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CM 2007/D:15

Seals, cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in NW Atlantic ecosystems.

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The facts: four NW Atlantic ecosystems, three cod stock collapses fifteen 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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Introduction

Giovanni Caboti anecdotally reported to Henry VII in the late 15th century that there were so many cod on the Grand Banks off Canada's east coast, that you could not catch them all in 500 years. He was wrong. Since the early 1990s, after 500 years of fishing, Atlantic cod (*Gadus morhua*) have been decimated on the Grand Banks, the northern Gulf of St. Lawrence, the southern Gulf of St.Lawrence and the eastern Scotian Shelf. The immediate response of the Canadian Department of Fisheries and Oceans was to close the cod fisheries in the early 1990s. Consequently, 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 (DFO 2007c) and the eastern Scotian Shelf (Fanning et al. 2003) there has been no recovery of cod and there is no directed fishery, although in Newfoundland there was a directed inshore fishery from 1998-2002 (DFO 2007c).

Essentially, these four marine ecosystems off the east coast of Canada (Figure 1) have suffered catastrophic change. Along with cod, many other groundfish species, such as white hake (*Urophycis tenuis*), American plaice (*Hippoglossoides platessoides*) and other flatfish also suffered serious declines, as reflected by steep declines in total landings (Figure 2). Meanwhile, other changes in these ecosystems were also occurring, such as large increases in seals and, at least in some areas, of forage fish.

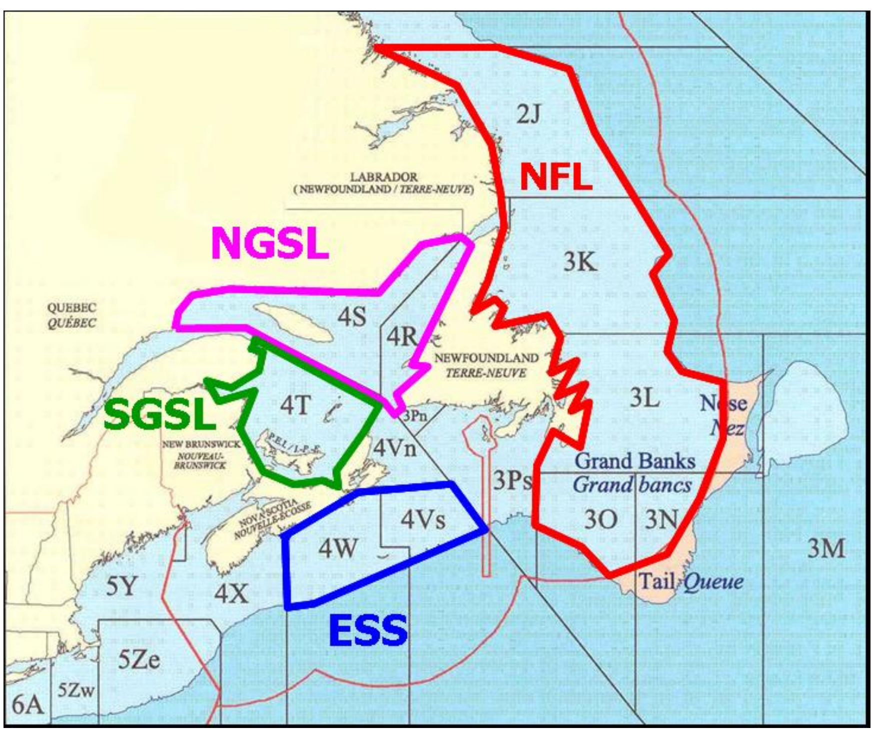


Figure 1. Map of the east coast of Canada, showing the 4 NW Atlantic ecosystems.

Comparative studies have proven useful in understanding how ecosystems change, and the impacts of perturbations (Cury et al. 2005, Bundy 2005, Bundy and Fanning 2005, Heymans et al. 2004, Savenkoff et al. 2007a,b). Here, we take a comparative ecosystem approach to ask, to what extent have these ecosystems changed, both structurally and functionally, and what are the implications for the recovery of cod? We approach this using modeling, empirical data and a suite of ecosystem indicators to determine how and why these systems have changed over time.

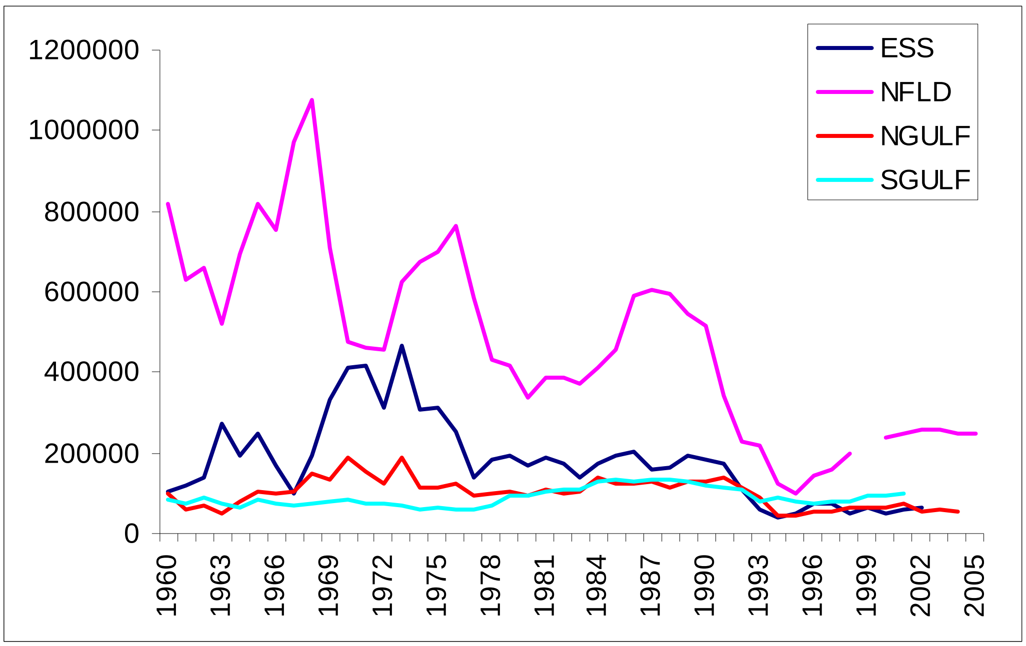


Figure 2: Total landings (t) from 1960 for the eastern Scotian Shelf (NAFO Divisions 4VsW), the Northern Gulf (NAFO Divisions 4RS), Southern Gulf (NAFO Division 4T) and Newfoundland-Labrador (NAFO Divisions 2J3KLNO). Note that NAFO data for Newfoundland in 1999 are incomplete and not included.

Methods

Balanced Ecopath models were developed for the four ecosystems areas for a period in the 1980s before the groundfish collapse and in the 1990s after the collapse, Table 1 (Heymans 2003, Bundy 2004, 2005, Savenkoff et al. 2004, Morissette et al. *Submitted,* Savenkoff et al. 2007a and b). The Newfoundland model covers the largest area and the widest degree of latitude; the northern Gulf and eastern Scotian Shelf models are around 100,000 km^2 and the southern Gulf is the smallest (Figure 2).

The nearshore regions of the study areas were not included in the models since shallower zones are not covered by annual bottom-trawl surveys and because exchanges between the infra-littoral and mid- to off-shore zones are still poorly understood. American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) were not included in the models. 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 (Table 1). Broadly, these can be distinguished into marine mammal groups, seabirds, fish groups, invertebrate groups, one phytoplankton group, and one detritus group (see Appendix 1 for more detailed definition of the groups, and Heymans 2003, Bundy 2004, Savenkoff et al. 2004, Morissette 2007 for additional details).

