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## Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems

Alida Bundy<sup>a,\*</sup>, Johanna J. Heymans<sup>b,1</sup>, Lyne Morissette<sup>c,2</sup>, Claude Savenkoff<sup>d,3</sup>

<sup>a</sup> Fisheries and Oceans Canada, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2

<sup>b</sup> Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban PA37 1QA, Scotland, United Kingdom

<sup>c</sup> Fisheries Centre, The University of British Columbia, Aquatic Ecosystems Research Laboratory (AERL), 2202 Main Mall, Vancouver, BC, Canada V6T 1Z4

<sup>d</sup> Pêches et Océans Canada, Institut Maurice-Lamontagne, 850 route de la Mer, Mont-Joli, Que., Canada G5H 3Z4

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### ABSTRACT

The facts: four Northwest Atlantic ecosystems, three cod stock collapses 15 years ago (plus one severely depleted), seals now top predator in all ecosystems, all had cod as a top predator before collapse, groundfish declines in all areas, forage base increased in most systems. No recovery in any system. Have these ecosystems fundamentally changed? Why? The challenge: compare and contrast these four ecosystems. The answer: using mass balance models, empirical data and a suite of ecosystem indicators, we explore how and why these systems have changed over time. At the ecosystem and community level, we see broad similarities between ecosystems. However, structurally and functionally these systems have shifted to an alternate state, with changes in predator structure, trophic structure and flow.

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### 1. Introduction

When Giovanni Cabotti returned from his voyage to the “New Found Land” in the late 15th century, he reported that there were vast amounts of cod in the seas off eastern Canada, that the seas were literally “teeming” with fish (cited in Kurlansky, 1997). It was considered a huge bounty which led to a “cod rush” by the Portuguese, French, Spanish and English (Kurlansky, 1997). Five hundred years later, in the early 1990s, Atlantic cod (*Gadus morhua*) stocks on the Grand Banks, the eastern Scotian Shelf and in the northern and southern Gulf of St. Lawrence finally collapsed after centuries of exploitation. The immediate response of the Canadian Department of Fisheries and Oceans was to close the cod fisheries in the early 1990s. Subsequently, there has been little recovery of cod in any of these areas, although the fisheries in the northern and southern Gulf of St. Lawrence were re-opened in the late 1990s and are now in a precarious state (DFO, 2007a,b): the biomass of mature cod in the northern Gulf will likely decrease with fishing during 2007 (DFO, 2007a) and in the southern Gulf, the current estimate of spawning stock biomass of cod (48,000 t) is the lowest observed (DFO, 2007b). In Newfoundland–Labrador,

where there has also been no recovery of cod (DFO, 2007c, 2008), there was a directed inshore fishery from 1998 to 2002 (DFO, 2007c), and two fisheries for cod (a “stewardship fishery” and a recreational fishery) were re-opened during 2006, and still continue. On the eastern Scotian Shelf (Fanning et al., 2003) there has been no recovery of cod and there is no directed fishery.

Essentially, these four Northwest (NW) Atlantic marine ecosystems off the east coast of Canada (Fig. 1) have undergone catastrophic change. Along with cod, many other groundfish species, such as white hake (*Urophycis tenuis*), redfish (*Sebastes* spp.), and flatfish such as American plaice (*Hippoglossoides platessoides*) suffered serious declines, as reflected by steep decreases in total landings (Fig. 2). Meanwhile, other changes in these ecosystems were also occurring, such as large increases in seals, due to population recovery from hunting (Mohn and Bowen, 1996; Hammill and Stenson, 2005) and, at least in some areas, of forage fish, which may be due to predation release (Lilly, 1991; Bundy, 2005).

The Newfoundland–Labrador shelf (Fig. 1) is the most northerly of the four ecosystems and extends from Labrador to the Grand Banks in the south encompassing Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KLNO, and a total area of 495,000 km<sup>2</sup>. The Grand Banks in the south extend to the 200 miles EEZ, whereas further north, the shelf area is narrower. The ocean environment is influenced by several factors including the Labrador Current, cross-shelf exchange with warmer continental slope water and bottom topography and large seasonal and inter-annual variations, particularly in ice cover (DFO, 2007d). The Gulf of St. Lawrence forms one of the most important estuarine shelves in the world (Therriault, 1991). It is a stratified semi-enclosed sea

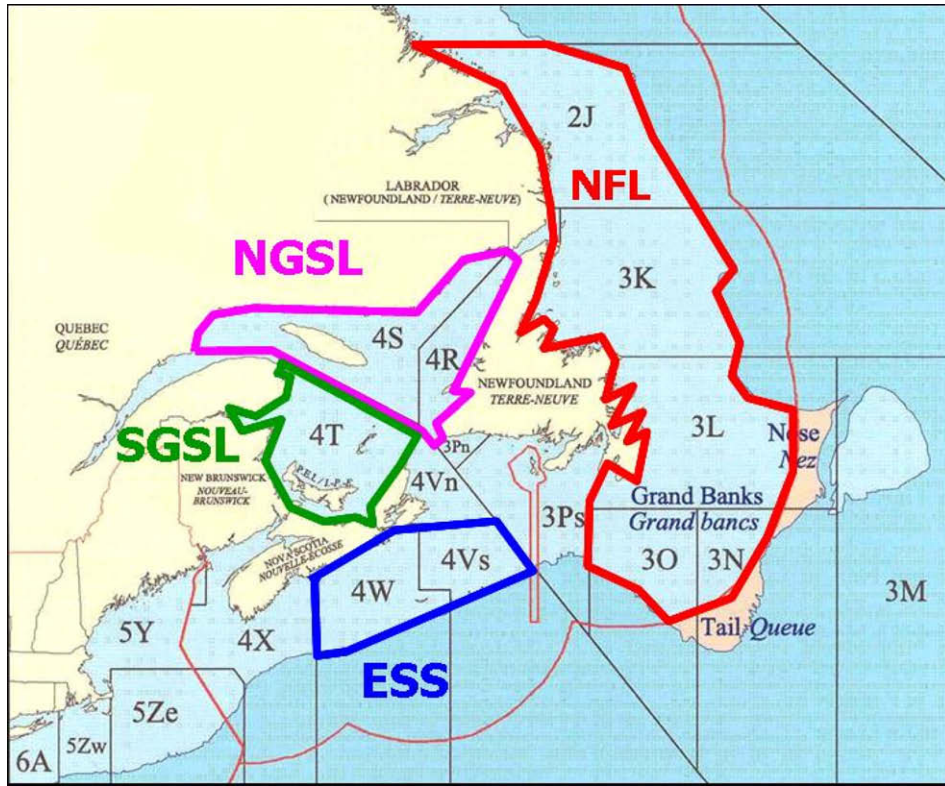
\* Corresponding author. Tel.: +1 902 426 8353; fax: +1 902 426 1506.

E-mail addresses: [bundy@mar.dfo-mpo.gc.ca](mailto:bundy@mar.dfo-mpo.gc.ca) (A. Bundy), [sheila.heyman@sams.ac.uk](mailto:sheila.heyman@sams.ac.uk) (J.J. Heymans), [lmorissette@fisheries.ubc.ca](mailto:lmorissette@fisheries.ubc.ca) (L. Morissette), [claudesavenkoff@dfo-mpo.gc.ca](mailto:claudesavenkoff@dfo-mpo.gc.ca) (C. Savenkoff).

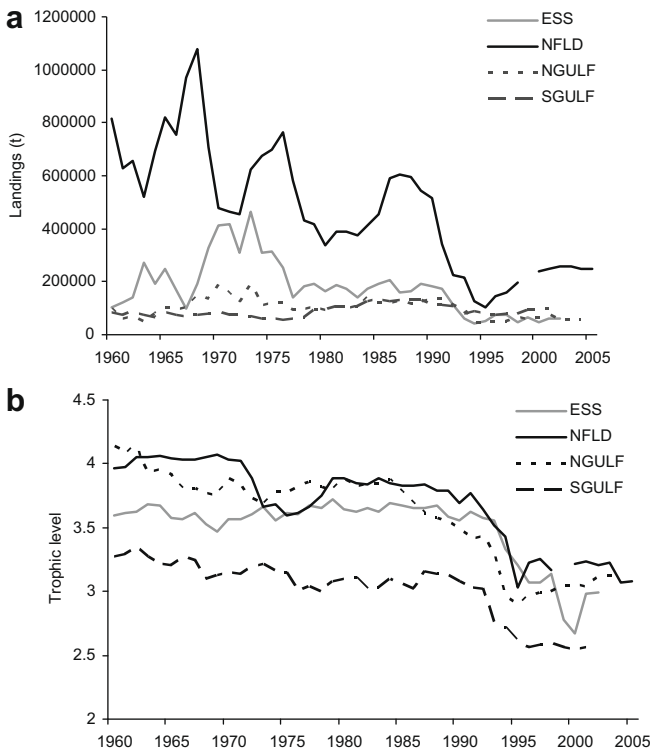
<sup>1</sup> Tel.: +44 1 631 559418.

<sup>2</sup> Tel.: +1 604 822 2731; fax: +1 604 822 8934.

<sup>3</sup> Tel.: +1 418 775 0764; fax: +1 418 775 0740.



**Fig. 1.** Map of the east coast of Canada, showing the four NW Atlantic ecosystems. NFL: Newfoundland–Labrador Shelf ecosystem (Northwest Atlantic Fisheries Organization [NAFO] Divisions 2J3KLNO); NGSL: northern Gulf of St. Lawrence (NAFO Divisions 4RS); SGSL: southern Gulf of St. Lawrence (NAFO Division 4T); ESS: eastern Scotian Shelf (NAFO Divisions 4VsW).



**Fig. 2.** (a) Total landings (t) from 1960 for the eastern Scotian Shelf, the northern Gulf, southern Gulf and Newfoundland–Labrador and (b) mean trophic level of landings (trophic level derived from Ecopath models). Note that NAFO data for Newfoundland in 1999 are incomplete and are not included.

connected to the North Atlantic Ocean through the Cabot Strait to the southeast and the Strait of Belle-Isle to the northeast. The bathymetry of the Gulf is dominated by the Laurentian Channel, which divides the Gulf into two very distinct systems: the deep northern Gulf, characterized by a number of deep channels with depths greater than 200 m, and the southern Gulf represented by a shallow shelf, the Magdalen Shallows, with depths mostly less than 100 m (Koutitonsky and Bugden, 1991). The northern Gulf of St. Lawrence (NAFO Divisions 4RS) covers an area of 103,812 km<sup>2</sup>. The nearshore region (depths < 37 m) was not included in the northern Gulf models. In the southern Gulf of St. Lawrence (NAFO Division 4T), our study area was defined as the region with depths between 15 and 200 m, covering an area of 64,075 km<sup>2</sup>, which excluded the deep parts of the Laurentian Channel and the St. Lawrence Estuary. The eastern Scotian Shelf is a broad continental shelf made up of a number of shallow off-shore banks and deeper inner basins. It extends from the Laurentian Channel in the northeast to a line from Halifax south to the shelf break in the southwest, encompassing NAFO Divisions 4VsW and has an area of approximately 100,000 km<sup>2</sup>. The physical environment of the eastern Scotian Shelf is governed by two primary factors: its location, near the meeting place of major currents of the Northwest Atlantic, the Labrador Current and the shelf current which brings cool fresh water from the Gulf of St. Lawrence; and its complex topography (Zwanenburg et al., 2006).

Comparative studies have proven useful in understanding how the structure and functioning of ecosystems change, and their response to perturbations (Neira et al., 2004; Bundy and Fanning, 2005; Cury et al., 2005; Savenkoff et al., 2007a,b; Pranovi and Link, in this issue). In the southern Benguela system, Shannon et al. (2003) compared a series of steady-state model outputs for the 1980s and 1990s, and concluded that the ecosystem functioned

in a similar way trophically in these two contrasted periods. Heymans et al. (2004) compared models for the northern Benguela systems and concluded that by the 1990s, energy was flowing through fewer pathways and trophic efficiency was lower than in the 1980s. Coll et al. (2006) compared five standardized mass balance models of different ecosystems (a Northwest Mediterranean exploited ecosystem and four models from coastal upwelling ecosystems). Among other results, they demonstrated the importance of pelagic–demersal coupling and of gelatinous zooplankton in the consumption of production in Namibian and Mediterranean ecosystems and evidenced the relative higher impacts of fisheries in the Mediterranean Sea. In the NW Atlantic, Bundy (2005) compared mass balance models for the eastern Scotian Shelf before and after the cod collapse and showed that despite similar total biomass and productivity, there were marked differences in the trophic structure and energy flows through the system. Similarly, Savenkoff et al. (2007a,b) compared changes in ecosystem structure and the effects of fishing and predation within the northern and southern Gulf of St. Lawrence before and after the cod collapse while Morissette et al. (2009) contrasted changes between these two areas, especially exploring the response of ecosystem indicators, the role of predation, and the trophic interactions, in the context of collapsing groundfish resources.

The lack of recovery of overfished Northwest Atlantic groundfish stocks points to the need to understand how ecosystems react to perturbations. Here, for the first time, we compare and contrast these four NW Atlantic ecosystems over time to investigate how they have changed structurally and functionally, and to explore the implications for the recovery of cod using empirical data, a suite of ecosystem indicators and a mass balance modelling approach. Where possible, we include the effects of uncertainty in the comparisons.

