mixed Trophic Impact Analysis

Figure 11 to Figure 14 show the mixed trophic impacts on major fish species in Sør fjord and Northern Gulf of St. Lawrence ecosystems. This analysis allows estimation of the relative impact of a change in the biomass of one group on other components of the ecosystem, under the assumption that the diet composition remains constant (Ulanowicz and Puccia 1990). When the whole food web is considered (all species together), the two elements having the most negative impact in the Sør fjord ecosystem are cod and the cod fishery (Figure 11). On the other hand, positive impacts are noted for phytoplankton, heterotrophic nano-flagellates and krill. In the NGSL, most piscivorous fish and marine mammals have a negative impact on the rest of the food web (Figure 12). However, we see also positive effects from phytoplankton, large zooplankton, benthic invertebrates and shrimp.

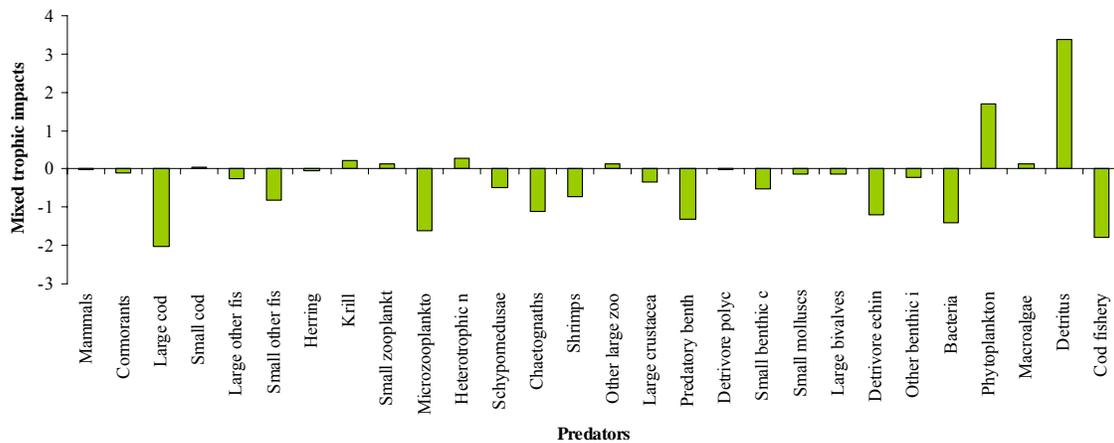


Figure 11. Mixed trophic impacts on all species of the Sør fjord ecosystem, for each predator.

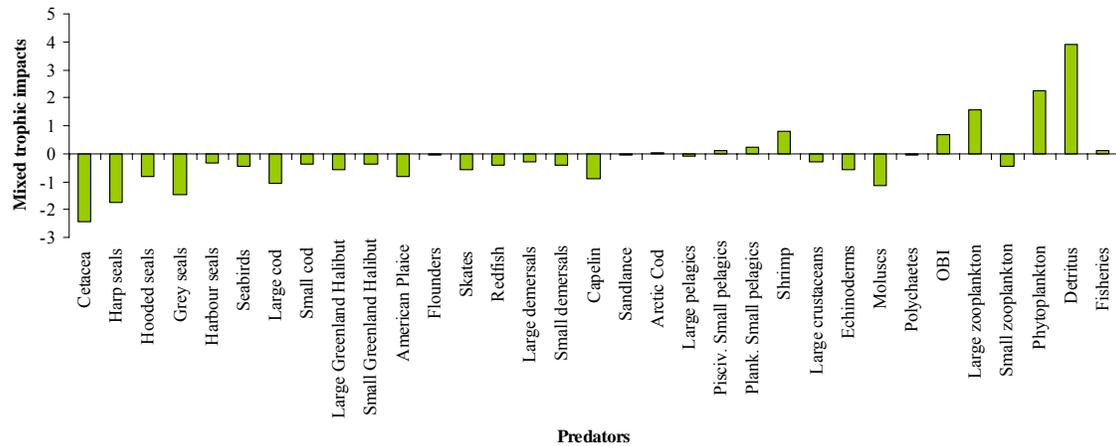


Figure 12. Mixed trophic impacts on all species of the NGSL ecosystem, for each predator.

When the same trophic impact analysis is done only for species impacting large and small cod, the most important negative impacts in Sørffjord are inflicted by marine mammals, large cod, chaetognaths and other large fish (Figure 13). The strongest negative impacts on small cod in the same ecosystem are caused by large cod, cormorants and chaetognaths. In the NGSL, large cod is negatively impacted mainly by marine mammals, Greenland halibut and skates, while small cod is negatively impacted mainly by large cod, marine mammals and redfish (Figure 14).