In order to explore the effects of uncertainty on the model results, a perturbation analysis was applied to the balanced models. Two methods were used: the "Autobalance" routine (Kavanagh et al. 2004) and the Pedigree routine in Ecopath (Morissette 2005), and in the case of the models for the Gulf of St. Lawrence, the inverse method (Savenkoff et al. 2007a and b). In the former, the pedigree routine is used the describe the range of uncertainty for the biomass and diet composition input parameters, then the autobalance routine randomly selects from this range (Bundy 2004). In the Inverse Method, each model input was perturbed to a maximum of its standard deviation (Vézina and Platt 1988). Each of these balanced inverse solutions were then transposed into Ecopath software to estimate mortality (due to fishing, predators, and other sources), the basic emergent properties and network analysis indices for the two time periods, and estimates of the associated uncertainties for the two Gulf models.
For all models, 31 balanced solutions were obtained for each ecosystem and period. These solutions corresponded to 31 random perturbations (including a response without perturbation).

Table 1: Descriptions of the models for the four NW Atlantic Ecosystems

	ESS	SGSL	NGSL	NFLD
NAFO Divisions	4VsW	4T	4RS	2J3KLNO
Area (km^2)	102,325	64,075	103,812	495,000
Inshore Limit (m)	100	15	37	
Depth Limit	400	200		
# 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

The four NW Atlantic ecosystems were compared at a number of levels using:

Ecological Indicators
Keystone Species
Functional Role Indicators
Whole System Indicators

Ecological Indicators

Methratta and Link (2005) recommended the use of eight indicators to describe the state of an ecosystem: total fisheries landings, total finfish biomass, planktivore biomass described here as pelagic fish biomass, benthivore biomass, described here as demersal fish biomass, mean individual fish length, mean individual fish weight, flatfish biomass, indicator species biomass. To these we add the mean trophic level of landings and commercial invertebrate biomass, the pelagic:demersal ratio and a commercial invertebrate: demersal biomass ratio. However, due to differences in survey protocols we were not able to use mean individual fish length or mean individual fish weight. Indicator species are defined here as keystone species – see below.

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). Given their important role, the keystone species in each ecosystem were used as indicators of ecosystem change. They were determined, following Libralato et al. (2006) from the trophic impact routine in the eight Ecopath models:

$$KS_i = \log[\varepsilon_i (1 - p_i)] \quad \text{Eq. 1}$$

Where KS_i = keystone species "i", p_i=proportion of the biomass total biomass that is group (i) and ε_i =total impact of group "i"= $\sqrt{\sum_{j\neq 1}^{n} m_{i,j}^2}$ where m_{ij}=impact of group "i"on group "j".

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

Functional Group Indicators – Predators and forage fish

Following from the keystone species, and ecological indicators, species were grouped into 3 functional groups to explore basic structural changes in the four ecosystems: marine mammals (seals and cetaceans), piscivorous fish (cod, halibut, American plaice, skates, redfish, large demersals, small demersals, large pelagics, small piscivorous pelagics, Greenland cod and salmon) and planktivorous fish (capelin, sandlance, Arctic cod and planktivorous small pelagics such as Atlantic herring). Changes in biomass, consumption and fish consumption were compared across models.

Interactions between marine mammals and fisheries were explored using the Marine Mammal Overlap Index (Morissette 2007). Modified from Kaschner (2004), the index uses Ecopath estimates of fisheries catches and marine mammal consumption to assess the overlap between marine mammal and fisheries. The resource overlap index ($\alpha_{f,m}$) is calculated as:

$$\alpha_{f,m} = \left(\frac{2\sum_k p_{m,k}\, p_{f,k}}{\sum_k p_{m,k}^2 + p_{f,k}^2} \right) * \left(pQ_m * pC_f \right) \quad \text{Eq. 2}$$

where $\alpha_{f,m}$ is the quantitative overlap between a fishery, f and a marine mammal group, m in each 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 $p_{j,k}$ representing the proportions of each prey in the diet of marine mammals or the catch by fisheries. This term is multiplied by the product of the proportion of total food consumption by marine mammals in the ecosystem Q and the total fisheries catches C in the ecosystem.

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 2003, Bundy 2005, Cury et al. 2005, Morissette et al. submitted). For the summary statistic and the network indices, each model was aggregated to a 30 group model to ensure that differences between models were real, and not due to structural differences.

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 and thus a measure of the size of the ecosystem. It is the sum of total consumption, total respiration, flows to detritus and total export. Total production is a 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 et al. 2005), 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 (OI) is an index of a functional groups feeds across the different trophic levels. A low value indicates feeding over a narrow range of trophic levels. Three catch indicators included were total catch, mean trophic level of the catch and the gross efficiency of the catch (catch/primary production).

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 with Ecosim models include statistical entropy (H), average mutual information (AMI), ascendancy:capacity (A:C), redundancy (R or overhead on internal flows, in % flowbits) and Finn cycling index (%) (Heymans 2003).

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 1998), and is calculated as:

$$H = \sum_{ij} \frac{T_{ij}}{TST} \cdot \log\left(\frac{T_{ij}}{TST}\right) \qquad \text{Eq.3}$$

where T_{ij} is the flow between any two compartments and it 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 #77]. Thus, the AMI is calculated as:

$$AMI = \sum_{i,j} (T_{ij}) \cdot \log\left(\frac{T_{ij} \cdot TST}{T_j \cdot T_i}\right) \qquad \text{Eq.4}$$

where Ti is the sum of all material leaving the ith component and Tj is the sum of all flows entering the jth component [Mageau, 1998 #138].

Ascendency describes both the growth (TST) and development (AMI) of the system [Ulanowicz, 1986 #156] and is therefore the product of TST and average mutual information (AMI), and in Ecopath is defined in terms of flow, or:

$$A = TST \cdot \sum_{i,j} \left(\frac{T_{ij}}{TST}\right) \cdot \log\left(\frac{T_{ij} \cdot TST}{T_j \cdot T_i}\right) \qquad \text{Eq.5}$$

The complement to the ascendency is the overhead, which gauges the inefficient degrees of freedom that a system retains [Ulanowicz, 2000 #139]. Overhead is divided into export, dissipation and internal flow [Ulanowicz, 2000 #139], 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 [Ulanowicz, 1997 #157]. 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 #95] linked the overhead to ecosystems stability and Heymans [, 2003 #277] proposed R as an index of the system's resilience. A trade-off develops between the increasing efficiency resulting from a network of exchanges dominated by only the most efficient transfers, and the vulnerability resulting from the rigidity of such a flow configuration. The redundancy is calculated as [Ulanowicz, 2004 #365]:

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

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

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 #183] or through time, and is calculated as:

$$FCI = \frac{TST_c}{TST_s} \qquad \text{Eq.7}$$

where TSTc is the total flow that is recycled, and TSTs is the total flow through the system.

PPR

The primary production required to sustain a fishery has been used to compare the effects of fishing globally (Pauly and Christensen 1995) and is calculated as

$$PPR_C = \sum_{Paths}\left[Y.\prod_{\Pr ed,prey}\frac{Q_{\Pr ed}}{P_{\Pr ey}}.DC'\,pred,prey\right] \qquad \text{Eq.8}$$

where P is production, Q consumption, and DC’ is the diet composition for each predator/ prey constellation in each path (with cycles removed from the diet compositions, (Christensen et al. 2005).

Results

Ecological Indicators

The results for the 8 indicators are summarized in Table 2 and presented in detail below.

Table 2: Summary of direction of change for ecological indicators (+ = increase, - = decrease and ~ = no significant change) S gulf least impacted, but no recovery of cod (as in ESS and NFLD).