## 2. Methods

Mass balance models were developed for the four NW Atlantic ecosystems for a period in the 1980s before the groundfish collapse and in the 1990s after the collapse (Table 1) (Heymans, 2003a; Bundy, 2005; Savenkoff et al., 2007a,b). The Newfoundland–Labrador model covers the largest area and the widest degree of latitude; the northern Gulf and eastern Scotian Shelf models are around 100,000 km<sup>2</sup> and the southern Gulf is the smallest (Fig. 1). The eastern Scotian Shelf and Newfoundland–Labrador were modelled using Ecopath with Ecosim (EwE, Christensen et al., 2005) and the two Gulf systems were first modelled using the Inverse method (Vézina and Platt, 1988; Savenkoff et al., 2001, 2007a,b). Results were subsequently imported into Ecopath with Ecosim (see below).

Based on data availability and the ecological and commercial significance of the species, the organisms inhabiting the different

ecosystems were divided into selected functional groups or compartments. Broadly, these can be distinguished into marine mammal groups, seabirds, fish groups, invertebrate groups, one phytoplankton group, and one detritus group (see Appendix A for more detailed definition of the groups, and Heymans, 2003a; Morissette et al., 2003; Bundy, 2004; Savenkoff et al., 2004a,b for additional details). The nearshore regions of the study areas were not included in three of the four modelled areas since shallower zones are not covered by annual bottom-trawl surveys and because exchanges between the infra-littoral and mid- to offshore zones are still poorly understood. However, although the models of the Newfoundland–Labrador Shelf ostensibly included the nearshore, other than American lobster (*Homarus americanus*), little heed was paid to the inshore ecosystem (e.g., macrophytes were not included in the model). Thus, this can also be considered a Shelf model.

In order to explore the effects of uncertainty on the model results, a perturbation analysis was applied to the balanced models. For the models developed using EwE, the Pedigree routine (Morissette, 2005) was first used to describe the range of uncertainty for the biomass and diet composition input parameters. Values ranged from  $\pm 80\%$  for poorly estimated parameters such as some diets and biomass estimates to  $\pm 10\%$  for parameters such as biomass estimates for seals and cod. The option to “nudge” the production to biomass ratio (P/B) and consumption to biomass ratio (Q/B) in steps of 10% of their original values was also used. The “Autobalance” routine (Kavanagh et al., 2004) was then used to randomly select parameters from this range (Bundy, 2004) and find a new balanced solution. For the Inverse method, all model parameters were perturbed to a maximum of their standard deviation (Savenkoff et al., 2007a,b) and a new optimal solution estimated. Each of these balanced inverse solutions was imported into EwE to estimate mortality (due to fishing, predation, and other sources), the basic emergent properties and network analysis indices for the two time periods, and estimates of the associated uncertainties for the Gulf models. Note that in the Inverse method, although biomass information is used in the calculation of flows, it is not a state variable as in the Ecopath models, thus there are no model estimates of the effects of uncertainty on biomass estimates for the four Gulf models.

For all models, 31 balanced solutions were obtained for each ecosystem and period corresponding to one solution without perturbation (the “initial solution”) and 30 iterations with random perturbations of the input data, so as to provide an overall view of the ecosystem and to identify robust patterns. When comparing models between time periods for each ecosystem, a Mann–Whitney *U*, two independent samples test was used to test whether differences between the models were significant, or an artifact created by the uncertainty of the input parameters.

The four NW Atlantic ecosystems were compared at a number of levels using: (1) ecological indicators; (2) keystone species; (3) functional role indicators; and (4) whole system indicators.

### 2.1. Ecological indicators

Methratta and Link (2006) recommended the use of eight indicators to describe the state of an ecosystem. We adapt their approach and use five of these indicators (fisheries landings, total finfish biomass, planktivore biomass, demersal (benthivore) fish biomass and flatfish biomass), drop two indicators (mean individual fish length and mean individual fish weight, due to differences in survey protocols) and redefine indicator species biomass as keystone species (see below). To these five indicators we added four; the mean trophic level of landings (Pauly et al., 1998), the commercial invertebrate:demersal (P:D) ratio, and the commercial invertebrate:demersal (I:D) biomass ratio. The latter two ratios integrate the individual data for planktivorous and demersals fish and commercial invertebrates and demersal fish,

**Table 1**  
Descriptions of the models for the four NW Atlantic ecosystems.

	ESS <sup>a</sup>	SGSL <sup>b</sup>	NGSL <sup>c</sup>	NFLD <sup>d</sup>
NAFO Divisions	4VsW	4T	4RS	2J3KLNO
Area (km <sup>2</sup> )	102,325	64,075	103,812	495,000
Inshore limit (m)	100	15	37	0
Greatest depth sampled (m)	400	200	530	1000
# Functional groups	39	30	32	50
Perturbation method	EwE autobalance	Inverse method	Inverse method	EwE autobalance
Pre-collapse	1980–1985	1985–1987	1985–1987	1985–1987
Post-collapse	1995–2000	1994–1996	1994–1996	1995–1997

<sup>a</sup> Eastern Scotian Shelf.

<sup>b</sup> Southern Gulf of St. Lawrence.

<sup>c</sup> Northern Gulf of St. Lawrence.

<sup>d</sup> Newfoundland and Labrador.



and are indicators of the negative effects of fishing (Rochet and Trenkel, 2003).

Data for the nine indicators were taken from the data used for the Ecopath models. For the eastern Scotian Shelf and Newfoundland–Labrador models, all the indicators except fisheries landings were averaged over the 30 balanced model solutions. For the two Gulf models, since biomass was not perturbed in the 30 model iterations, only the mean trophic level of landings was averaged over the 30 balanced model solutions.

## 2.2. Keystone species

Rather than use one indicator species, we chose to use a suite of indicator species defined here as keystone species. Keystone species are species which have a strong role in the structure and function of ecosystems, despite having a relatively low biomass and low food intake (Power et al., 1996). Thus they impact the ecosystems that they inhabit disproportionately to their abundance. This definition thus excludes species which structure ecosystems through their high biomass, such as plankton. Given this important role, the keystone species in each ecosystem were used as indicators of ecosystem changes. They were determined from the eight Ecopath models using the trophic impact routine, following Libralato et al. (2006):

$$KS_i = \log_{10}[\varepsilon_i(1 - p_i)] \quad (1)$$

where  $KS_i$  is the keystone species  $i$ ,  $p_i$  the proportion of the total biomass attributable to group  $i$  (excluding detritus), and  $\varepsilon_i$  the total impact of group  $i$  defined as  $\sqrt{\sum_{j \neq i}^n m_{ij}^2}$  with  $m_{ij}$  the impact of group  $i$  on group  $j$  where the impact of group  $i$  on itself is not included. Keystone species were defined as species with a  $KS$  close to, or greater than zero (Libralato et al., 2006).

The following keystone species indicators were compared across the models: biomass or abundance trends, total mortality, predation mortality, and their main prey and predators. When available, empirical data were used for the biomass or abundance trends, otherwise Ecopath estimates were used.

## 2.3. Functional role indicators

Following from the keystone species, and ecological indicators, species were grouped into three functional groups to explore basic structural changes in the four ecosystems: marine mammals (seals, cetaceans), piscivorous fish (e.g., cod, Greenland halibut *Reinhardtius hippoglossoides*, American plaice *Hippoglossoides platessoides*, skates, redfish *Sebastes* spp., large demersals, small demersals, large pelagics, small piscivorous pelagics, etc.) and planktivorous fish (capelin *Mallotus villosus*, sandlance *Ammodytes* spp., Arctic cod *Boreogadus saida*, and planktivorous small pelagics such as Atlantic herring *Clupea harengus*). Changes in biomass, consumption and fish consumption were compared across models.

An overlap index between marine mammals and fisheries for each ecosystem was developed by Morissette (2007), using a modified version of the resource overlap index of Kaschner (2004), to explore the degree of interaction between marine mammals and fisheries. The marine mammal overlap index presented here ( $\alpha_{f,m}$ ) uses a weighting factor representing the relative importance of fisheries versus marine mammals as consumers within a given ecosystem:

$$\alpha_{f,m} = \left( \frac{2 * \sum_k (p_{m,k} * p_{f,k})}{\sum_k p_{m,k}^2 + \sum_k p_{f,k}^2} \right) * \left( \frac{Q_m}{(Q_m + C_f)} * \frac{C_f}{(Q_m + C_f)} \right) \quad (2)$$

where  $\alpha_{f,m}$  is the quantitative overlap between a fishery  $f$  and a marine mammal group  $m$  in the ecosystem, and the first term expresses the qualitative similarity in diet/catch composition between the

marine mammal group  $m$  and fisheries  $f$  sharing the resource or food type  $k$ , with  $p_{m,k}$  and  $p_{f,k}$  representing the proportions of group  $k$  in the diet of marine mammals  $m$  or the catch by fishery  $f$ . This term is multiplied by the product of the proportion of total food consumption by marine mammals  $Q_m$  and the proportion of total fisheries catches  $C_f$  in the ecosystem. This index scales from 0 (no overlap) to 0.250 (identical resource). When resource use is identical between two groups, the first term of Eq. (2) is equal to 1 and each proportion of the second term is 0.5 (or 0.25 for the product).

## 2.4. Whole system indicators

So far we have looked at ecological indicators of individual keystone species and functional group. In the last series of comparisons, we look at changes to the whole ecosystem, using a series of metrics including ecosystem summary statistics and network analysis, as have been described in several comparative studies (Heymans, 2003b; Shannon et al., 2003; Bundy, 2005; Cury et al., 2005; Morissette et al., 2009). For the summary statistics and the network indices, the number of functional groups in each model was aggregated into 30 groups to ensure that the model comparisons were valid and that any differences detected were not due to structural differences (Abarca-Arenas and Ulanowicz, 2002).

### 2.4.1. Summary statistics

The summary statistics provided by Ecopath are well described in Christensen et al. (2005). They summarise various attributes of the ecosystem and several can be associated with the maturity of an ecosystem *sensu* Odum (1969) and Christensen (1995). The total system throughput (TST) is the sum of all the flows in an ecosystem (total consumption, total export, total respiration and total flows to detritus) and thus a measure of the size of the ecosystem. Total production is the sum of all production in the ecosystem and the net system production is the total primary production minus total respiration. Values close to zero indicate a mature system, larger values an immature system. The ratio of primary production to total biomass (PP/B) is a measure of ecosystem maturity (Christensen, 1995), where an increase represents an increase in maturity. The total biomass/total system throughput (B/TST) ratio represents the amount of biomass in a system that can be supported by the available energy flow in a system. Here an increase represents an increase in maturity. The connectance index (CI) is a measure of how connected an ecosystem is and is measured as the ratio of the number of actual links to the number of possible links (Christensen et al., 2005). An increase in connectance indicates more branching in the ecosystem, and a more mature system (Odum, 1971). The system omnivory index (SOI) is an index of how widely a functional group feeds across the different trophic levels. A low value indicates a narrow trophic feeding range. Together, the connectance index and SOI give an overall indicator of complexity and diversity of feeding interactions.

### 2.4.2. Network indices

Network analysis incorporates analytical techniques for studying indirect trophic effects and the structure of recycling pathways by assessing overall ecosystem characteristics as a set of mathematical measures to quantify its organization and redundancy (Ulanowicz and Kay, 1991). The network analysis indicators used to examine the status of the four ecosystems as depicted by their Ecopath models include statistical entropy (H), average mutual information (AMI), ascendancy:capacity ratio (A:C), redundancy (R or overhead on internal flows, in % flowbits) and Finn cycling index (%) (Heymans, 2003b).

The diversity of flows or systems entropy (H) is an indication of the uncertainty of the system and represents the total number and

diversity of flows in a system (Mageau et al., 1998), and is calculated as:

$$H = - \sum_{ij} \frac{T_{ij}}{TST} \cdot \log \left( \frac{T_{ij}}{TST} \right) \quad (3)$$

where  $T_{ij}$  is the flow between any two compartments and TST includes all outflows (respiration, catch, export) from each compartment.

The average mutual information (AMI) measures the organization of the exchanges among components. A rise in AMI signifies that the system is becoming more constrained and is channeling flows along more specific pathways (Ulanowicz, 1997). Thus, the AMI is calculated as:

$$AMI = \sum_{ij} \left( \frac{T_{ij}}{TST} \right) \cdot \log \left( \frac{T_{ij} \cdot TST}{T_j \cdot T_i} \right) \quad (4)$$

where  $T_i$  is the sum of all material leaving the  $i$ th component and  $T_j$  is the sum of all flows entering the  $j$ th component (Mageau et al., 1998).

Ascendency describes both the growth (TST) and development (AMI) of the system (Ulanowicz, 1986) and is therefore the product of TST and average mutual information (AMI), and in Ecopath is defined in terms of flow, or:

$$A = \sum_{ij} (T_{ij}) \cdot \log \left( \frac{T_{ij} \cdot TST}{T_j \cdot T_i} \right) \quad (5)$$

Here we express ascendency as the A:C ratio, that is the proportion of the development capacity which is the upper limit for the size of the ascendency. The development capacity is estimated as the product of entropy and the total throughput of the system ( $C = H * TST$ ).

The complement to the ascendency is the overhead, which gauges the inefficient degrees of freedom that a system retains (Ulanowicz, 2000). Overhead is divided into import, export, respiration and internal flow (Ulanowicz, 2000), and the internal flow overhead (IFO or R) seems to be the best indicator of a change in degrees of freedom of the system, i.e. what is the distribution of energy flow among the pathways in the ecosystem. It is also defined as the pathway redundancy (R) (Ulanowicz, 1997). Thus, if the R is high the flows among the pathways are not concentrated in one or two main pathways but there are many ways for energy to get from one compartment to another. Christensen (1995) linked the overhead to ecosystem stability and Heymans (2003b) proposed R as an index of the system's resilience. The redundancy is calculated as (Ulanowicz, 2004):

$$R = - \sum_{i=1}^n \sum_{j=1}^n (T_{ij}) \cdot \log \left( \frac{T_{ij}^2}{\sum_{j=1}^n T_{ij} \cdot \sum_{i=1}^n T_{ij}} \right) \quad (6)$$

**Table 2**

Summary of changes in ecological indicators from the 1980s to 1990s for the four NW Atlantic ecosystems (+ = increase, – = decrease and ~ = no significant change). All values are  $t \text{ km}^{-2}$ , with the exception of the ratios which are dimensionless. Values are the average of the 31 estimated models, with the exception of the biomass estimates for the two Gulf models. See text for further details.