However, some species in food webs can also have a positive impact on cod. This is the case for krill, herring and phytoplankton impacting large cod in Sørffjord, as well as krill, cod fishery and other large fish positively impacting small cod in the same system (Figure 13). In the NGSL, groups such as large crustaceans, fisheries and shrimp have a positive impact on large cod, while shrimp, large zooplankton and phytoplankton have a positive impact on small cod (Figure 14).

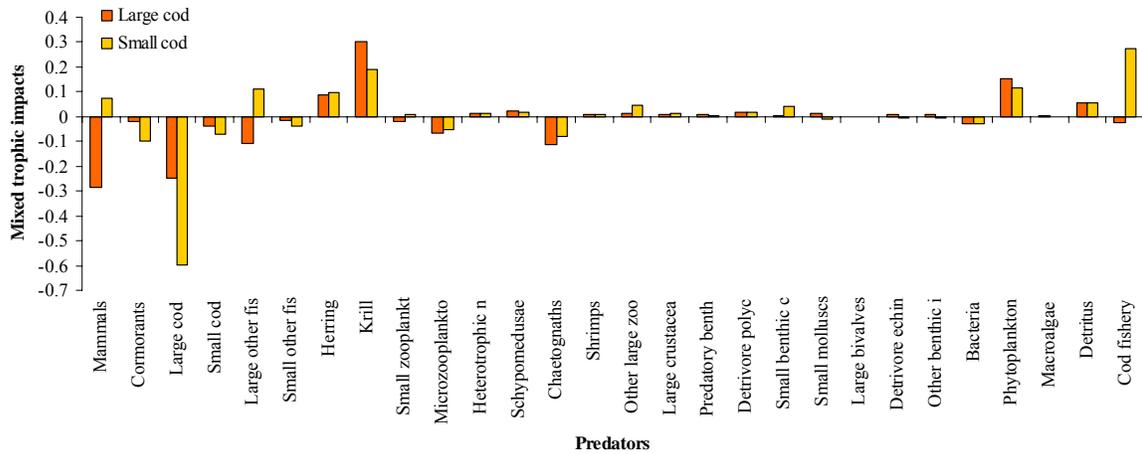


Figure 13. Mixed trophic impacts on cod in Sør fjord.

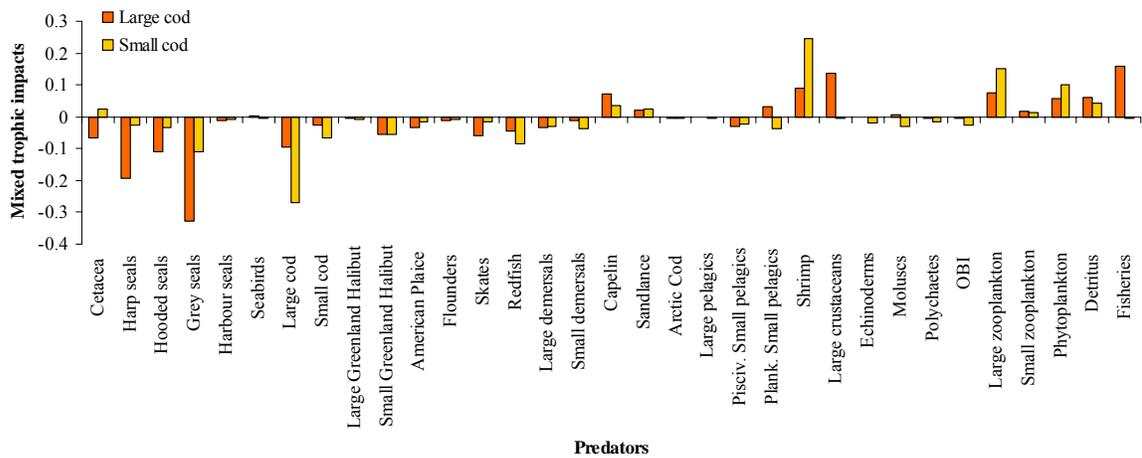


Figure 14. Mixed trophic impacts on cod in the NGSL.