	ESS	NFLD	NGULF	SGULF
Total Landings	–	–	–	–~
Finfish biomass	+	–	–	–
Pelagic biomass	+	–	–	–
Demersal biomass	–	–	–	–
Flatfish biomass	–	–	–	~
Pelagic:demersal biomass ratio	+	–	+	+
Invertebrate Biomass	+	~	~	+
commercial invertebrate:demersal fish biomass ratio	+	+	+	+

Commercial Landings

When landings are expressed on a per area basis (Figure 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 4 systems, has suffered the least reduction in catch since the 1980s. Indeed catches have increased since the mid-1990s and are similar to, or higher than, levels in the 1960s and 1970s.

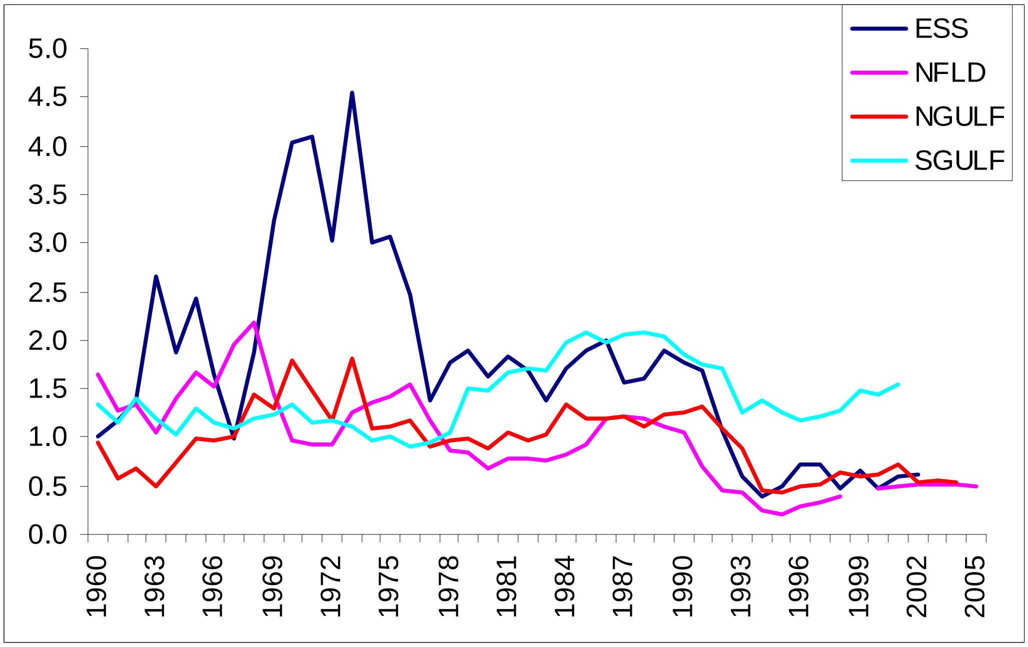


Figure 3: Total landings from 1960 as in Figure 2, expressed as t km^2 yr^{-1}. Note that NAFO data for Newfoundland in1999 are incomplete and not included.

Mean Trophic Level of Landings
Since the cod collapse, fisheries in all areas have switched their focus to lower trophic level invertebrates and this is reflected in the mean trophic level of the catch, which has declined in all areas (Figure 4).

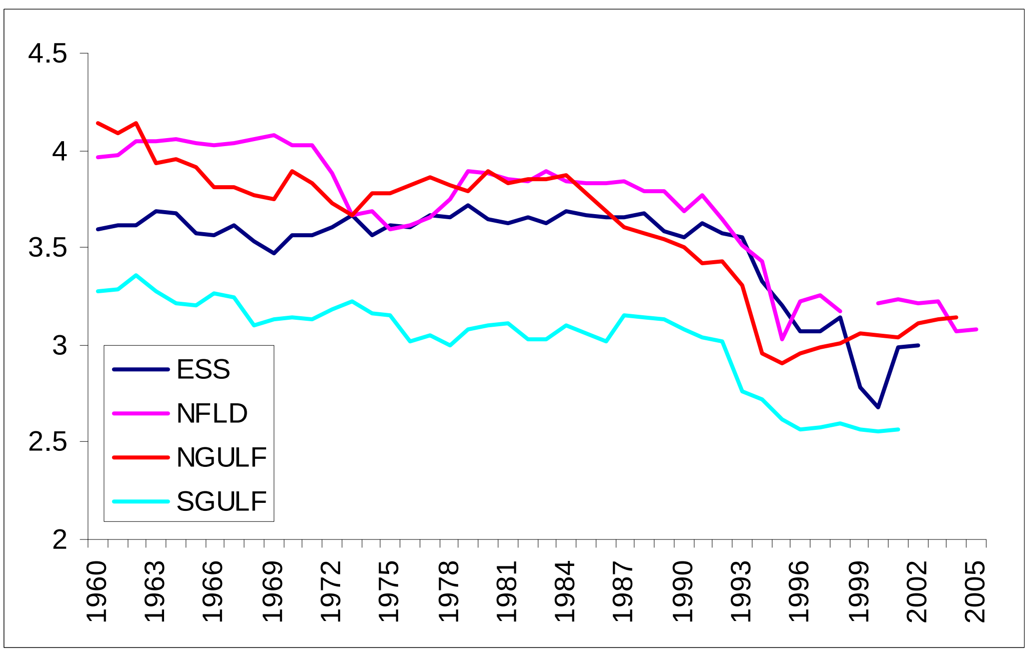


Figure 4. Mean trophic level of landings (trophic level derived from Ecopath models). Note that NAFO data for Newfoundland in1999 are incomplete and not included.

Total finfish biomass

Estimated total finfish biomass decreased in all ecosystems, with the exception of the eastern Scotian Shelf, where there was a substantial increase (Figure 5). The greatest decrease occurs in the northern Gulf of St. Lawrence.

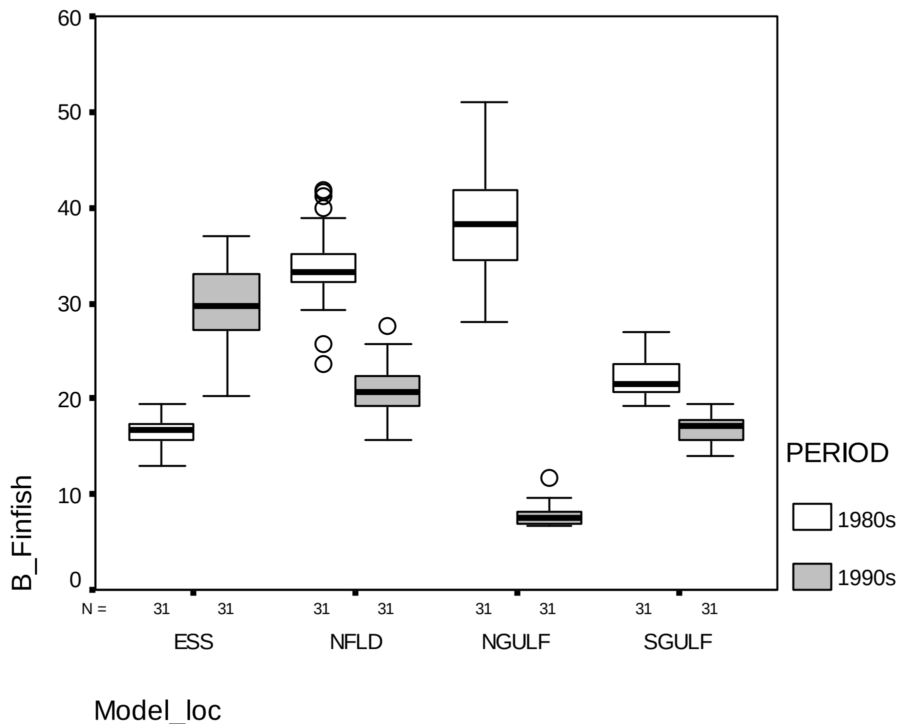


Figure 5: Total finfish biomass (values from Ecopath models).