	ESS			NFLD			NGSL			SGSL		
	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change
Total landings	1.73	0.49	–	1.31	0.28	–	1.89	0.48	–	2.81	1.99	–
Mean trophic level of landings	3.54	3.29	–	3.81	3.16	–	3.83	3.1	–	3.33	3.17	–
Finfish biomass	16.46	30.07	+ <sup>a</sup>	34.57	20.65	–	46.41	22.41	– <sup>b</sup>	29.95	22.55	– <sup>b</sup>
Planktivorous biomass + capelin	2.43	22.13	+ <sup>a</sup>	17.45	9.97	– <sup>a</sup>	22.12	17.96	~	10.24	13.02	~
Demersal biomass	12.83	7.25	– <sup>a</sup>	12.42	8.10	– <sup>a</sup>	21.78	3.85	– <sup>b</sup>	14.74	8.24	– <sup>b</sup>
Flatfish biomass	1.81	1.41	– <sup>a</sup>	3.28	2.79	– <sup>a</sup>	1.58	1.46	~	6.92	5.74	– <sup>b</sup>
Pelagic:demersal biomass ratio	0.19	3.13	+ <sup>a</sup>	1.44	1.22	– <sup>a</sup>	1.02	4.67	+ <sup>b</sup>	0.69	1.58	+ <sup>b</sup>
Invertebrate biomass	3.90	19.24	+ <sup>a</sup>	4.70	4.04	– <sup>a</sup>	1.69	1.48	~	3.35	3.61	~
Commercial invertebrate:demersal fish biomass ratio	0.42	3.80	+ <sup>a</sup>	0.53	0.69	+ <sup>a</sup>	0.08	0.38	+ <sup>b</sup>	0.23	0.44	+ <sup>b</sup>

<sup>a</sup> Significant change (Mann–Whitney  $U$  test).

<sup>b</sup> Significant change (Student's  $t$ -test).

Similar to the ascendency, it is here presented as a percentage of the development capacity.

There is a trade-off in ecosystem functioning between resilience and efficiency. Resilience is gained by increasing the diversity of pathways, but this leads to decreased efficiency in energy flow. Efficiency is gained by reducing the number of pathways to those which are most efficient. However, the rigidity of such an efficient configuration makes the system is more vulnerable.

The Finn cycling index (FCI) quantifies the relative amount of recycling and is an indication of stress and structural differences either among models (Finn, 1976) or through time, and is calculated as:

$$FCI = \frac{TST_c}{TST_s} \quad (7)$$

where  $TST_c$  is the total flow that is recycled, and  $TST_s$  is the total flow through the system.

### 2.5. Multivariate analysis

In order to systematically integrate and explore the results for the keystone species indicators and for all the indicators described here, a multivariate analysis of the percentage change in the indicators from the 1980s to the 1990s was conducted. We used principle components analysis (PCA, SPSS (vers. 11.5.0)), where the data were first 4th root transformed.

## 3. Results

### 3.1. Ecological indicators

Of the nine ecological indicators (Table 2), two are directly related to exploitation, total landings and the mean trophic level of the catch (Fig. 2). Both decreased from the 1980s to the 1990s in the four ecosystems, indicating loss in fisheries production and fishing down of the food web (Pauly et al., 1998). Since the collapse or near collapse of cod stocks in the early 1990s, fisheries in all areas have switched their focus to lower trophic levels (forage fish and invertebrates such as shrimp, scallops and lobster). However, productivity at these levels does not match earlier productivity. When landings are expressed on a unit area basis (Fig. 3), the most productive system in terms of fishery landings until the early 1990s was the eastern Scotian Shelf. The southern Gulf of St. Lawrence also supported very productive fisheries during the 1980s, and of the four systems, has experienced the least reduction in catch since the 1980s. Indeed catches have increased since the mid-1990s (high landings of herring and snow crab *Chionoecetes*

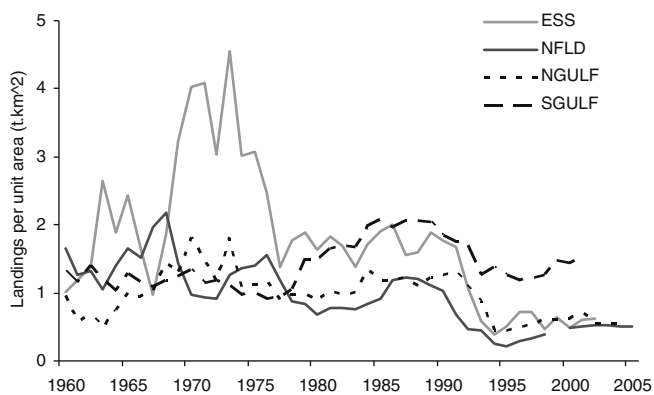


Fig. 3. Total landings from 1960 as in Fig. 2, expressed as  $t\ km^{-2}\ yr^{-1}$ . Note that NAFO data for Newfoundland in 1999 are incomplete and are not included.

opilio) and are similar to, or higher than, levels in the 1960s and 1970s.

Total finfish biomass decreased in all ecosystems, with the exception of the eastern Scotian Shelf (Table 2). Planktivore biomass decreased in Newfoundland–Labrador, did not change in the northern or southern Gulf of St. Lawrence, but increased substantially in the eastern Scotian Shelf, resulting in the increase in total finfish. The greatest decrease in total finfish biomass occurred in the northern Gulf of St. Lawrence. The biomass of demersal fish decreased in all ecosystems; the greatest decrease occurred in the northern Gulf of St. Lawrence, the smallest change in Newfoundland–Labrador. Flatfish biomass decreased in the eastern Scotian Shelf and Newfoundland–Labrador ecosystems, slightly in the southern Gulf of St. Lawrence, but did not change in the northern Gulf. The biomass of commercial invertebrates increased on the eastern Scotian Shelf, decreased in Newfoundland–Labrador and there was no change in the northern or southern Gulf of St. Lawrence models.

The P:D and I:D ratios increased in all ecosystems, except in Newfoundland–Labrador where there was a decrease in the P:D ratio. The indicators demonstrate a switch from a demersal fish dominated ecosystems to ecosystems dominated by forage species.

The four NW Atlantic ecosystems follow similar trends in total landings, mean trophic level of landings, biomass of demersal fish and the P:D and I:D ratios. However, there are also some differences. All indicators except the I:D ratio decreased in Newfoundland–Labrador and most decreased in the northern Gulf of St. Lawrence whereas the southern Gulf of St. Lawrence has undergone the least change, and catches have improved since the mid 1990s. Finfish biomass only increased on the eastern Scotian Shelf, due to a large increase in planktivorous fish; it decreased elsewhere.

### 3.2. Keystone species

Nine functional groups were identified as “keystone” in the four ecosystems over the two time periods (Table 3). The results suggest that no one species or functional group was keystone in all four ecosystems, although notably, large cod had high keystone indices in the 1980s in all ecosystems except Newfoundland–Labrador. Planktivorous small pelagics and capelin were common to three of the four ecosystems, and when taken together as a functional group, the eastern Scotian Shelf is the one ecosystem where neither had a keystone role in the 1980s. Capelin were keystone species in Newfoundland–Labrador and the northern Gulf of St. Lawrence in both time periods, and planktivorous small pelagics were keystone in the southern Gulf of St. Lawrence for both time periods.

The results indicate that three species of seal, grey, hooded and harp seals, were keystone species in one or more ecosystems. Grey

Table 3

(a) Ranking of functional groups according to their index of “keystoneness” (Eq. (1)), where grey represents a keystone group and the number represents the rank order of keystoneness in each ecosystem; (b) ranking of “high impact” functional groups, where grey represents a high impact group and the number represents the rank order of high impact in each ecosystem.

Functional group	ESS 80s	ESS 90s	4T 80s	4T 90s	4RS 80s	4RS 90s	NFLD 80s	NFLD 90s
(a)								
Cetaceans	2					2	1	1
Grey seals		1		2		4		
Harp seals					4	1	3	2
Hooded seals							4	
Lcod	1		2		1			
Skates								3
Sm Pels <sup>a</sup>			1	1				
Capelin					2	3	2	4
Shrimp		2						
(b)								
Large zooplankton	3	3					3	4
Small zooplankton	4			2	1			
Phytoplankton	1	1					6	

<sup>a</sup> Sm Pels = planktivorous small pelagics.

seals were keystone in the 1990s for the more southerly ecosystems (eastern Scotian Shelf, and southern Gulf of St. Lawrence) while harp seals were keystone over both time periods for the more northern ecosystems (northern Gulf of St. Lawrence and Newfoundland–Labrador). Harp seals do not occur on the eastern Scotian Shelf, and hooded seals were only keystone in Newfoundland–Labrador in the 1980s.

In general, the keystone species remained the same from one time period to another, with some notable exceptions. Grey seals became keystone species on the eastern Scotian Shelf and in the two Gulf ecosystems in the 1990s, while the large cod ceased to be a keystone species in these ecosystems. In the northern Gulf of St. Lawrence, cetaceans became keystone in the 1990s, where as in Newfoundland–Labrador they were keystone in both time periods. Finally in Newfoundland–Labrador, hooded seals ceased to be keystone in the 1990s, while skates became keystone. Of the four ecosystems, Newfoundland–Labrador was the most consistent from one period to the next, the eastern Scotian Shelf the least.

Three groups, skates, shrimp and hooded seals, were keystone in only one ecosystem. The hooded seals were not considered further here since their abundance is low in the northern and southern Gulf of St. Lawrence and they do not occur on the eastern Scotian Shelf. Skates and shrimp were included as “keystone” species since they occur in all ecosystems and skate, like flatfish, can be considered an indicator species.

Thus eight species/functional groups were identified as keystone species and occur in all or most of the ecosystems. They represent top predators (marine mammals and cod) and mid-trophic levels or forage fish (small planktivorous fish and capelin) in the ecosystems.

Although keystone species do not include species with a large biomass at the lower trophic levels, phytoplankton, and large and small zooplankton were collectively identified as keystone species in all four ecosystems (Table 3) by Eq. (1). We have included them in the analysis of biomass trends below as “high impact” species, with  $\varepsilon_i$  the total impact of group  $i > 0.9$ . In addition, cod were analysed as large and small cod.

#### 3.2.1. Biomass/abundance trends

Estimates of phytoplankton and zooplankton abundance were derived from the continuous plankton recorder data series for the Scotian Shelf (eastern Scotian Shelf) and the Western Atlantic (New-

foundland–Labrador) (Sameoto, 2001; Pepin et al., 2007; AZMP, 2007), from the mackerel egg survey in the southern Gulf (Runge et al., 1999; Ringuette et al., 2002). No zooplankton data that extended from the 1980s to the 1990s were available for the northern Gulf (Patrick Ouellet, DFO, personal communication). In the Gulf of St. Lawrence, there were no available phytoplankton data for the modelled time periods. For the areas with data, phytoplankton increased, and large and small zooplankton decreased (Table 4).

Shrimp increased in all areas, although in the northern Gulf, shrimp decreased slightly from the 1980s to the 1990s (Savenkoff et al., 2006), but have since increased (DFO, 2007e). In Newfoundland–Labrador, the estimate of shrimp abundance from the 1980s is based on CPUE data (DFO, 2005a), while more recent survey data indicates an increase since the early 1990s (M. Koen-Alonso, DFO, personal communication).

Planktivorous small pelagics were discussed above. Estimates of capelin abundance are uncertain in the Gulf of St. Lawrence (see below). Overall they appear to have increased in the eastern Scotian Shelf and the southern Gulf, remained unchanged in the northern Gulf and decreased in Newfoundland–Labrador. Large cod and skates decreased every where, harp and grey seals increased everywhere they occur, except for grey seals in Newfoundland–Labrador, where they are at the northern extent of their range. There are no data for abundance trends of cetaceans in these areas.

There is a general concordance in the direction of change in keystone species abundance in all four ecosystems over time (Table 4). The general pattern consists of an increase in seals, a decrease in cod and skates, an increase in shrimp, a decrease in large and small zooplankton and an increase in phytoplankton in the eastern Scotian Shelf and Newfoundland–Labrador. This is less evident for the two Gulf of St. Lawrence ecosystems where there is currently no plankton data to verify this trend. However, the four ecosystems differ in the abundance trends of the forage fish, as seen above. Planktivorous small pelagics and capelin increased in the eastern Scotian Shelf, but decreased in Newfoundland–Labrador and remained unchanged in the southern and northern Gulf. In the northern Gulf, capelin biomass (the main forage species) was assumed to be the same in both periods, but this may reflect the lack of information on this and other forage species (e.g., sand lance and Arctic cod) in this region.

**Table 4**  
Biomass/abundance trends of keystone species from the 1970s to the 1990s for the four NW Atlantic ecosystems, based mainly on empirical survey data. Grey boxes indicate where there is no data, or the data is uncertain.