Discussion

The use of a common modelling approach to compare of the Northern Gulf of St. Lawrence and the Sør fjord ecosystems represents a new way of addressing the problem of collapsing fish stocks. This approach allowed the exploration of new indicators that could explain which differences in ecosystem structure could be related to such collapses. The two *Ecopath* models presented here correspond to our "best" estimates of the components of the ecosystems and the ways in which they interact, though we recognize

that they only represent one possible solution of a balanced model. No model can ever duplicate reality (Moloney *et al.* 2005), and there may be many uncertainty related to this modelling approach (Morissette 2005).

Strengths and weaknesses of modelling efforts

The synthesis of existing ecosystem information is designed to enable a whole-system view using parameters that are basic to understanding populations and the ecosystem. The use of a common modelling technique and sets of ecosystem indicators to compare two sub-arctic food webs represents a new and useful approach to address ecosystem changes issues.

Unfortunately, an ecosystem model is not a perfect representation of the reality. The uncertainties remaining in the understanding of the ecosystem may come from incorrect values as well as from unknown mechanisms occurring in the ecosystem (Morissette 2001). Indeed, the only mechanism used to represent interactions is direct consumption. It ignores the fact that consumers often do more than skim production off their prey; they can shift composition to species with lower productivity and alter the P/B ratio of the group (Ruesink 1998). However, these errors are important only if the questions addressed by the model are drawn on aspects of the model that are importantly wrong. For instance, it would be imprudent to try to set fisheries quotas with this kind of model.

On the other hand, the structure of the model provides an overall view of all the data of the ecosystem and to see where are the uncertainties that could be filled for future studies. These uncertainties may occur because no data exists, because the confidence limits are too large, because of an inaccurate aggregation of species within one ecological box, or either because the ecotrophic efficiency is unlikely (Ruesink, 1998).

A common problem in ecosystem modelling is that less information is available for the lower trophic levels (Walline *et al.* 1993; Morissette 2001). However, this is not the case for Sør fjord model. Indeed, in the Sør fjord model, biomass is estimated from predation for predatory benthos and large crustaceans, whereas for the other groups, biomass is sampled by grab and considered relatively precise.

On the other hand, some progress is still needed in understanding and refining the structure of the Sør fjord and NGSL ecosystems. Nevertheless, this lack of information is

less important in the top-down modelling approach, because it is assumed that apex predators drive the system, so having detailed information for these species is more important.

Model structure is also different between Sør fjord and NGSL. First, there are 32 trophic groups in the NGSL while only 27 groups are represented in Sør fjord model. This is primarily due to various degrees in aggregation of benthic and marine mammals components. Having different group numbers can lead to differences in linking, connectance, and other global indices. However, based on the number of trophic levels covered and the similarity in species composition, these two models can be assumed to be comparable.

Part of the difference in the total amount of trophic groups is due to the fact that the Sør fjord model has only one marine mammal group, while the NGSL covers 5 groups. As a result, there are 4 extra sets of trophic links towards higher trophic levels in the NGSL model. To compensate for that, the five groups of cetaceans and seals in the NGSL were aggregated to analyse all results involving marine mammals and their impact on the food web.

Finally, the microbial loop plays a major role in food web models (Vézina and Savenkoff 1999). In the Sør fjord model, it was characterized by a distinct trophic group, while in the NGSL bacteria was considered as part of the detritus group (bacterial remineralization of detritus & respiration were included as extra-parameters for benthos to represent the microbial loop).

Trophic structure

Sør fjord appeared to be a larger ecosystem in terms of biomass density. As in the NGSL, most of the biomass was composed by benthic invertebrates. When only vertebrate species were considered, the biomass was higher in the NGSL. In fact, information about benthic invertebrates was very scarce in NGSL and thus this group may be less important than what was projected by the model. Since the uncertainty related to benthic invertebrates is very high, it is not clear if Sør fjord really had a higher biomass than NGSL. In the Sør fjord model, however, the quantity and quality of information on benthic invertebrates is higher (Nilsen *et al.* 2006).

Primary producers were similar in terms of biomass proportions and production Sør fjord and in NGSL. However, higher trophic levels (such as fish and marine mammals) were more important in the NGSL in terms of proportions of total biomass.

When we have a closer look at the structure of the food web, we see that in Sør fjord, most biomass was located at intermediate trophic levels. Most species had TL between 2.5 and 3.0, and there were fewer groups at higher TL of 3.5 – 5.0. In the NGSL the overall structure of the system was different, with more species at higher trophic levels, between 3.5 and 4.0. This is partly due to the fact that marine mammals were described through 5 groups in the NGSL, but even without that effect, higher trophic levels seemed to be more abundant in the NGSL.