Total Planktivore biomass

Like the trend seen for total biomass, estimated planktivore biomass decreased in all ecosystems, except the eastern Scotian Shelf (Figure 6).

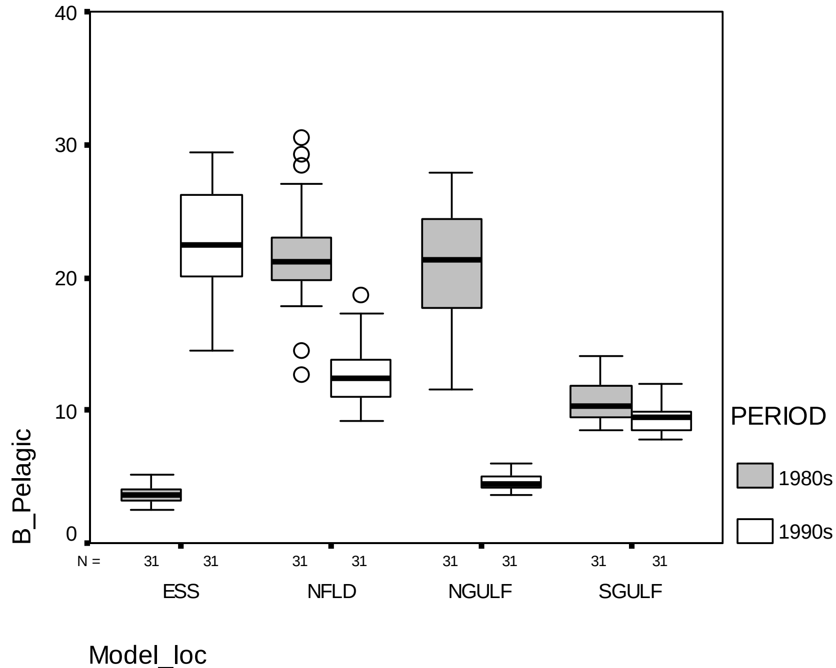


Figure 6: Total planktivore biomass in the 1980s and 1990s for the 4 NW Atlantic Ecosystems

Demersal fish biomass

The estimated biomass of demersal fish decreased in all ecosystems, and the greatest decrease occurred in the northern Gulf of St. Lawrence (Figure 7). The smallest change was in the southern Gulf of St. Lawrence.

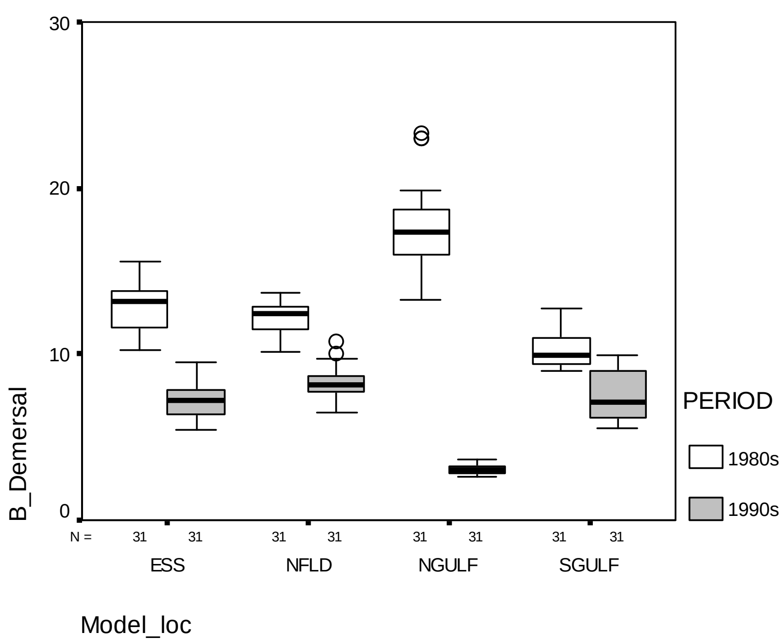


Figure 7: Total demersals fish biomass in the 1980s and 1990s for the 4 NW Atlantic Ecosystems

Flatfish biomass
Estimated flatfish biomass decreased in all ecosystems, with the exception of the southern Gulf of St. Lawrence where it did not change (although there is increased uncertainty in the model estimates, Figure 8).

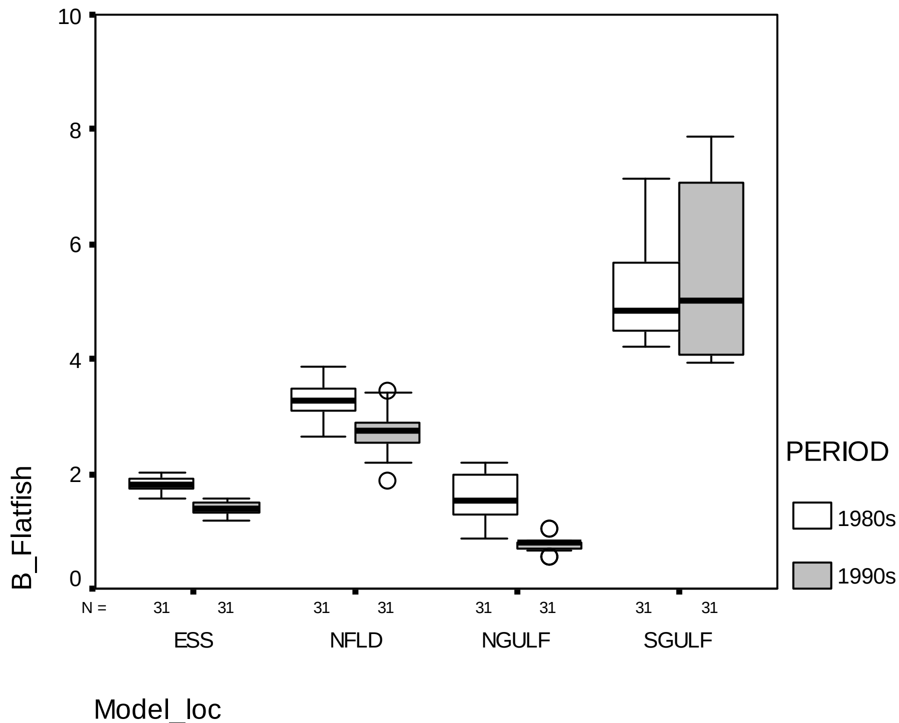


Figure 8: Total flatfish biomass in the 1980s and 1990s for the 4 NW Atlantic Ecosystems

Commercial invertebrate biomass
Estimated commercial invertebrates increased in the eastern Scotian Shelf and the southern Gulf of St. Lawrence (Figure 9). There was no change in the Newfoundland or northern Gulf of St. Lawrence models. The large increase in the eastern Scotian Shelf was estimated by Ecopath, although empirical data do indicate that shrimp increased – see keystone species below.