	ESS	SGSL	NGSL	NFLD
Phytoplankton	+ <sup>a</sup>	?	?	+ <sup>b</sup>
Small zooplankton	- <sup>a</sup>	- <sup>c,d</sup>	?	- <sup>b</sup>
Large zooplankton	- <sup>a</sup>	?	?	- <sup>b</sup>
Shrimp	+ <sup>e</sup>	+ <sup>f</sup>	- <sup>f,g</sup>	+ <sup>h</sup>
Planktivorous small pelagics	+	-	-	-
Capelin	+	+	~	-
Skates	-	-	-	-
Large cod	-	-	-	-
Grey seals	+ <sup>i</sup>	+ <sup>i</sup>	+ <sup>i</sup>	~
Harp seals	NA	+ <sup>j</sup>	+ <sup>j</sup>	+ <sup>j</sup>
Cetaceans	?	?	?	?

<sup>a</sup> Sameoto (2001).

<sup>b</sup> Pepin et al. (2007).

<sup>c</sup> Ringuette et al. (2002).

<sup>d</sup> Runge et al. (1999).

<sup>e</sup> DFO (2006).

<sup>f</sup> Ecopath value.

<sup>g</sup> DFO (2007).

<sup>h</sup> DFO (2005a).

<sup>i</sup> Mohn and Bowen (1996).

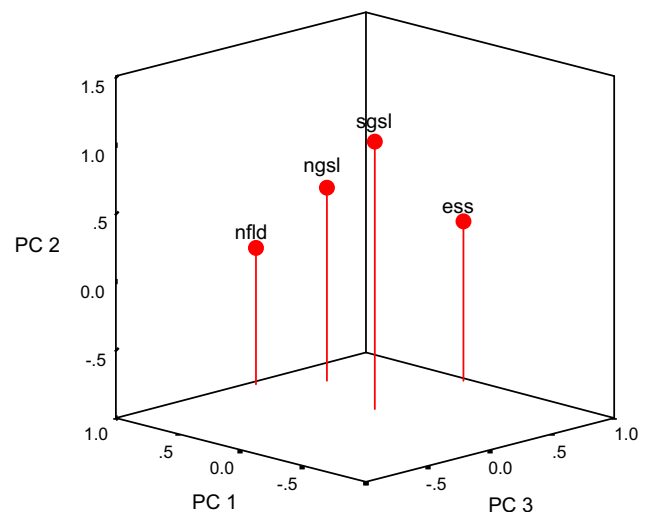
<sup>j</sup> Hammill and Stenson (2005).

### 3.2.2. Total mortality, predation mortality and predators of keystone species

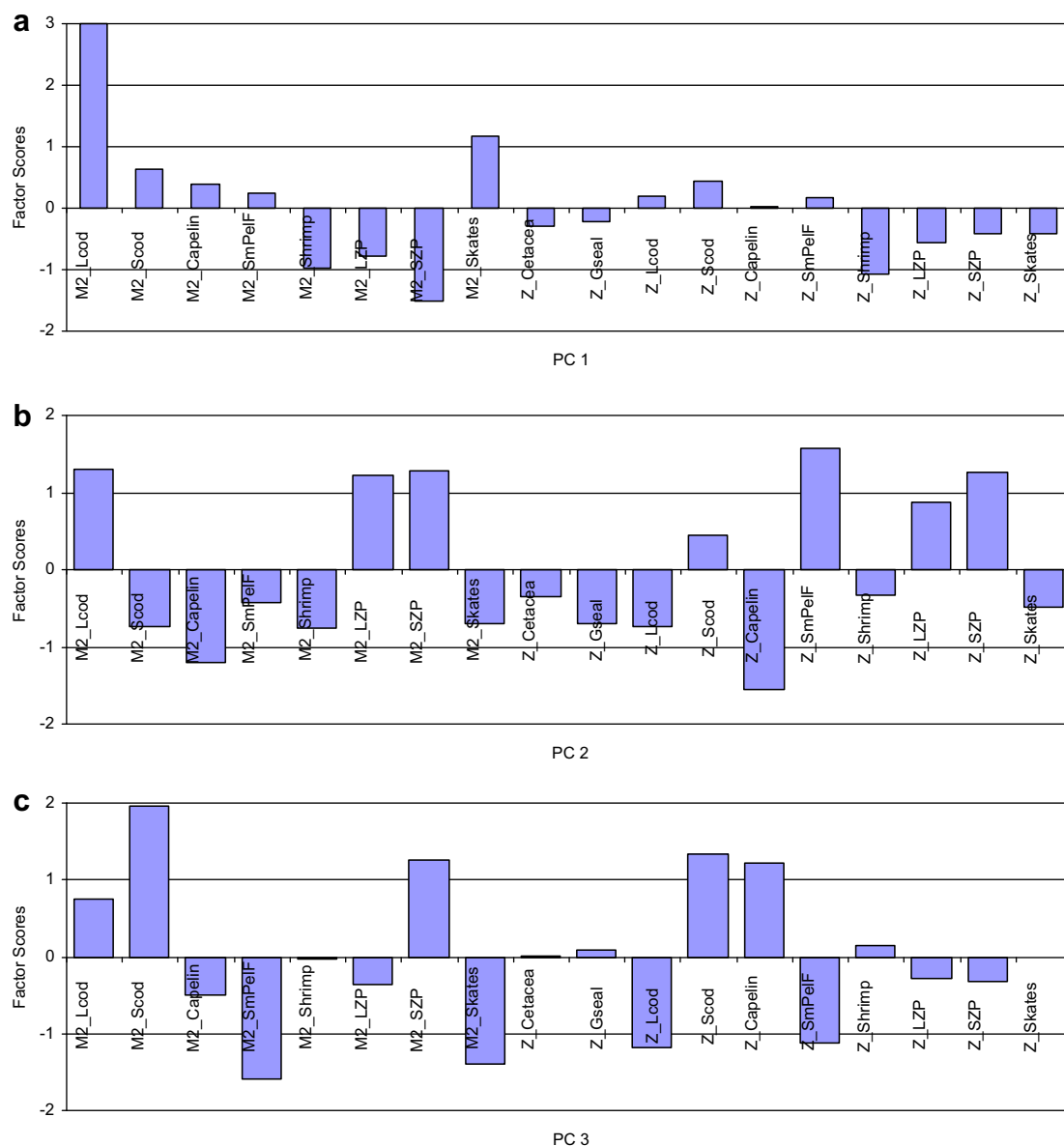
The PCA analysis of the mortality and predation mortality indices (derived from mass balance model estimates) for the keystone species and the 3 “high impact” species indicated that there are differences across the four ecosystems (note harp seals were not included in the PCA since they do not occur on the eastern Scotian Shelf). The first principle component, PC, (after varimax rotation) explained 37% of the variance in the data, the second 29%, and the third 28%, making a total of 93% of the variance explained. The four ecosystems were positively loaded on all three axes except Newfoundland–Labrador which was slightly negative on PC2. The first PC grouped Newfoundland–Labrador and the northern Gulf of St. Lawrence, and the eastern Scotian Shelf and southern Gulf of St. Lawrence together (Fig. 4). PC2 separated the southern Gulf of St. Lawrence from the other three areas, and PC3 separated the eastern Scotian Shelf.

Of the 18 indices included in the PCA, only a few influenced the principle components, and thus the differentiation between the four ecosystems. The separation of Newfoundland–Labrador and northern Gulf of St. Lawrence on PC1 was due to the high positive and negative factor scores for predation mortality of large cod and small zooplankton, respectively (Fig. 5a). The greatest estimated increases in predation mortality occurred in Newfoundland–Labrador and the northern Gulf of St. Lawrence, the least on eastern Scotian Shelf. Total mortality of large cod was high in all the ecosystems in both the 1980s but decreased everywhere in the 1990s except Newfoundland–Labrador (Table 5). In the 1980s, the high large cod mortality was due to fishing. This was not the case in the 1990s when over 50% of large cod mortality was due to predation in the northern and southern Gulf of St. Lawrence and in Newfoundland–Labrador. Harp and grey seals were the main predators in the northern and southern Gulf, and harp and hooded seals in Newfoundland–Labrador. However, large cod had few predators on the eastern Scotian Shelf, and while grey seals were their main predators, this predation was very low and the cause of the high mortality was not attributable to predation (unexplained mortality; Bundy and Fanning, 2005).

Estimates of the predation mortality of small zooplankton decreased in Newfoundland–Labrador and northern Gulf of St. Lawrence, and increased in the other two areas. Many species prey on zooplankton and their main predators varied to some degree



**Fig. 4.** PCA results for the change in keystone species mortality indicators. Scatter plot shows the loadings of the four ecosystems on the first three principle components which explained 93% of the total variance in the data. See Fig. 1 for further details.



**Fig. 5.** PCA results for the change in keystone species mortality indicators showing the factor scores of the indicators on (a) the first principle component, (b) the second principle component and (c) the third principle component. M2 = predation mortality, Z = total mortality, Lcod = large cod, Scod = small cod, SmPelF = small planktivorous plankton feeders, lzp = large zooplankton and szp = small zooplankton.

in the different ecosystems. The main predator of small zooplankton on the eastern Scotian Shelf and Newfoundland–Labrador was large zooplankton, accounting for 75–85% of total mortality in both time periods, whereas in both Gulf models, small zooplankton themselves were the principal consumers of the small zooplankton compartment (between 46% and 90% of total mortality). Other main predators included large zooplankton and forage fish (Gulf models) and shrimp and forage fish (eastern Scotian Shelf and Newfoundland–Labrador).

The southern Gulf of St. Lawrence had the highest loading on PC2, followed by the northern Gulf of St. Lawrence (Fig. 5b). This axis is more multivariate than PC1, with high factor scores for 7 of the indices: total mortality of capelin, small pelagic feeders and small zooplankton, and predation mortality of large cod, capelin large zooplankton and small zooplankton.

Estimated total mortality and predation mortality of capelin decreased in the southern and northern Gulf of St. Lawrence, both increased in Newfoundland–Labrador and on the eastern Scotian Shelf total mortality increased while predation mortality de-

creased. In all areas capelin was an important forage species, and most of the mortality was due to predation. They were preyed on by predators such as cetaceans, seals, cod, redfish and Greenland halibut.

Changes in estimated total mortality of planktivorous small pelagics from the 1980s to the 1990s were inconsistent between the four ecosystems; total mortality decreased on the eastern Scotian Shelf, increased in the two Gulf ecosystems and did not change in Newfoundland–Labrador. However, predation mortality was estimated to decrease on the eastern Scotian Shelf and the southern Gulf but the estimates for northern Gulf and Newfoundland–Labrador did not change (Table 5). Predation accounted for most of the mortality on this forage group, though there is a great degree of variation in estimates, especially in Newfoundland–Labrador. Declines in the northern and southern Gulf were less severe. They were preyed on by a wide array of predators in all systems, including redfish, large cod, cetaceans, Greenland halibut, and demersal feeders. In the Gulf of St. Lawrence, fishing was also an important source of mortality of planktivorous small pelagics, accounting for



**Table 5**  
Summary of changes in mortality of keystone species and high impact species indicators from the 1980s to 1990s for the four NW Atlantic ecosystems (+ = increase, – = decrease and ~ = no change). All mortality values are the average of estimates from the 31 models ( $\text{yr}^{-1}$ ). Note estimates of total mortality frequently did not vary across the 31 model solutions (in the eastern Scotian Shelf and Newfoundland–Labrador models, total mortality was not directly perturbed) and thus changes could not be tested for statistical significance. See text for further details.

	ESS			NFLD			NGSL			SGSL		
	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change
M2_Lcod	0.01	0.02	+ <sup>a</sup>	0.01	0.43	+ <sup>a</sup>	0.02	0.18	+ <sup>a</sup>	0.04	0.12	+ <sup>a</sup>
M2_Scod	0.42	1.26	+ <sup>a</sup>	1.35	1.71	+ <sup>a</sup>	0.62	0.88	+ <sup>a</sup>	0.52	0.51	~
M2_Capelin	0.54	0.68	+ <sup>a</sup>	1.06	1.43	+ <sup>a</sup>	0.73	0.95	+ <sup>a</sup>	0.87	0.68	– <sup>a</sup>
M2_SmPelF	0.43	0.10	– <sup>a</sup>	0.21	0.20	~	0.31	0.32	~	0.36	0.26	– <sup>a</sup>
M2_Shrimp	1.49	1.49	~	1.52	1.23	– <sup>a</sup>	1.63	0.61	– <sup>a</sup>	3.19	2.63	– <sup>a</sup>
M2_LZP	2.61	2.83	~	3.00	3.32	~	2.76	2.93	+ <sup>a</sup>	5.20	2.88	– <sup>a</sup>
M2_SZP	5.52	7.40	+ <sup>a</sup>	7.38	7.11	~	3.96	3.01	– <sup>a</sup>	3.24	4.00	+ <sup>a</sup>
M2_Skates	0.11	0.07	– <sup>a</sup>	0.02	0.10	+ <sup>a</sup>	0.23	0.25	~	0.24	0.24	~
Z_Cetaceans	0.04	0.04	~	0.10	0.10	~	0.07	0.06	– <sup>a</sup>	0.08	0.08	~
Z_Grey seals	0.12	0.12	~	0.12	0.12	~	0.06	0.04	– <sup>a</sup>	0.16	0.15	~
Z_Large cod	0.63	0.50	–	0.65	0.67	~	0.45	0.28	–	0.46	0.27	–
Z_Small cod	0.76	1.43	+	1.61	1.87	+	0.48	0.94	+	0.58	0.58	~
Z_Capelin	0.70	1.08	+	1.18	1.66	+	0.81	0.23	– <sup>a</sup>	1.13	0.15	– <sup>a</sup>
Z_SmPelF	0.53	0.47	–	0.28	0.28	~	0.29	0.33	+	0.35	0.41	+ <sup>a</sup>
Z_Shrimp	1.81	1.83	~	1.76	1.49	–	1.77	0.95	–	4.76	3.79	–
Z_LZP	3.19	3.20	~	3.53	3.59	~	3.89	2.52	–	3.96	3.20	– <sup>a</sup>
Z_SZP	8.45	8.64	~	8.72	8.57	~	6.65	6.43	~	5.58	6.55	+ <sup>a</sup>
Z_Skates	0.20	0.20	~	0.29	0.30	~	0.30	0.23	–	0.23	0.23	~
Z_Harp seals				0.10	0.10	~	0.07	0.06	~	0.07	0.05	~

<sup>a</sup> Significant change (Mann–Whitney *U* test).

between 24% and 43% of total mortality, whereas in Newfoundland–Labrador and the eastern Scotian Shelf, it had little to no impact.