Production and cycling

Ecopath modelling allowed us to analyse a series of parameters on the systems' production and cycling, which represented a useful way of comparing different ecosystems and to show important differences of food web structure. There was a strong indication that the sum of flows was higher in Sør fjord than in the NGSL (respiratory flows, total system throughput, and total production). All these indices represent the size of the entire system in terms of flow (Ulanowicz 1986), meaning that less energy is flowing in the entire Sør fjord ecosystem compared to the NGSL. Moreover, the ascendancy, the overhead and the capacity are indices based on thermodynamics and information theory representing ecosystem growth and development (Christensen 1995). They were strong indicators that the Sør fjord ecosystem is closer to maturity than the NGSL. This difference in internal flows certainly indicates that the overall structure of the Sør fjord and NGSL ecosystems was different.

The primary production required (PPR) to sustain the fisheries (excluding marine mammals catches) was lower in Sør fjord than in the NGSL (2% *versus* 4%, respectively). However, PPR to sustain marine mammals consumption was higher in Sør fjord than in NGSL (36% *versus* 22%, respectively). As marine mammals can be seen as two “top-predators” in these marine ecosystems, we clearly see that they had a higher impact in Sør fjord where fishery was less important.

Sources of mortality

In both ecosystems, the higher total mortalities (Z) were observed for lower trophic levels, and particularly for zooplankton. This suggests that species at lower trophic levels are smallest, fast-growing organisms, with a highest production and thus a higher total mortality.

The highest proportions of predation mortality (M_2) were seen at lower trophic level in Sør fjord ecosystem than in the NGSL ecosystem. Predators in the NGSL seemed to consume larger fish, including cod, while in Sør fjord, species most impacted by predation were molluscs and other benthic invertebrates. As an exception to that, the group with the highest proportion of predation mortality in the Sør fjord ecosystem was herring. This clearly represents a key species for Sør fjord. As a matter of fact, herring abundance was relatively low during the modelled period (1993-1996), probably due to the high predation on that species by marine mammals, but was much higher during 1990-1992, when krill was low (T. Pedersen, Norwegian College of Fishery Science, pers. comm.). This could reflect the result of a diet switch for marine mammals in this ecosystem.

In the NGSL, the mortality graph showed us that most fishing mortality was directed towards lower trophic levels since the collapse of larger groundfish species in the early 1990s. Shrimp and small pelagic fish were the most important species caught by the fishery.

Top predators

Cod was an important top predator in both Sør fjord and NGSL ecosystems, with only marine mammals and seabirds higher in the food web. However, in both ecosystems, predation by marine mammals was also important.

In the NGSL model, seals were very important in terms of biomass and they replaced cod (that was more abundant in the 1980s; see Morissette *et al.* [2003] for a description of this model) as the main predator in the ecosystem. In Sør fjord ecosystem, sea otters are more and more abundant, and there was an invasion of harbour seals in the late 1980s. Despite this increase of marine mammals in the ecosystem, cod remained abundant, and the structure of the ecosystem had not yet shifted towards a new

equilibrium where seals are predominant. It may be because the Sør fjord's complex ecosystem structure makes it more resilient to such changes, or because this process would take more time and will eventually happen.

Trophic impact of fishing

One surprising result from the NGSL model was that the fishery seemed to benefit cod. However, this was possibly due to the fact that the NGSL fishing fleet included anything that was catching any species in the ecosystem and thus comprised seal hunt and cetaceans bycatches. With an average of 0.009 t*km^{-2} of seals and cetaceans caught (or accidentally trapped in fishing nets) in NGSL for the 1990s, this could represent an important release in predation for cod. Moreover, since fishing for cod has been stopped by the moratoria in the early 1990s, there is no cod catches to compensate for this release in predation and drive the trophic impact of the fisheries to expected negative values.

Since the collapse of cod and other groundfish species in NGSL, fishing effort was more directed towards shrimp and crab. This is why we see a lower TL of the catch in this ecosystem, even if the fishery is relatively intense, and partly directed on species that were prey for cod before the collapse (Morissette *et al.* 2003).

On the opposite, our results clearly showed that Sør fjord has been exploited lightly compared to the NGSL. Even if the model representing NGSL in the 1990s is supposed to represent a reduced fishing level (compared to the 1980s, before the moratorium), the exploitation level in this ecosystem was still ten times higher than the exploitation level seen in Sør fjord for the same period.