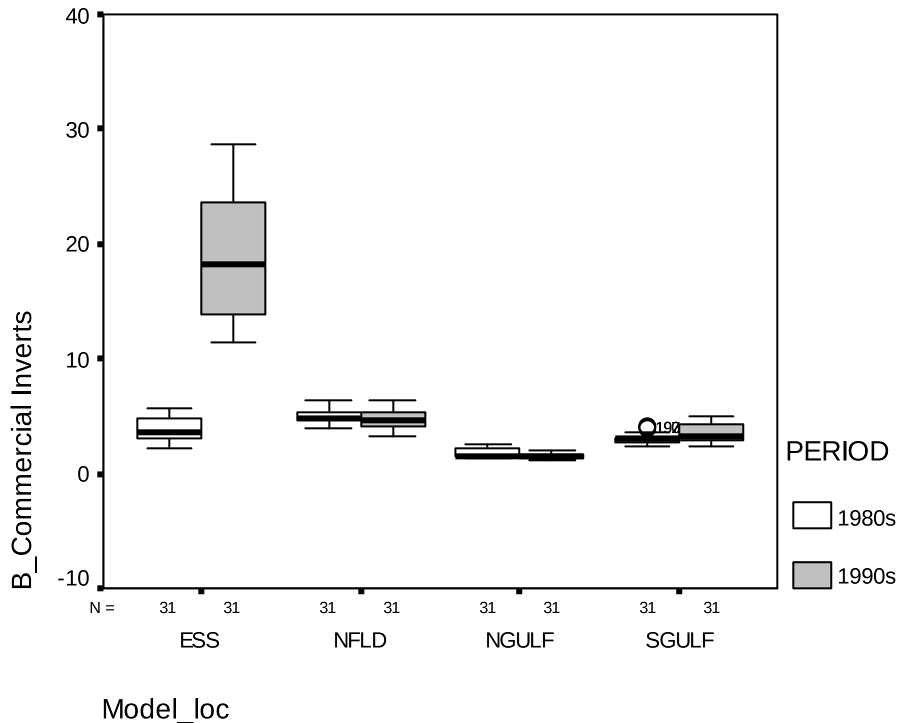


Figure 9: Total commercial invertebrate biomass in the 1980s and 1990s for the 4 NW Atlantic Ecosystems

Pelagic: demersal ratio and Commercial invertebrate: demersal biomass ratio
These ratios integrate the individual data for pelagics and demersals and commercial invertebrates and demersals fish. Both indicator show similar strong signals: a switch from a demersal fish dominated ecosystem to a pelagic and commercial invertebrate dominated system (Figure 10 and 11), with the exception of Newfoundland that did not show the former.

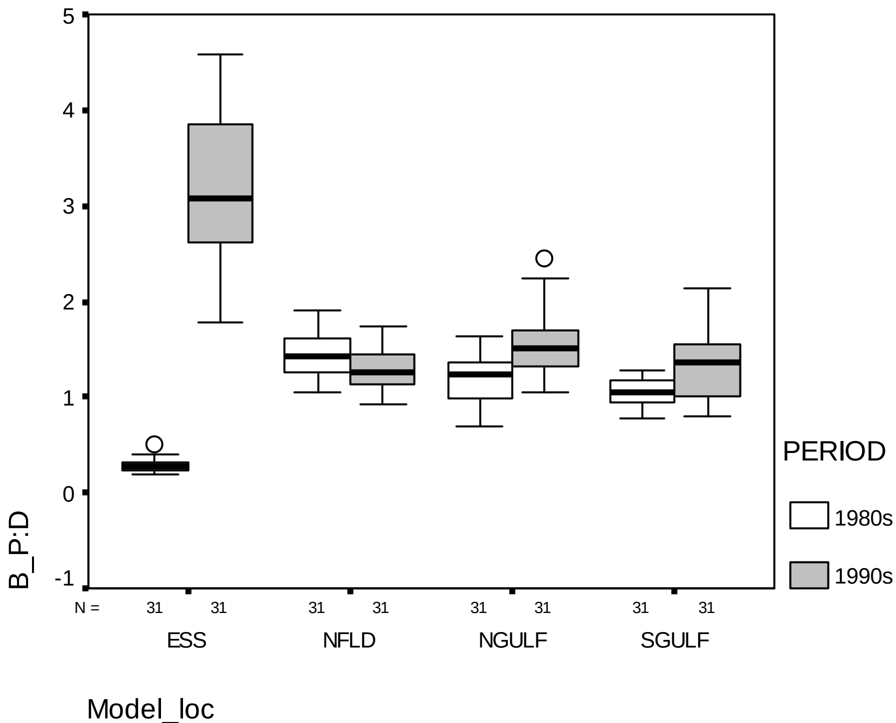


Figure 10. Pelagic fish:demersal fish ratio

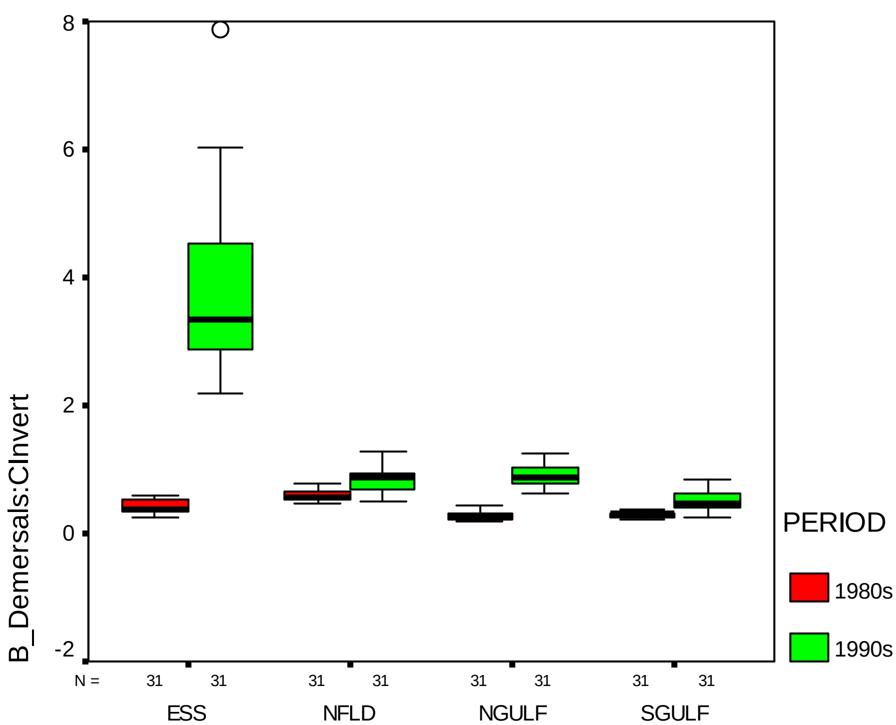


Figure 11: Commercial invertebrate:demersals fish ratio

~~*Seal:demersal fish biomass ratio – I have not done this yet*~~

~~As expected the 4 ecosystems follow similar trends in total landings, demersal fish and flatfish biomass, and pelagic or commercial invertebrate to demersals fish biomass ratios (Table XX). However, there are some differences between the systems. The northern Gulf of St. Lawrence appears to have suffered the greatest decline in finfish biomass, while the fishery in southern Gulf of St. Lawrence has improved since the mid 1990s, and has a healthy flatfish fishery. Pelagic fish biomass only increase in the eastern Scotian Shelf; it decreased elsewhere.~~

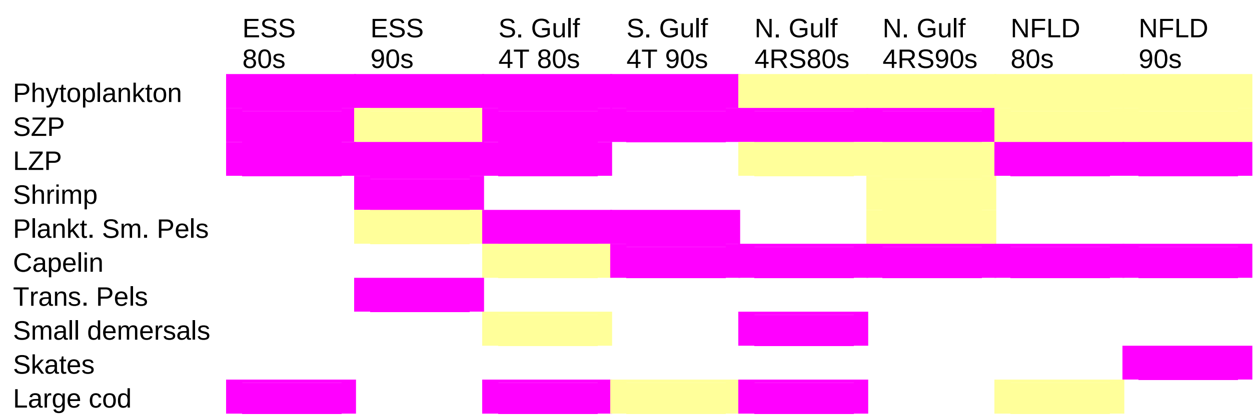
~~Table XX: Summary of direction of change for ecological indicators (+ = increase, - = decrease and ~ = no significant change) S gulf least impacted, but no recovery of cod (as in ESS and NFLD).~~