The indices above affect the northern and southern Gulf of St. Lawrence similarly. The separation of these two areas on PC2 can be explained by the mortality of large and small zooplankton; both total and predation mortality for the two groups increased in the southern Gulf of St. Lawrence, but decreased in the northern Gulf of St. Lawrence.

The third principle component separated the eastern Scotian Shelf from the other ecosystems, primarily due to the predation mortality of small cod (Fig. 5c). Model estimates of predation mortality on small cod increased in all ecosystems except the southern Gulf, with the greatest increase occurring on the eastern Scotian. In all cases, predation mortality accounted for most of the total mortality in the 1990s, thus predation mortality approximated total mortality. In the 1980s, one of the main predators of small cod in all systems was large cod (Table 6). Demersal predators were the other main predator of small cod, except in the southern Gulf, where it was seals. In the 1990s, seals were important predators

of small cod in all the ecosystems, although large cod were still important predators in the two Gulf models, and demersal predators were important in the eastern Scotian Shelf and Newfoundland–Labrador models. The latter two systems had a greater diversity of predators accounting for 75% of the predation on small cod in both time periods.

### 3.3. Functional role indicators

#### 3.3.1. Consumption by functional groups

There were common trends in biomass of the three functional groups across the four ecosystems; the biomass of marine mammals increased in all areas; piscivorous fish biomass decreased everywhere while planktivorous fish biomass only increased on the eastern Scotian Shelf. Changes in the total consumption by these functional groups reflect these trends. In the 1980s, piscivorous fish were the main predators of fish in all areas (Fig. 6a). By the 1990s, their influence as predators declined in all systems and marine mammals consumed slightly more fish than piscivorous fish in the northern and southern Gulf of St. Lawrence and they consumed around 66% as much fish as was consumed by piscivorous fish in Newfoundland–Labrador (Fig. 6b). On the eastern Scotian Shelf the situation was a little different. The amount of fish eaten by piscivorous fish increased, although total consumption by piscivorous fish decreased. This reflects an increase in piscivory on the eastern Scotian Shelf (Bundy, 2005), due to the increased availability of forage fish as prey.

#### 3.3.2. Marine mammal overlap index

For each ecosystem, all marine mammals were grouped and compared to the fisheries in terms of their overlap for food resources (Table 7). The global resource overlap index,  $\alpha$ , for all four ecosystems, decreased between the two time periods (0.043 in the 1980s versus 0.029 in the 1990s). This decrease in overlap was also found in the eastern Scotian Shelf (–26%), Newfoundland–Labrador (–71%), and the southern Gulf (–62%) ecosystems, but not in the northern Gulf, where the overlap between marine mammals and fisheries increased by 15%. The ecosystem where the highest overlap occurred is the southern Gulf, in the 1980s as in the 1990s. The lowest overlap occurred on the eastern Scotian Shelf.

**Table 6**  
The main predators accounting for over 75% of predation on small cod in the 1980s and the 1990s.

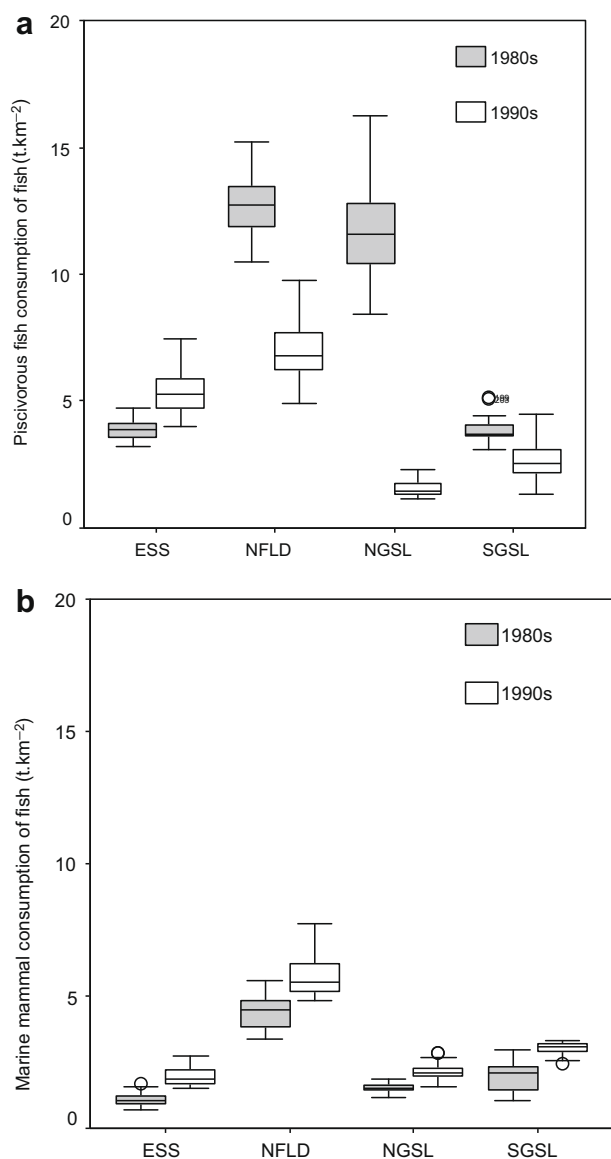
Time period	ESS	NFLD	NGSL	SGSL
1980s	Sm. Dem. Pisc.	Squid	Large cod	Large cod
	Grey seals	Large cod	L. demersals	Harp seals
	Large cod	Sm. Dem. Pisc	Harp seals	Grey seals
	Dem. Piscivores	Skates		
	Haddock	L.G. halibut		
	Squid Cetaceans			
1990s	Grey seals	Squid	Grey seals	Large cod
	Silver hake	SM. Dem. Pisc	Large cod	Grey seals
	Sm. Dem. Pisc.	Harp seals	Harp seals	Harp seals
	Squid	L.G. halibut		
	Cetaceans	Cetaceans Dem. Pisc		

Sm. Dem. Pisc. – small demersals piscivores.

Dem. Piscivores – demersals piscivores.

L. demersals – large demersals.

L.G. halibut – large Greenland halibut.



**Fig. 6.** Box and Whisker plots showing total consumption of fish by (a) piscivorous fish and (b) marine mammals in the 1980s and 1990s in the four NW Atlantic ecosystems. Horizontal lines represent the median, the boxes represent 50% of the values, the whiskers extend to the highest and lowest values and the circles represent outliers.

**Table 7**

Estimated resource overlap index between marine mammals and fisheries from four Northwest Atlantic ecosystem models.

Ecosystem model	$\alpha_{j,l}$ 1980s	$\alpha_{j,l}$ 1990s
Eastern Scotian Shelf	0.008	0.006
Newfoundland	0.028	0.008
Northern Gulf of St. Lawrence	0.021	0.030
Southern Gulf of St. Lawrence	0.128	0.048
GLOBAL (average)	0.043	0.029

### 3.4. Whole system indicators

#### 3.4.1. Summary statistics

All the whole system indicators are derived from model estimates. Total biomass of the ecosystem increased in the eastern Scotian Shelf, decreased in the northern Gulf and did not significantly

change in the southern Gulf or Newfoundland–Labrador (Table 8). Total consumption increased, and total respiration remained stable in the southern Gulf and eastern Scotian Shelf, whereas in Newfoundland–Labrador and the northern Gulf, both decreased. Flow to detritus decreased on the eastern Scotian Shelf but remained the same elsewhere. Total system throughput measures the overall size of flows in the ecosystem, and did not change in the eastern Scotian Shelf or southern Gulf, but decreased in Newfoundland–Labrador and the northern Gulf. Total production decreased in Newfoundland–Labrador and the northern Gulf, increased in the southern Gulf and did not significantly change on the eastern Scotian Shelf. Net system production did not change significantly in any of the ecosystems from the 1980s to the 1990s, except the northern Gulf where it increased. The ratio of primary production to total biomass decreased in all systems except the southern Gulf where there was no significant change. Biomass/total system throughput increased in all ecosystems except the southern Gulf where there was no significant change, indicating that the ecosystems became more mature. The connectance index decreased in all ecosystems except in Newfoundland–Labrador, where it did not change. The omnivory index increased in Newfoundland–Labrador and the northern Gulf and decreased in the eastern Scotian Shelf and the southern Gulf (see Table 8).

Overall, many of the summary metrics for the northern Gulf and Newfoundland–Labrador decreased whereas there was little change in any of the summary metrics for the southern Gulf. The eastern Scotian Shelf showed some similar trends, or lack of, to the southern Gulf.

#### 3.4.2. Network indices

**3.4.2.1. Entropy ( $H$ ).** In the eastern Scotian Shelf and southern Gulf, model estimates of  $H$  increased significantly, indicating that the system flows have become more diverse, whereas in the northern Gulf, it decreased significantly, indicating that the system has become more organized, but that there is less diversity and more of the flows are being channeled through pathways, potentially making the system less resilient (Table 9).  $H$  is very stable in Newfoundland–Labrador, indicating that the flow diversity did not change over time. It is likely that the reduction in flows from groundfish was replaced by flows to invertebrates.

**3.4.2.2. Average mutual information.** Average mutual information measures organization and exchanges among components. An increase in AMI indicates that the system is becoming more constrained and channeling flows among more specific pathways. The eastern Scotian Shelf was the only ecosystem where this was estimated to increase, whereas it decreased in the southern Gulf (Table 9). AMI values are higher in the eastern Scotian Shelf and Newfoundland–Labrador models than in the Gulf models, suggesting that these ecosystems are more constrained.

**3.4.2.3. The ascendancy:capacity ratio.** Model estimates of the ascendancy:capacity ratio increased in the northern Gulf and decreased in the eastern Scotian Shelf and in the southern Gulf (Table 9). There was no significant difference in Newfoundland–Labrador. However, both the Gulf models have a lower A:C than the eastern Scotian Shelf or Newfoundland–Labrador. This suggests that the latter ecosystems were more channel like with very little variations in flow.

**3.4.2.4. Redundancy ( $R$ ).** Redundancy ( $R$ ) or internal flow overhead (IFO in % flowbits) seems to be the best indicator of a change in degrees of freedom of the system, i.e. what is the distribution of energy flow among the pathways in the ecosystem. It is also defined as the pathway redundancy (Ulanowicz, 1997). Thus, a high  $R$  indicates that flows among the pathways are not concentrated in one

**Table 8**  
Summary of changes for summary statistic metrics. All values are the average of estimates from the 31 models, units are  $t\ km^{-2}\ yr^{-1}$  for the first seven metrics, and the last four are dimensionless. A “+” indicates an increase, a “–” a decrease and ~ no change in the metrics from one time period to the next.

Summary statistics	ESS			NFLD			NGSL			SGSL		
	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change
Total biomass	244	312	+ <sup>a</sup>	315	295	~	304	280	–	280	292	~
Total consumption	2653	3509	+ <sup>a</sup>	3367	2799	– <sup>a</sup>	2083	1845	– <sup>a</sup>	1677	2018	+ <sup>a</sup>
Total respiration	2801	2613	~	2557	2010	– <sup>a</sup>	1400	1142	– <sup>a</sup>	1251	1374	~
Flow to detritus	2236	1723	– <sup>a</sup>	1938	1980	~	1311	1414	~	1476	1395	~
Total System Throughput (TST)	7696	7846	~	7879	6812	– <sup>a</sup>	4796	4569	– <sup>a</sup>	4622	1970	~
Total production	3272	3280	~	3229	2531	– <sup>a</sup>	1907	1787	– <sup>a</sup>	1904	4897	+ <sup>a</sup>
Net system production	0.90	0.56	~	17.08	22.90	~	3.60	16.22	+ <sup>a</sup>	8.57	9.58	~
PP/B	11.55	8.39	– <sup>a</sup>	8.18	6.94	– <sup>a</sup>	4.62	4.68	– <sup>a</sup>	5.24	5.08	~
B/TST	0.03	0.04	+ <sup>a</sup>	0.04	0.04	+ <sup>a</sup>	0.06	0.06	~	0.06	0.06	~
CI	0.38	0.33	–	0.23	0.23	~	0.30	0.28	– <sup>a</sup>	0.28	0.26	– <sup>a</sup>
OI	0.16	0.14	– <sup>a</sup>	0.13	0.14	+ <sup>a</sup>	0.12	0.14	+ <sup>a</sup>	0.13	0.12	– <sup>a</sup>

<sup>a</sup> Significant change (Mann–Whitney *U* test).

**Table 9**  
Summary of changes for the network analysis. All values are the average of estimates from the 31 models, units are  $t\ km^{-2}\ yr^{-1}$  for the first seven metrics, and the last four are dimensionless. A “+” indicates an increase, a “–” a decrease and ~ no change in the metrics from one time period to the next.