Interestingly, large cod was the main predator in the NGSL during the 1980s, before the collapse of most groundfish species. At that time, Figure 10 would have been similar to what we now see in Sør fjord (Morissette *et al.*, submitted). However, when the stock collapsed in the early-1990s, this part of the predation was taken up by the increasing seals population, which are now the top and most important predators in the northern Gulf of St. Lawrence ecosystem (Morissette *et al.* 2006).

Mixed trophic impacts

In the NGSL ecosystem, more fish species had a positive impact on the overall structure of the ecosystem than in Sør fjord. This was the case for all pelagic groups (large, small piscivorous and small planktivorous), as well as for shrimp, benthic invertebrates and plankton. In Sør fjord, the groups that showed the most important positive impacts were lower trophic levels such as krill, nano-flagellates, and zooplankton.

Surprisingly, the overall effect of fishery on all species considered together in NGSL was positive. However, as stated before, this was probably due to the fact that this fishing includes seal hunt, which represents an important release in predation for many species in the ecosystem.

The impact of predation in marine ecosystems was is always a negative one. Indeed, predators can have indirect positive effects on their prey through different processes such as pre switching, competition, or cascading effects (Morissette *et al.* 2006; Morissette 2007) that may overall result in unintended outcomes, including beneficial predation. In Sør fjord, it was prey such as krill and herring that had the most positive impact on cod populations. In the NGSL, some predators such as cetaceans had a similar positive impact on small cod, even if they were also their predators.

Ecosystems complexity and resilience

The connectance index only represents the number of trophic links in the food web. If we just examine this index, we would tend to think that the Sør fjord system would be less complex than the NGSL. However, connectance is correlated to the number of trophic groups in the model, and thus can be erroneous. On the other hand, the system omnivory index (SOI) is calculated for all consumers and weighted by the logarithm of each consumer's food. This is more precise, and represents better the complexity of the models (Morissette 2007). The SOI clearly indicated that the Sør fjord ecosystem was more complex than the NGSL. According to a recent study by Morissette (2007), food webs' SOI is positively related to ecosystems' resilience, as it is seen in natural environments (Yodzis 1981; Neutel *et al.* 2002). This means that Sør fjord would be more resilient, and could thus recover better from perturbations such as environmental

changes, alteration of the structure of the food web, etc. This concept of resilience is also linked to maturity, as ecosystems are thought to be more stable when they reach maturity. In the NGSL, this loss in complexity was reflected by the loss in maturity (ascendancy, overhead and capacity). Also, since both ecosystems differed in their communities (NGSL was dominated by capelin and herring in the mid-1990s while Sør fjord was dominated by cod, krill, chaetogaths, and benthic invertebrates), we might suppose that recovery from the current level of exploitation can be different for each ecosystem.

The Ascendancy, also used as an indicator of ecosystem's maturity, corroborates the suggestion that Sør fjord ecosystem would be more mature and thus resilient than the NGSL. Sør fjord was probably a more mature ecosystem because it has not been overexploited and its structure was more intact.

The lack of recovery of many important stocks of the NGSL that underwent drastic declines leading to fishing moratoria clearly points to the need to understand how ecosystems react to perturbations. One argument is that more complex ecosystems will cope better with perturbations (McNaughton 1978). For example, major decreases in abundance of gadoid predators on the Eastern shelf/Georges Bank ecosystem of the United States was offset by increased abundance of elasmobranchs and large demersal predators (i.e., various sculpins) such that total consumption of forage fishes changed remarkably little (Fogarty and Murawski 1998; Link and Garrison 2002).

Regime shift, a process of density compensation of some species after the removal of some other species in an ecosystem (Cury *et al.* 2003), is also a phenomenon that could explain the changes in the trophic structure of Sub-Arctic ecosystems. As fisheries have removed extensive amounts of predatory fishes in many Sub-Arctic ecosystems during the last decades, one must carefully consider the implications for the other components of these systems. Comparing with the Sør fjord, an ecosystem that was not affected by overexploitation, represents an asset in understanding such processes. However, the NGSL model suggest that fishing did not lead to clear compensatory of biomass or consumption of other species resulting from the removal of predatory fishes (Morissette *et al.*, submitted). The population of Atlantic cod in The Gulf of St. Lawrence has not increased in abundance despite greatly reduced fishing pressure since 1993/94, and the failure of strong year-classes to develop is currently perplexing. On the other

hand, cod in a lightly exploited such as the Sør fjord didn't suffered from any collapse, and the structure of this system seem to be more complex and mature. Not only overexploitation changes the structure of the ecosystem, but it now seems that these structural changes can affect the resilience of ecosystems, and the ability of collapsed species to return to their original equilibrium.

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