	~~ESS~~	~~NFLD~~	~~NGULF~~	~~SGULF~~
~~Total Landings~~	~~–~~	~~–~~	~~–~~	~~–~~ ~
~~Finfish biomass~~	~~+~~	~~–~~	~~–~~	~~–~~
~~Pelagic biomass~~	~~+~~	~~–~~	~~–~~	~~–~~
~~Demersal biomass~~	~~–~~	~~–~~	~~–~~	~~–~~
~~Flatfish biomass~~	~~–~~	~~–~~	~~–~~	~~\~~~
~~Pelagic:demersal biomass ratio~~	~~+~~	~~–~~	~~+~~	~~+~~
~~Invertebrate Biomass~~	~~+~~	~~\~~~	~~\~~~	~~+~~
~~commercial invertebrate:demersal fish biomass ratio~~	~~+~~	~~+~~	~~+~~	~~+~~

Keystone Species

Fourteen functional groups were identified as keystone in the four ecosystems for the two time periods (Table 3). Those with a keystone index (KS) close to 1 are termed keystone species, and are indicated by pink in Table 3.

Table 3: Ranking of functional groups according to their index of "keystoneness" (Eq. 1), where pink represents a keystone group and yellow represents a group with high impact.



No one species or functional group was keystone in all four ecosystems. Some groups such as phytoplankton, small zooplankton, large zooplankton, capelin, harp seals and cetaceans are common to all ecosystems and are either keystone or high impact in all or most. Cod is a keystone species on the eastern Scotian Shelf, southern Gulf and northern Gulf in the 1980s (high impact in Newfoundland in the 1980s) and in the southern Gulf in the 1990s.

Planktivorous small pelagics are common to all ecosystems, but are not keystone or high impact in Newfoundland. If taken together as a functional group, the 1980s eastern Scotian Shelf stands out as the one ecosystem where capelin and planktivorous small pelagics did not have an important functional role. Harp seals do not occur in the eastern Scotian Shelf.

In general, the keystone species remain the same from one time period to another, with some notable exceptions. On the eastern Scotian Shelf, cod, cetaceans and small zooplankton ceased to be keystone, whereas shrimp, transient pelagics and grey seals became keystone; in the southern Gulf of St. Lawrence, large cod and large zooplankton ceased to be keystone, while grey seals and capelin became keystone; in the northern Gulf of St. Lawrence, small demersals and large cod ceased to be keystone, while grey seals and cetaceans became keystone; in Newfoundland, hooded seals ceased to be keystone, while skates became keystone. Of the four ecosystems, Newfoundland was the most consistent from one period to another.

Grey seals were keystone in the 1990s for the more southern ecosystems (ESS and SGSL) while harp seals were keystones in both time periods for the more northern ecosystems (NGSL and NFLD).

Three functional groups are only keystone in one ecosystem, transient pelagics (ESS 90s), skates (NFLD 90s) and hooded seals (NFLD 80s). The transient pelagics and hooded seals were not considered further here since the abundance of transient pelagics is not well known (although they occur in most ecosystems), and hooded seal abundance is low in the northern and southern Gulf of St Lawrence and they do not occur on the eastern Scotian Shelf. Skates however occur in all ecosystems and like flatfish, can be considered an indicator species.

Thus the other 12 species/functional groups were determined to be keystone species and occur in all or most of the ecosystems. These consist mainly of top predators (marine mammals and cod), forage fish (small planktivorous fish and capelin) and secondary and primary producers.

Biomass/Abundance Trends

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 (in the eastern Scotian Shelf and Newfoundland; there is no time series of plankton data available for the Gulf of St. Lawrence), and an increase in phytoplankton in the eastern Scotian Shelf and

Newfoundland. Where the systems differ are in the forage fish. Planktivorous small pelagics and capelin increased in the eastern Scotian Shelf, but decreased in Newfoundland. In the southern and northern Gulf, planktivorous small pelagics decreased while capelin increased in the southern 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., sandlance and Arctic cod) in this region.

Table 4: Biomass/Abundance Trends of keystone Species from the 1980s to the 1990s, based on empirical survey and remote sensing data. Green boxes indicate where there is not data, or it is uncertain.

	ESS	S Gulf	N Gulf	NFLD
Phytoplankton	+	?	?	+
SZP	-	?	?	-
LZP	-	?	?	-
Shrimp	+	+	-	+
Planktivorous small pelagics	+	-	-	-
Capelin	+	+	~	-
Small Demersals	+	-	-	~
Skates	-	-	-	-
Large Cod	-	-	-	-
Grey Seals	+	+	+	~
Harp Seals	NA	+	+	+
Ceteaceans	?	?	?	?

Proportion of total mortality due to predation and predators of Keystone Species

Cetaceans, harp seals and grey seals have no predation mortality in these models. Total mortality of large cod is high in all the ecosystems in both the 1980s and 1990s. In the 1980s, this high mortality was due to fishing, but this is not the case in the 1990s. In the northern and southern Gulf of St. Lawrence and Newfoundland in the 1990s, over 50% of large cod mortality is due to predation (Figure 12). Harp seals, grey seals and hooded seals are the main predators in the northern and southern Gulf, and harp and hooded seals in Newfoundland. However, large cod have few predators on the eastern Scotian Shelf, and while grey seals are their main predator, this predation is very low and the cause of the high mortality is not attributable to predation (Bundy and Fanning 2005).

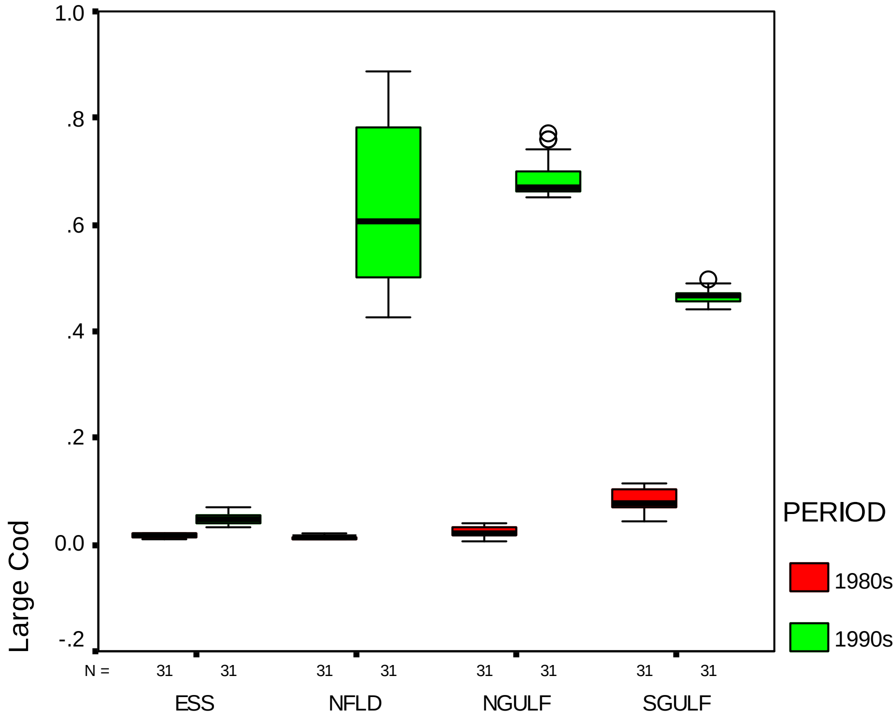


Figure 12. Proportion of large cod total mortality due to predation.