	ESS			NFLD			NGSL			SGSL		
	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change
Entropy	4.00	4.40	+	4.16	4.12	~	4.31	3.72	–	3.94	4.10	+
AMI	0.94	1.00	+ <sup>a</sup>	1.09	1.09	~	0.78	0.80	~	0.80	0.75	– <sup>a</sup>
A:C	23.56	22.64	– <sup>a</sup>	26.35	26.51	~	18.03	21.69	+ <sup>a</sup>	20.71	18.48	– <sup>a</sup>
Redundancy	47.17	49.20	+ <sup>a</sup>	45.32	46.67	+ <sup>a</sup>	53.89	53.29	~	53.92	55.76	~
Finn's cycling index	5.12	5.93	+ <sup>a</sup>	7.22	8.75	+ <sup>a</sup>	13.86	18.57	+ <sup>a</sup>	14.12	14.96	~

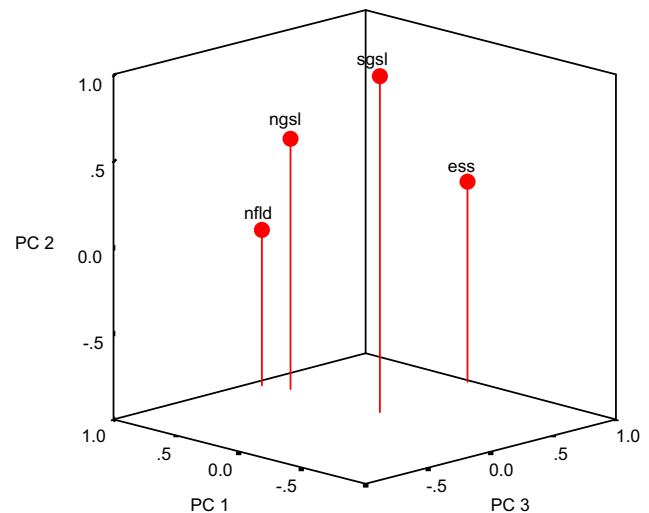
<sup>a</sup> Significant change (Mann–Whitney *U* test).

or two main pathways but there are many ways for energy to get from one compartment to another. Redundancy was estimated to increase a little in the eastern Scotian Shelf and Newfoundland–Labrador models but did not significantly change in the Gulf models where *R* had higher values (Table 9).

**3.4.2.5. Finn's cycling index.** Estimates of Finn's cycling index (%) increased in the eastern Scotian Shelf, Newfoundland–Labrador and the northern Gulf, indicating that these systems became more efficient in the 1990s (Table 9). However, Finn's cycling index is much higher in the Gulf models than in Newfoundland–Labrador or the eastern Scotian Shelf, indicating that these ecosystems are more efficient.

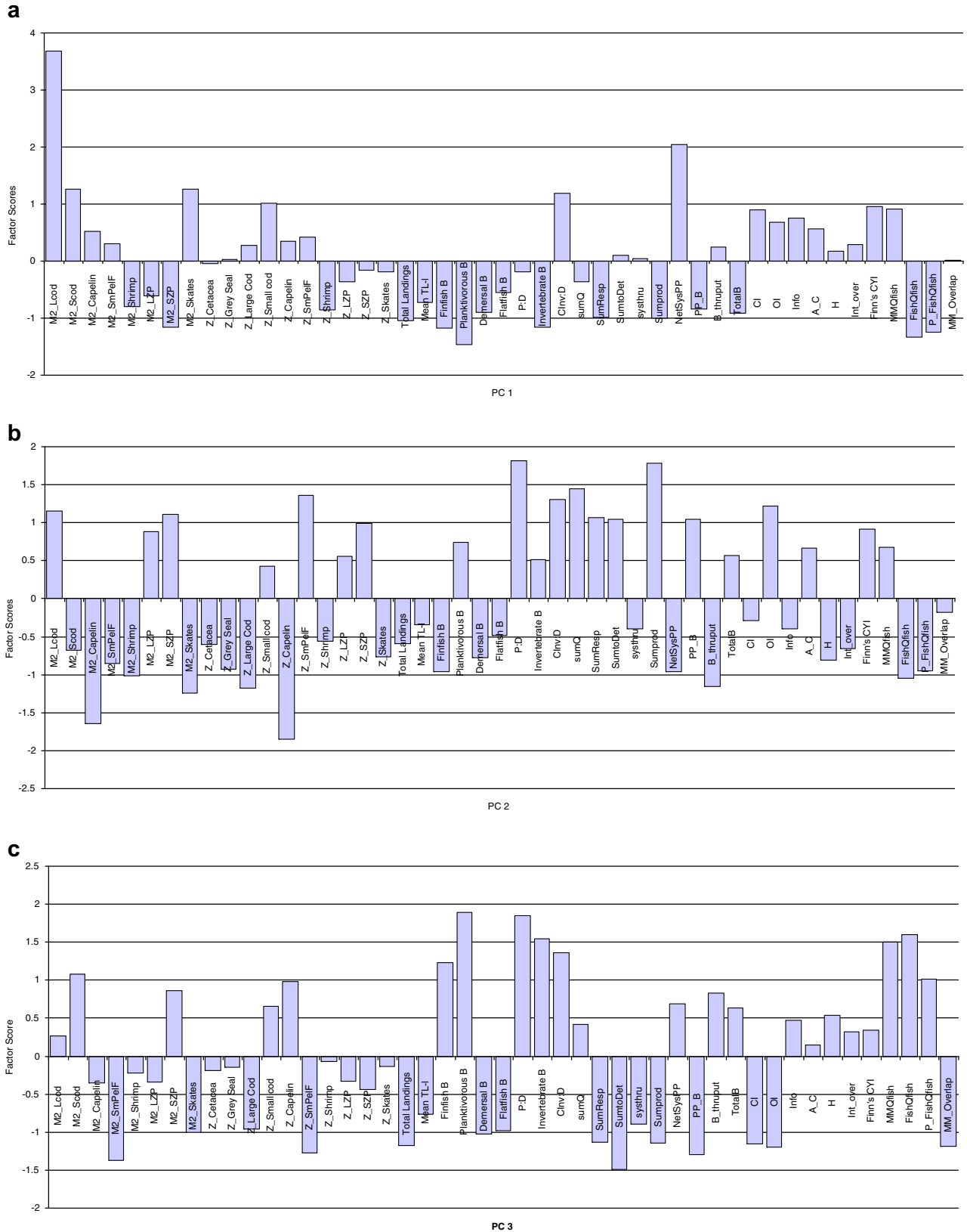
### 3.5. Multivariate analysis

The PCA analysis of all the indicators discussed above was consistent with the results for the keystone species: the first principle component grouped the northern Gulf of St. Lawrence and Newfoundland–Labrador, the second separated the southern Gulf of St. Lawrence and the third distinguished the eastern Scotian Shelf (Fig. 7). The loadings of the four ecosystems were positive on all three axes, with the exception of a slight negative loading of Newfoundland–Labrador on PC 2. These three axes explained 90% of the variation in the data (PC 1, 35.5%; PC 2, 28.7% and PC 3, 25.2%). On PC 1, the keystone species indicator, the factor score for predation mortality of large cod dominated the other indices (Fig. 8a), and separated Newfoundland–Labrador and northern Gulf of St. Lawrence from the other ecosystems, due to their large increases in predation mortality of cod. PC 2 and PC 3 were more multivariate. On PC 2, the highest factor scores were due to keystone species



**Fig. 7.** PCA results for the 48 indicators used in this study. Scatter plot shows the loadings of the four ecosystems on the first three principle components which explained 93% of the total variance in the data. See Fig. 1 for further details.

indices, total mortality and predation mortality of capelin (both negative), the ecological indicator, P:D ratio, and the whole system indicator, sum of all production (both positive, Fig. 8b). Ecological indicators planktivorous fish biomass, the P:D ratio and invertebrate biomass, and the functional role indicator, piscivorous fish consumption of fish had the highest factor scores on PC 3 (Fig. 8c).



**Fig. 8.** PCA results for the 48 indicators used in this study showing the factor scores of the indicators on (a) the first principle component, (b) the second principle component and (c) the third principle component. Species names as in Fig. 5, and Mean TL = mean trophic level of landings; Finfish B = finfish biomass; P:D = pelagic:demersal biomass ratio; Clnv:D = commercial invertebrate:demersal fish biomass ratio; sum Q = total consumption; Sum Respiration = total respiration; SumtoDet = total flow to detritus; systhru = total system throughput; sumprod = total production; NetSysPP = net system production; PP\_B = total primary production/total biomass; B\_Thruput = total biomass/total system throughput; Total B = total biomass; CI = connectance index; SOI = system omnivory index; Info = average mutual information; A\_C = ascendancy to capacity ratio; H = entropy; Int\_over = redundancy; Finn's CYI = Finn's cycling index; MMQfish = marine mammal consumption of fish; FishQfish = fish consumption of fish; P\_fishQfish = piscivorous fish consumption of fish; MM\_Overlap = marine mammal overlap.



## 4. Discussion

### 4.1. Changes in the ecosystem structure

The four NW Atlantic ecosystems followed similar broad trends in the nine ecological indicators that assess the general state of an ecosystem. The changes in total landings, demersal fish biomass, flatfish biomass, and pelagic or commercial invertebrate to demersals fish biomass ratios indicate that the structure of all four ecosystems has switched from long-lived demersal, commercial fish dominated ecosystems to shorter lived pelagic and invertebrate dominated ecosystems. The northern Gulf of St. Lawrence has suffered the greatest decline in finfish biomass, while eastern Scotian Shelf total fish biomass increased due to an increase in planktivorous fish biomass. The mean trophic level of landings declined in all systems, similar to the declines reported in many other ecosystems of the world (Pauly et al., 1998; Myers and Worm, 2003; Pauly and Maclean, 2003). However, there are some differences between the systems. The fisheries landings in all systems decreased, but in the southern Gulf of St. Lawrence, that decrease was less. Furthermore, on a per unit area basis, landings were twice as high in the southern Gulf as in the other ecosystems during the 1990s. Compared to the northern Gulf, the lower decline in total landings in the southern Gulf may have occurred because the fishery in the southern Gulf was more diverse (37 species versus 25) during the mid-1980s. However, this may also reflect the fact that forage fish and invertebrates already represented 52% of total landings in the mid-1980s.

#### 4.1.1. Trends in keystone species

The eight keystone species identified from this analysis represented the middle and top trophic levels of the food web (TL = 3 and 4+). The commonality in keystone species among the four NW Atlantic ecosystems was remarkable, as was the similarity in their biomass trends. Perhaps most striking was the presence of large cod as a keystone species in three of the four ecosystems in the 1980s, and their absence as a keystone species anywhere in the 1990s. However, despite modelling efforts and scientific surveys, there is still great uncertainty over the abundance estimates for some of these species, such as cetaceans and some of the planktivorous forage fish (capelin and sand lance).

While there was a great deal of consistency in the response of most keystone species to ecosystem change, changes in the abundance of forage species differed in the four systems. This was highlighted by the PCA of all the indicators which resulted in high factor scores for the planktivorous biomass on the third principle component. The only ecosystem where small planktivorous pelagics increased from the 1980s to the 1990s was the eastern Scotian Shelf (sand lance and herring). While we are confident of these increases, the absolute biomass values are uncertain. Until recently, small planktivores were not exploited on the eastern Scotian Shelf, whereas in the other three ecosystems there have been fisheries for capelin, herring or both for decades if not centuries, which may account for the differences observed.

Taking a more recent perspective, small planktivores have also increased in the southern Gulf of St. Lawrence. Capelin increased from the 1980s to the 1990s and has shown a significant expansion in geographical distribution in the entire Gulf of St. Lawrence in the 1990s (DFO, 2001). Since the mid-1990s, herring have also increased in the southern Gulf (DFO, 2005b), so it too has seen an overall increase in forage fish in more recent years.

Bundy and Fanning (2005) and Frank et al. (2005) have already noted the trophic cascade on the eastern Scotian Shelf and the trends in abundance of keystone species confirms this. Is there evidence for this elsewhere? The data from Newfoundland–Labrador also show evidence of a trophic cascade; seals increased, cod and

skates decreased, forage species increased (shrimp), zooplankton decreased and there was an increase in phytoplankton. The increase in forage species however is not as great as on the eastern Scotian Shelf. There is less evidence for this in the Gulf of St. Lawrence due to lack of empirical information at lower trophic levels. However, there was an increase in abundance of seals, a decrease in cod and skate abundance, an increase in forage species (shrimp, herring and capelin) and a decrease in small zooplankton in the southern Gulf. In the northern Gulf, seals increase, but all other keystone species decrease or remain the same (capelin), except for shrimp which has increased since the mid-1990s (Bourdages et al., 2007). However, modelling results for the northern Gulf do support a general top-down view of species interactions found by Myers and Worm (2003) in the North Atlantic; they indicated that a change in predation structure or flows at the top of the trophic system led to changes in predation at all lower trophic levels (Savenkoff et al., 2007a).

Overall, keystone species had similar predators in the four NW Atlantic systems, although there were differences in total predation mortality and the proportion of mortality due to predation. One key difference, highlighted by both of the PCAs, was the predation mortality of large cod. The largest increases were observed in Newfoundland–Labrador and northern Gulf of St. Lawrence, where predation by seals accounts for up to 70% of mortality in the 1990s. On the eastern Scotian Shelf, large cod had few predators, but mortality was high, but the cause was not known. Predation mortality on small cod was also highlighted by the PCA of the keystone species. In the 1990s, this was higher on the eastern Scotian Shelf and Newfoundland–Labrador than in the Gulf of St. Lawrence ecosystems, and at the same time they had a greater range of predators, indicating that in these areas, small cod face greater challenges to survival. Zooplankton had a similar range of predators, but in the case of small zooplankton, cannibalism was the main source of mortality in the northern and southern Gulf models.

#### 4.1.2. Functional role indicators

Species interactions are central to ecosystem management considerations. In marine ecosystems, predation can be the major ecological process affecting fish populations and piscivory is often the largest source of fish removals, usually larger than fishing mortality (Bax, 1998; Link and Garrison, 2002). Also, multispecies predation models indicate that fish can consume more fish than marine mammals do (Overholtz et al., 1991; Trites et al., 1997). Prior to the collapse of cod, piscivory was the largest source of fish removals in all four NW Atlantic ecosystems and consumption of fish by marine mammals was lower than consumption of fish by predatory fishes. However, since the collapse, piscivorous fish have been at least partly replaced by marine mammals (seals) as the top predators in these ecosystems, particularly in the northern and southern Gulf of St. Lawrence. However, though marine mammal consumption increased, the marine mammal overlap index indicated that in general, marine mammals consumed food resources that were not the main targets of fisheries. In areas where competition between marine mammals and fisheries was higher (southern Gulf of St. Lawrence), the results indicate that the resource overlap was higher than the global average (L. Morissette, personal communication). Most overlap appeared to occur between fisheries and seals.

In the eastern Scotian Shelf, Newfoundland–Labrador and southern Gulf models, the overlap of marine mammals versus fisheries for food resources decreased from the 1980s to the 1990s. This is counterintuitive since this decrease is associated with an increase in marine mammal consumption of fish in all ecosystems. However, since there were no groundfish species to prey on in the 1990s, seals species have shifted their consumption towards lower trophic level species, which are not the main target of fisheries.

The overlap with the fishery slightly increased from the 1980s to the 1990s in the northern Gulf. This may be due to increased consumption by marine mammals. However, in the northern Gulf during the 1980s, fisheries mainly targeted large cod, redfish, planktivorous small pelagics, and shrimp (90% of total landings) that were not heavily eaten by marine mammals (at most 18% of total consumption of seals), which were consuming smaller fish. This resulted in relatively weak resource overlap index between marine mammals and fisheries in the 1980s. In the 1990s, fisheries targeted capelin and small planktivorous pelagics (herring), increasing the overlap with marine mammals.

#### 4.2. Ecosystem analysis

Based on the ecological indicators, keystone species and functional species analyses, there were both broad similarities in trends among the four NW Atlantic ecosystems, but also differences. The summary statistics and network analyses largely confirmed these observations.

The eastern Scotian Shelf was unique because total biomass and total consumption increased, although total system throughput remained the same (due to a decrease in flows to detritus). In Newfoundland–Labrador and the northern Gulf virtually all these statistic decreased, indicating that the whole systems have decreased in size. In the southern Gulf, most of the summary flow statistics did not change.

The connectance index decreased in all ecosystems except in Newfoundland–Labrador, indicating decreased complexity. In Newfoundland–Labrador there was no change. However, connectance is based only on linking, and can be erroneous since it does not take into account the size of the links (i.e. how much matter flows between the compartments). In contrast, 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 is a better representation of the complexity of the models (Morissette, 2007). Like the connectance index, the SOI decreased in the southern Gulf and on the eastern Scotian Shelf, indicating that feeding interactions in these systems have become less diverse and complex. However, SOI increased in Newfoundland–Labrador and the northern Gulf. For the latter there are two contrary signals, suggesting that while there may be fewer connections, feeding occurred across a wider range of trophic levels. In Newfoundland–Labrador, it is likely that complexity overall increased.

The network indicators require some explanation and should be interpreted as a group for each ecosystem. On the eastern Scotian Shelf, systems entropy (H) increased, indicating that the system flows became more diverse, signifying increased resilience. This is reflected by the low A:C, showing that the system became less organized. However, the increase in AMI is a sign that channeling of the pathways increased (in contradiction to the increase in entropy just described). The increase in R indicates that the system has more strength in reserve in the 1990s, which is also shown by the increase in the FCI. In the eastern Scotian Shelf most of the indicators point to greater diversity in flows.

Entropy (H), AMI and A:C did not change from the 1980s to the 1990s in the Newfoundland–Labrador models, indicating stability in this ecosystem. Redundancy however increased, suggesting that the changes within the ecosystem show that it could withstand greater perturbation in the 1990s than in the 1980s, and that it might have moved to a new stable state. The lack of change in A:C indicates that the reduction in flows from groundfish may have been replaced by flows to invertebrates, but without the large pelagic increase observed in the eastern Scotian Shelf.

In the northern Gulf, entropy decreased significantly, but A:C and FCI increased. The former indicates a decrease in uncertainty and a reduction in number and diversity of flows in the system.

Similarly, the increase in A:C indicates that the system was getting more organized with more flows going along fewer pathways and little redundancy in the system. However, given the lack of change in AMI or R, this result is not too robust, but suggests that the system is getting less resilient.

In the southern Gulf there were small changes in entropy, AMI and A:C, indicating that the system flows became a little more diverse (increase in entropy and decrease in AMI and A:C). However, these changes were small and there was no change in R or the FCI. This suggests that the flow diversity has changed little over that time, which means that the reduction in flows from groundfish was replaced by flows to pelagics and invertebrates, but without the large pelagic increase observed in the eastern Scotian Shelf. H is quite flat usually in ecosystems where increases in some species are replacing decreases in others.

The higher A:C in Newfoundland–Labrador and the eastern Scotian Shelf indicates that these ecosystems are more channel like and organized than the Gulf models with most flows going along fewer pathways and less redundancy in the system. Given earlier similarities between Newfoundland–Labrador and the northern Gulf, one would have expected the Northern Gulf to be similar to Newfoundland–Labrador but it is not. This might be due to differences in the model construction between the inverse modelling methodology and the Ecopath methodology.

Despite best attempts to use a standard approach to modelling (Ecopath estimates of network and summary statistics, models of same size and structure), the results indicate that for several indicators the two mass balance models for the Gulf of St. Lawrence are different from the Newfoundland–Labrador and eastern Scotian Shelf mass balance models. This could be due to the differences in methodology, or it could be due to real differences. Some indicators, such as H are ratios, and results are comparable across the four systems. A:C is also a ratio, but the two Gulf models have much lower values than the eastern Scotian Shelf and Newfoundland–Labrador models. This is also true of the AMI and R indices and Finn's cycling index, which indicates that cycling is much higher in the Gulf models than the other two models. This difference in the cycling index could be due to the large amount of flow consumed in cannibalistic cycles of small zooplankton in these models. In the two Gulf models, small zooplankton, phytoplankton, and detritus were assumed to be potentially accessible to small zooplankton. In the eastern Scotian Shelf and Newfoundland–Labrador models, the diet was assumed to be 100% phytoplankton. The consistent differences between the Inverse and Ecopath derived results of the network analysis is concerning and until it is resolved whether these differences are model derived or real, robust conclusions about differences between ecosystem network indices cannot be made.

Within each ecosystem, we can conclude that in eastern Scotian Shelf and Newfoundland–Labrador the systems were very concentrated in a few flows in the 1980s, but after the ground fish collapse both those systems seem to have found ways for energy to move to higher trophic levels, with the eastern Scotian Shelf perhaps more successful than Newfoundland–Labrador (bigger increase in R than Newfoundland–Labrador). The two Gulf systems on the other hand have changed little. Since the southern Gulf did not have such a large groundfish collapse as the other systems, it does not appear to have changed as dramatically as the other ecosystems.

#### 4.3. Coherent changes across the four NW Atlantic ecosystems

The multivariate analysis of the 48 indicators of change in the four ecosystems raises several issues: (i) only a few indicators strongly differentiated between the four ecosystems, which suggests that a reduced set of indicators may be used to monitor ecosystem change. Gaichas et al. (in this issue) compared five

ecosystems and also found that only few indicators differed between ecosystem, including the P:D ratio; (ii) based on this analysis, the most informative indicators were the ecological indicators and the keystone species indicators; (iii) the indices from the network analysis had consistently low factor scores on the principle components, suggesting that these are conservative ecosystem properties. This implies that where a negative change is detected, serious concerns should be raised about potential changes in the functioning of the ecosystem and (iv) although there are a few differences between these ecosystems, these four ecosystems have undergone very similar changes from the 1980s to the 1990s.

#### 4.4. Implications for cod

Structurally and functionally these systems have shifted to an alternate state, with changes in predator structure, trophic structure and flow. Overfishing in the late 1980s greatly reduced the abundance of large piscivorous fish, which have not recovered 20 years after the cessation of heavy fishing in the four ecosystems (Rice and Rivard, 2003). This decline has left marine mammals such as seals as top predators of many species during the mid-1990s and had profound effects over all trophic levels (top-down effects) in Newfoundland–Labrador, the northern Gulf and the southern Gulf. This, coupled with the re-opening of fisheries before stocks had recovered, may explain why cod biomass is still at extremely low levels in these ecosystems. On the eastern Scotian Shelf, top-down predation by seals does not appear to be a significant energy flow or cause of mortality of cod, nor has there been a fishery since 1993. However, the high abundance of forage fish may be out-competing small cod for food (small zooplankton), and larval cod may be consumed by forage fish. This is a variant of the cultivation–depensation hypothesis suggested by Bundy and Fanning (2005), where cod are caught in a trophic vise: with

the exponential increase of grey seals, and the large reduction of cod due to fishing, cod were squeezed, and as the small pelagics increased, competition from small pelagics with young cod causing the loss of the cultivation effect. There is no evidence for this effect in Newfoundland–Labrador or the northern Gulf since the forage fish biomass did not increase, although there is scope for further investigation in the southern Gulf. All systems show evidence of a potential trophic cascade, a result of the removal of the top fish predators by fishing.

Thus, the changes in top-predator abundance driven by human exploitation of selected species resulted in a major perturbation of the structure and functioning of the four Northwest Atlantic ecosystems. Each represents a case of fishery-induced regime shift, to alternate states that may not be reversible in the short-term.

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#### Appendix A

See Tables A.1–A.3.

**Table A.1**  
Functional groups used in modelling in the eastern Scotian Shelf for the two time periods.

30 Groups	39 Groups	Species
Cetaceans	Cetaceans	<i>Megaptera novaeangliae</i> , <i>Balaenoptera physalus</i> , <i>B. acutorostrata</i> , <i>B. borealis</i> , <i>B. musculus</i> , <i>Physeter catodon</i> , <i>Globicephala melanaea</i> , <i>Lagenorhynchus acutus</i>
Seals	Grey seals	<i>Halichoerus grypus</i>
Seabirds	Seabirds	<i>Alle alle</i> , <i>Puffinus griseus</i> , <i>P. Gravis</i> , <i>Uria lomvia</i> , <i>U. aalge</i> , <i>Fratercula arctica</i> , <i>Fulmarus glacialis</i> , <i>Larus hyperboreus</i> , <i>L. glaucooides</i> , <i>Larus argentatus</i> , <i>L. marinus</i> , <i>Morus bassanus</i> , <i>Oceanodroma leucorhoa</i> , <i>Oceanites oceanicus</i> , <i>Caleonectris diomedea</i> , <i>Puffinus puffinus</i> , <i>Rynchops niger</i> , <i>Catharacta maccormicki</i>
Large cod	Cod > 40 cm	<i>Gadus morhua</i>
Small cod	Cod ≤ 40 cm	Juveniles of above
Large Silver hake	Silver hake > 30 cm	<i>Merluccius bilinearis</i>
Small Silver hake	Silver hake ≤ 30 cm	Juveniles of above
Haddock	Haddock	<i>Melanogrammus aeglefinus</i>
Plaice	American plaice	<i>Hippoglossoides platessoides</i>
Large halibut	Halibut > 65 cm	<i>Reinhardtius hippoglossoides</i> , <i>Hippoglossus hippoglossus</i>
Small halibut	Halibut < 65 cm	Juveniles of above
Flatfish	Flounders	<i>Limanda ferruginea</i> , <i>Glyptocephalus cynoglossus</i> , <i>Pseudopleuronectes americanus</i>
Skates	Skates	<i>Raja laevis</i> , <i>R. radiata</i> , <i>R. senta</i> , <i>R. ocellata</i> , <i>Leucoraja erinacea</i>
Redfish	Redfish	<i>Sebastes mentella</i> , <i>S. fasciatus</i>
Large pelagics	Transient mackerel	<i>Scomber scombrus</i>
	Spiny dogfish	<i>Squalus acanthias</i>
	Transient pelagics	<i>Thunnus thynnus</i> , <i>Xiphias gladius</i> , <i>Lamna nasus</i> , <i>Cetorhinus maximus</i> , <i>Elasmobranchii</i>
Large demersals	Large demersal piscivores > 40 cm	<i>Urophycis tenuis</i> , <i>Lophius americanus</i> , <i>Hemitripterus americanus</i> , <i>Brosme brosme</i>
	Large demersal piscivores ≤ 40 cm	Juveniles of above
	Large demersals feeders > 30 cm	Zoarcidae, <i>Macrozoarcus americanus</i> , Macouridae, Anarhichadidae, <i>Urophycis sps</i> , <i>Cylopterus lumpus</i>
	Large demersal feeders ≤ 30 cm	Juveniles of above
	Pollock	<i>Pollachius virens</i>
Small demersals	Small demersals	e.g., sculpins (Cottidae), shannies and blennies (Stichaeidae)
Sand lance	Sand lance	<i>Ammodytes dubius</i>
Small pelagics	Capelin	<i>Mallotus villosus</i>
	Small pelagics	<i>Clupea harengus harengus</i> , <i>Argentina silus</i> , <i>Alosa sapidissima</i> , <i>Alosa pseudoharengus</i> , <i>Poronotus triacanthus</i> , juvenile <i>Scomber scombrus</i>

## Appendix A.1 (continued)

30 Groups	39 Groups	Species
Squid	Small mesopelagics	Myctophidae, Sternoptychidae
Large crustaceans	Squid	<i>Illex illecebrosus</i> , <i>Loligo pealeii</i>
	Large crabs (>50 mm CW)	<i>Chionoecetes opilio</i> , <i>Cancer borealis</i> , <i>Chaceon quinquegens</i> , <i>Lithodes maia</i> , <i>Cancer borealis</i>
	Small crabs (<50 mm)	<i>Hyas areneus</i> , <i>H. coarctatus</i> , <i>Pagurus</i> spp., <i>Cancer irroratus</i> , juveniles of large crabs
Shrimp	Shrimp	<i>Pandalus</i> spp., <i>Pasiphaea</i> sp., <i>Crangon</i> sp., <i>Spirontocaris</i> sp., <i>Eualus</i> sp., <i>Sabinea</i> sp., <i>Argis</i> sp., <i>Lebbeus</i> sp.
Echinoderms	Echinoderms	<i>Strongylocentrotus pallidus</i> , <i>Echinarachnius parma</i>
Polychaetes	Polychaetes	<i>Prionospio steenstrupi</i> and others
Bivalves	Bivalves	<i>Placopecten magellanicus</i> , <i>Chlamys islandicus</i> , <i>Cyrtodaria siliqua</i> , <i>Macoma calcarea</i>
Other benthic invertebrates	Other benthic invertebrates	<i>Ophiura sarsi</i> and others
Large zooplankton	Zooplankton (large)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians, ctenophores, mysids, tunicates >5 mm and ichthyoplankton
Small zooplankton	Zooplankton (small)	Copepods (mainly <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , and <i>Oithona similis</i> ), tunicates <5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates) and meroplankton
Phytoplankton	Phytoplankton	Diatoms ( <i>Cahetoceros decipiens</i> , <i>Thalassiosira</i> sp.)
Detritus	Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

Table A.2

Functional groups used in modelling in the Newfoundland Shelf for the two time periods.