Predation mortality on small cod increased in all ecosystems except the southern Gulf (Figure 13). It is highest in Newfoundland and the eastern Scotian Shelf, and about half the level in the two Gulf systems. In all cases, predation mortality accounts for most of the total mortality in the 1990s, thus predation mortality approximates total mortality. In the 1980s, one of the main predators of small cod in all systems was large cod. Demersals predators were the other main predators (Table 5), except in the southern Gulf, where it was seals. In the 1990s, seals became important predators of small cod in all the ecosystems, although large cod were still important predators in the two Gulf models, and demersals predators were important in the eastern Scotian Shelf and Newfoundland models. The latter two systems had a greater diversity of predators accounting for 75% of the predation on small cod in both time periods.

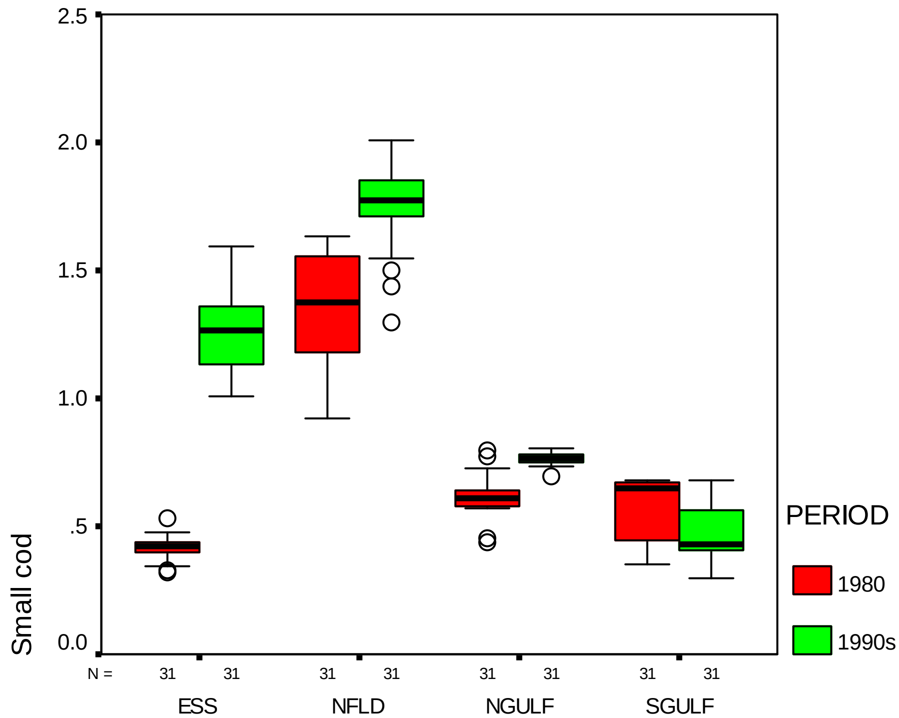


Figure 13. Predation mortality of small cod

Table 5. The main predators accounting for over 75% of predation on small cod in the 1980s and the 1990s. Colour codes depict common species/functional groups.

Time Period	ESS	SGULF	NGULF	NFLD
1980s	Juv. Dem.Pisc.	Large cod	Large cod	Squid
	Grey seals	Harp seals	L. demersals	Cod + 40cm
	Large cod	Grey seals	Harp seals	Juv. Dem. Pisc
	Dem. Piscivores			Skates
	Haddock			L_G. Halibut
	Squid			
	Ceteaceans			
1990s	Grey seals	Large cod	Grey seals	Squid
	Silver hake	Grey seals	Large cod	Juv. Dem. Pisc
	Juv. Dem.Pisc.	Harp seals	Harp seals	Harp Seals
	Squid			L_G. Halibut
	Ceteaceans			Cetacceans
				Dem. Pisc

Like large cod, skates have few predators. In all areas, demersals fish are important predators, and in the southern and northern Gulf and the eastern Scotian Shelf, grey seals are also important predators. Total predation mortality is lower in the eastern Scotian Shelf and Newfoundland than in the 2 Gulf regions for both time periods. It decreases in the eastern Scotian Shelf, increased in Newfoundland and effectively did not change in the Gulf. Predation mortality accounted for around 90% of mortality of skates in the northern Gulf and southern Gulf (although it decreased in the latter in the 1990s) where as in the eastern Scotian Shelf and Newfoundland it was lower.

Total mortality of capelin increased in all ecosystems except the southern Gulf, where is decreased. In Newfoundland and the northern Gulf, most of this mortality is due to predation by Harp seals, Greenland halibut, large cod, capelin and cetaceans, and similarly in the northern Gulf by cetaceans, harp seals, redfish and capelin. On the eastern Scotian Shelf where capelin are a recent addition to the ecosystem (Frank et al. 1996), and in the southern Gulf of St. Lawrence, predation only accounts for 60-70% of total mortality (Figure 14). Like the other two systems, predation by seals and cannibalism is important. Additional significant predators on the eastern Scotian Shelf include silver hake and in the southern Gulf small pelagic piscivorous in the mid-1990s.

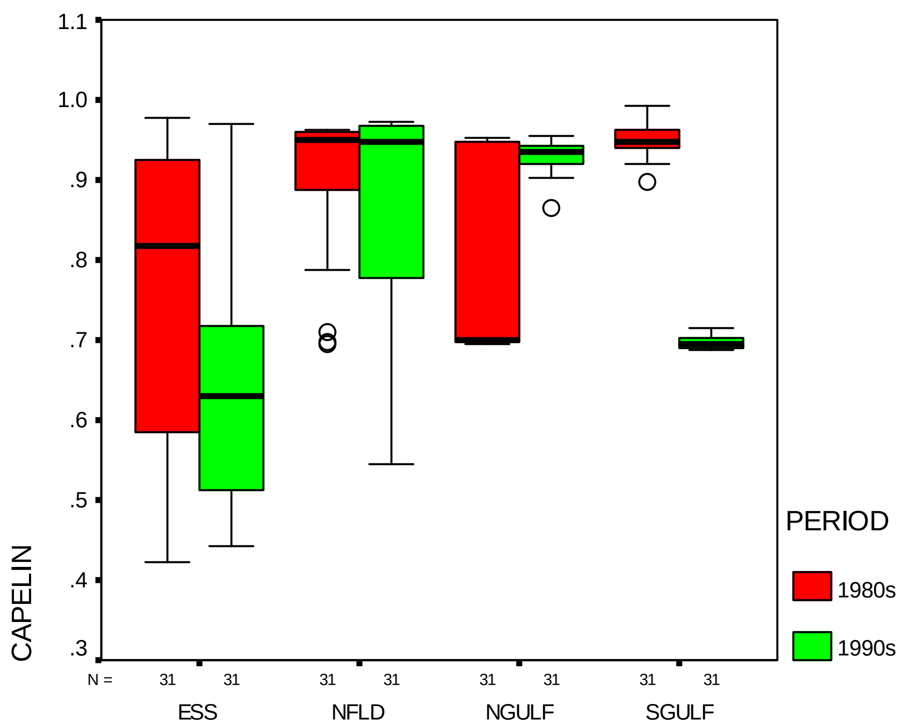


Figure 14. Proportion of capelin total mortality due to predation.