30 Groups	50 Groups	Species
Cetaceans	Walrus Cetaceans	<i>Odobenus rosmarus</i> <i>Megaptera novaeangliae</i> , <i>Balaenoptera physalus</i> , <i>B. acutorostrata</i> , <i>B. borealis</i> , <i>B. musculus</i> , <i>Physeter catodon</i> , <i>Globicephala melaena</i> , <i>Phocoena phocoena</i>
Harp seals	Grey seals	<i>Halichoerus grypus</i>
Hooded seals	Harp seals	<i>Phoca groenlandica</i>
Birds	Hooded seals	<i>Cystophora cristata</i>
	Ducks	<i>Somateria mollissima</i> , <i>Melanitta</i> sp., <i>Clangula hyemalis</i>
	Piscivorous birds	<i>Pinguinus impennis</i> , <i>Sula bassana</i> , <i>Phalacrocorax carbo</i> , <i>P. auritus</i> , <i>Larus argentatus</i> , <i>L. delawarensis</i> , <i>L. ridibundus</i> , <i>Rissa tridactyla</i> , <i>Sterna hirundo</i> , <i>S. paradisaea</i> , <i>Sterna caspia</i> , <i>Uria aalge</i> , <i>U. lomvia</i> , <i>Cephus grille</i> , <i>Alca torda</i> , <i>Fratrula arctica</i> , <i>Fulmarus glacialis</i> , <i>Puffinus puffinus</i> , <i>P. gravis</i> , <i>P. griseus</i>
Large cod	Planktivorous birds	<i>Oceanodroma leucorhoa</i> , <i>Alle alle</i>
Small cod	Cod > 35 cm	<i>Gadus morhua</i>
Large plaice	Cod < 35 cm	Juveniles of above
Small plaice	American Plaice >35 cm	<i>Hippoglossoides platessoides</i>
Large G halibut	American Plaice <35 cm	Juveniles of above
Small G halibut	Greenland Halibut > 40 cm	<i>Reinhardtius hippoglossoides</i>
Yellowtail flounder	Greenland Halibut < 40 cm	Juveniles of above
Other flounders	Yellowtail flounder	<i>Limanda ferruginea</i>
	Witch flounder	<i>Glyptodentophalus cynoglossus</i>
	Winter flounder	<i>Pseudopleuronectes americanus</i>
Skates	Skates	<i>Raja laevis</i> , <i>R. radiata</i> , <i>R. senta</i> , <i>R. ocellata</i> , <i>Leucoraja erinacea</i>
Large pelagics	Dogfish	<i>Squalus acanthias</i>
	Mackerel (>29 cm)	<i>Scomber scombrus</i>
	Transient pelagics	<i>Thunnus thynnus</i> , <i>Xiphias gladius</i> , <i>Lamna nasus</i> , <i>Cetorhinus maximus</i> , <i>Elasmobranchii</i>
Redfish	Redfish	<i>Sebastes mentella</i> , <i>S. fasciatus</i>
Large demersals	Dem. and BP > 40 cm	<i>Urophycis tenuis</i> , <i>Merluccius bilinearis</i> , <i>Lophius americanus</i> , <i>Hemitripterus americanus</i> , <i>Brosme brosme</i> , <i>Hippoglossus hippoglossus</i>
	Other Dem. >30 cm	<i>Melanogrammus aeglefinus</i> , <i>Phycis chesteri</i> , <i>Urophycis chuss</i> , <i>Anarhichas</i> sp., <i>Coryphaenoides</i> sp., <i>Lycodes</i> sp., <i>Ogcocephalidae</i>
	Lumpfish	<i>Cyclopterus lumpus</i>
	Greenland cod	<i>Gadus opac</i>
	Salmon	<i>Salmo salar</i>
Small demersals	Dem. and BP < 40 cm	Juveniles of <i>Urophycis tenuis</i> , <i>Merluccius bilinearis</i> , <i>Lophius americanus</i> , <i>Hemitripterus americanus</i> , <i>Brosme brosme</i> , <i>Hippoglossus hippoglossus</i>
	Other Dem. <30 cm	Juveniles of <i>Melanogrammus aeglefinus</i> , <i>Phycis chesteri</i> , <i>Urophycis chuss</i> , <i>Anarhichas</i> sp., <i>Coryphaenoides</i> sp., <i>Lycodes</i> sp., <i>Ogcocephalidae</i>
	Small Dem.	<i>Enchelyopus</i> sp., <i>Pholis gunnellus</i> , <i>Ulcina olriki</i> , <i>Leptagonus decagonus</i> , <i>Lumpenus lamprettaeformis</i> , <i>Leptoclinus</i> sp., <i>Myoxocephalus</i> sp., <i>Prionotus</i> sp., <i>Anisarchus</i> sp.
Forage fish	Capelin	<i>Mallotus villosus</i>
	Arctic cod	<i>Boreogadus saida</i>
Small pelagics	Sand lance	<i>Ammodytes dubius</i>
	Herring	<i>Clupea harengus harengus</i>
	Small pelagics	<i>Alosa sapidissima</i> , <i>Peprilus triacanthus</i> , <i>Argentina silus</i> , juvenile <i>Scomber scombrus</i> , <i>Osmerus mordax mordax</i>
	Small mesopelagics	Myctophidae, <i>Maurolucis muelleri</i> , <i>Paralepis elongata</i>

(continued on next page)



## Appendix A.2 (continued)

30 Groups	50 Groups	Species
Squid	Arctic squid	<i>Gonatus</i> sp.
	Shortfinned squid	<i>Illex illecebrosus</i>
Large crustaceans	Large crabs (>50 mm CW)	<i>Chionoecetes opilio</i> , <i>Cancer borealis</i> , <i>Chaceon quinque-dens</i> , <i>Lithodes maia</i>
	Small crabs (<50 mm)	<i>Hyas areneus</i> , <i>H. coarctatus</i> , <i>Pagurus</i> spp., <i>Cancer irroratus</i> , juveniles of large crabs
	American lobster	<i>Lomarus americanus</i>
Shrimp	Shrimps	<i>Pandalus borealis</i> , <i>P. montagui</i>
Echinoderms	Echinoderms	<i>Strongylocentrotus pallidus</i> , <i>Echinarachnius parma</i>
Polychaetes	Polychaetes	<i>Prionospio steenstrupi</i> and others
Bivalves	Bivalves	<i>Placopecten magellanicus</i> , <i>Chlamys islandicus</i> , <i>Cyrtodaria siliqua</i> , <i>Macoma calcarea</i>
Other inverts	Other benthic inverts.	<i>Ophiura sarsi</i> and others
Large zooplankton	Zooplankton (large)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians, ctenophores, mysids, tunicates > 5 mm and ichthyoplankton
Small zooplankton	Zooplankton (small)	Copepods ( <i>Calanus finmarchicus</i> , <i>Oithona similis</i> ), tunicates < 5 mm and meroplankton
Phytoplankton	Phytoplankton	Diatoms ( <i>Cahetoceros decipiens</i> , <i>Thalassiosira</i> sp.)
Detritus	Detritus	

Table A.3

Functional groups used in modelling in the northern and southern Gulf of St. Lawrence for the two time periods.

Group name	Main species
Cetaceans	<i>Balaenoptera physalus</i> , <i>B. acutorostrata</i> , <i>Megaptera novaeangliae</i> , <i>Phocoena phocoena</i> , <i>Lagenorhynchus acutus</i> , <i>L. albirostris</i>
Harp seals	<i>Phoca groenlandica</i>
Hooded seals	<i>Cystophora cristata</i>
Grey seals	<i>Halichoerus grypus</i>
Harbour seals	<i>Phoca vitulina</i>
Seabirds	<i>Phalacrocorax carbo</i> , <i>P. auritus</i> , <i>Larus delawarensis</i> , <i>L. argentatus</i> , <i>L. marinus</i> , <i>Sterna hirundo</i> , <i>S. paradisaea</i> , <i>Cephus grylle</i> , <i>Oceanodroma leucorhoa</i> , <i>Morus bassanus</i> , <i>Rissa tridactyla</i> , <i>Uria aalge</i> , <i>Alca torda</i> , <i>Fratercula arctica</i>
Large Atlantic cod (>35 cm)	<i>Gadus morhua</i>
Small Atlantic cod (≥35 cm)	<i>Gadus morhua</i>
Large Greenland halibut (>40 cm) <sup>a</sup>	<i>Reinhardtius hippoglossoides</i>
Small Greenland halibut (≥40 cm) <sup>a</sup>	<i>Reinhardtius hippoglossoides</i>
Large American plaice (>35 cm) <sup>b</sup>	<i>Hippoglossoides platessoides</i>
Small American plaice (≥35 cm) <sup>b</sup>	<i>Hippoglossoides platessoides</i>
Flounders	<i>Limanda ferruginea</i> , <i>Glyptocephalus cynoglossus</i> , <i>Pseudopleuronectes americanus</i>
Skates	<i>Amblyraja radiata</i> , <i>Malacoraja senta</i> , <i>Leucoraja ocellata</i>
Redfish	<i>Sebastes mentella</i> , <i>Sebastes fasciatus</i>
Large demersal feeders	<i>Urophycis tenuis</i> , <i>Melanogrammus aeglefinnus</i> , <i>Centroscyllium fabricii</i> , <i>Anarhichas</i> spp., <i>Cyclopterus lumpus</i> , <i>Lycodes</i> spp., <i>Macrouridae</i> , <i>Zoaridae</i> , <i>Lophius americanus</i> , <i>Hippoglossus hippoglossus</i>
Small demersal feeders	<i>Myoxocephalus</i> spp., <i>Tautoglabrus adspersus</i> , <i>Macrozoarces americanus</i> , juvenile large demersals
Capelin	<i>Mallotus villosus</i>
Sand lance <sup>c</sup>	<i>Ammodytes</i> spp.
Arctic cod <sup>d</sup>	<i>Boreogadus saida</i>
Large pelagic feeders	<i>Squalus acanthias</i> , <i>Pollachius virens</i> , <i>Merluccius bilinearis</i>
Piscivorous small pelagic feeders	<i>Scomber scombrus</i> , piscivorous myctophids and other mesopelagics, <i>Illex illecebrosus</i> , piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	<i>Clupea harengus harengus</i> , planktivorous myctophids and other mesopelagics, <i>Scomberesox saurus</i> , <i>Gonatus</i> spp., planktivorous juvenile large pelagics
Shrimp	<i>Pandalus borealis</i> , <i>P. montagui</i> , <i>Argis dentata</i> , <i>Eualus macilentus</i> , <i>E. gaimardi</i>
Large crustaceans	<i>Chionoecetes opilio</i> , other non-commercial species (e.g., <i>Hyas</i> spp.)
Echinoderms	<i>Echinarachnius parma</i> , <i>Strongylocentrotus pallidus</i> , <i>Ophiura robusta</i>
Molluscs	<i>Mesodesma deauratum</i> , <i>Cyrtodaria siliqua</i>
Polychaetes	<i>Exogone hebes</i>
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (>5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (<5 mm)	Copepods (mainly <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , and <i>Oithona similis</i> ), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)
Phytoplankton	Diatom species such as <i>Chaetoceros affinis</i> , <i>C. spp.</i> , <i>Leptocylindrus minimus</i> , <i>Thalassiosira nordenskiöldii</i> , <i>T. spp.</i> , <i>Fragilariopsis</i> spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

<sup>a</sup> Aggregated as Greenland halibut for the southern Gulf models.<sup>b</sup> Aggregated as American plaice for the northern Gulf models.<sup>c</sup> Included in the planktivorous small pelagic feeders for the southern Gulf models.<sup>d</sup> Included in the capelin group for the southern Gulf models.

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