Planktivorous small pelagics

As would be anticipated for a forage group, predation mortality accounts for most of the mortality, although there is a great degree of variation in estimates, especially in Newfoundland (Figure 15). The large drop in the eastern Scotian Shelf in the 1990s is due to the large increase in biomass of planktivorous small pelagics (sandlance and herring) and the lack of predators (demersals fish). Declines in the northern and southern Gulf are less severe. They are preyed on by a wide array of predators in all systems, including redfish, large cod, cetacean, Greenland halibut and demersals feeders. In the Gulf of St. Lawrence, fishing is also an important source of mortality of planktivorous small pelagics, accounting for between 24 and 43% of total mortality, where in Newfoundland and the eastern Scotian Shelf, it has little to no impact. Total mortality decreased on the eastern Scotian Shelf and the southern Gulf, but remained stable in Newfoundland and the northern Gulf.

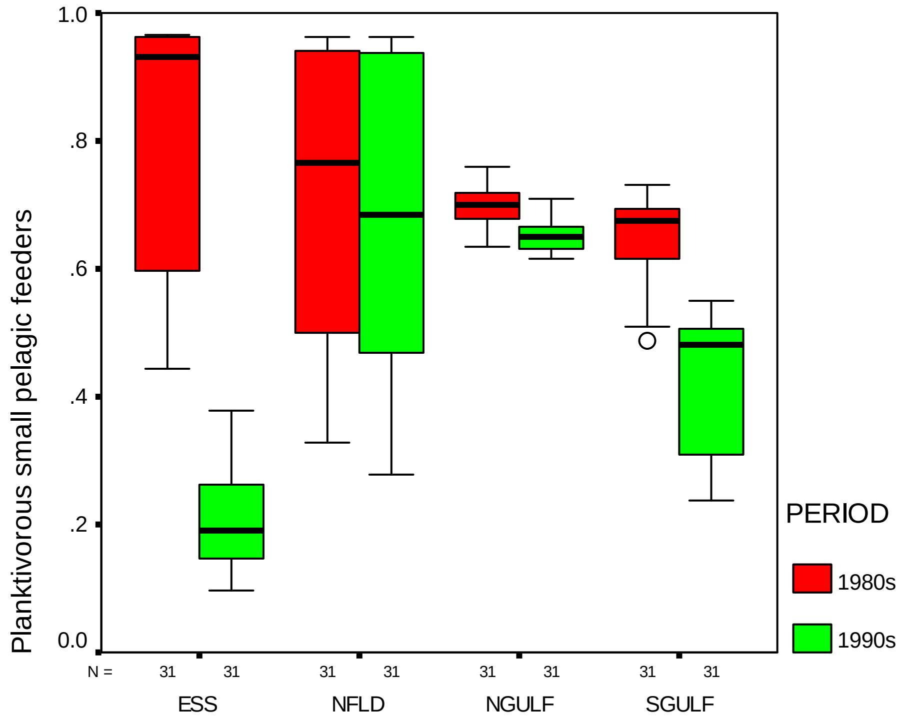


Figure 14. Proportion of planktivorous small pelagics total mortality due to predation.

Shrimp

Shrimp are important an important prey group in all the ecosystems, in both time periods, and most of mortality is due to predation. Fishing accounts for a small percentage of mortality. Total mortality is relatively low in the eastern Scotian Shelf, Newfoundland and the northern Gulf, but is higher in the southern Gulf (Figure 15) where large cod, American plaice, and small cod were the main predators for the two time periods. In the 1990s, American plaice, piscivorous small pelagics and large crustaceans all increased their consumption of shrimp. In the northern Gulf, redfish, small cod, and Greenland halibut, were the main predators in both time periods. Cod and demersals fish were the main predators in the eastern Scotian Shelf and Newfoundland in the 1980s, but in the 1990s, sand lance were the main predator of shrimp.

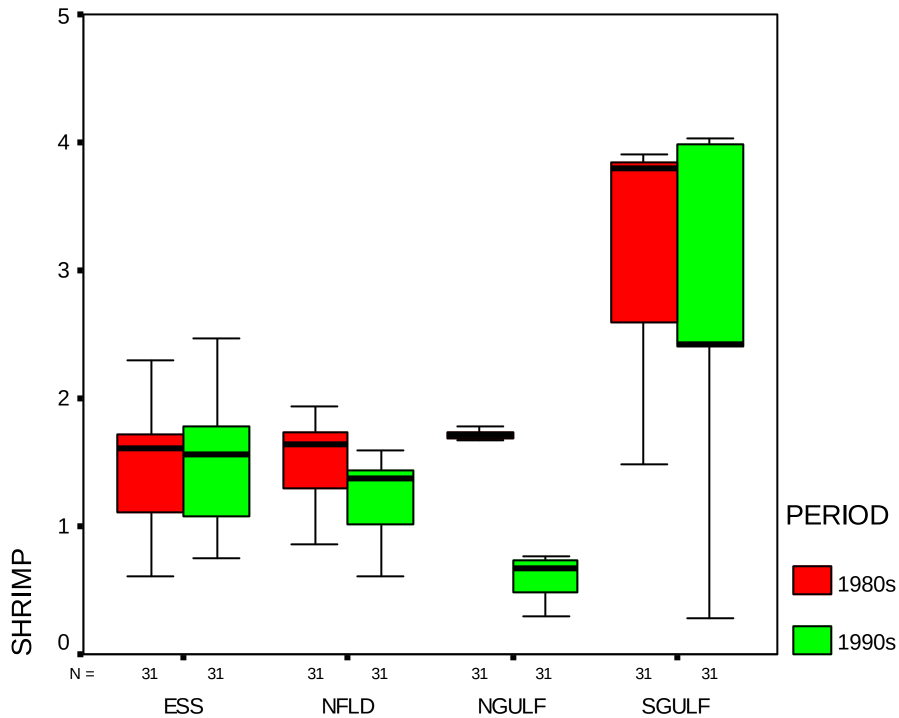


Figure 15. Total mortality of shrimp

Large zooplankton and small zooplankton are ubiquitous and form the prey of most species at some point in their life cycle. As such, most of their mortality is due to predation, although this decreased in the northern Gulf in the 1990s, which could be due to a considerable decrease in predation by fish on small zooplankton. While many species prey on zooplankton, their main predators vary to some degree in the different ecosystems, although forage fish play on dominant role in all. In the eastern Scotian Shelf, the main prey of large zooplankton are small silver hake, cannibalism and shrimp in the 1980s and in the 1990s, sandlance, shrimp and small pelagics, reflecting the increase in biomass of these species. In Newfoundland the main predators were capelin, sand lance and cannibalism in both time periods. In the southern Gulf, planktivorous small pelagics, small American plaice, and piscivorous small pelagics were the main predators of large zooplankton in the 1980s and in the 1990s, when cannibalism also became an important source of mortality. Similarly in the southern Gulf, the main predators were capelin, redfish and small cod in the 1980s and capelin, cannibalism and planktivorous small pelagics in the 1990s.

The main predator of small zooplankton in the eastern Scotian Shelf and Newfoundland was large zooplankton, accounting for 75% to 85 % of total mortality in both time periods, whereas in both Gulf models, cannibalism within the small zooplankton group accounted for between 45% and 65% of mortality. Other main predators included large zooplankton and forage fish (Gulf models) and shrimp and forage fish (eastern Scotian Shelf and Newfoundland).

Functional Role Indicators

As might be expected from the results above, the biomass of marine mammals increased in all areas. Piscivorous fish biomass decreased everywhere while forage fish biomass decreased in

Newfoundland and the northern Gulf, but increased in the eastern Scotian Shelf and the southern Gulf. Changes in total consumption reflect these trends (Figure 16), but there are some differences in the consumption of fish by piscivorous fish and forage fish. In the eastern Scotian Shelf, the amount of fish eaten increased, although total consumption decreased (Figure 17). This reflects an increase in piscivory on the eastern Scotian Shelf (Bundy 2005), due to the increased availability of forage fish as prey. Since forage fish are mainly planktivorous, they eat very little fish.

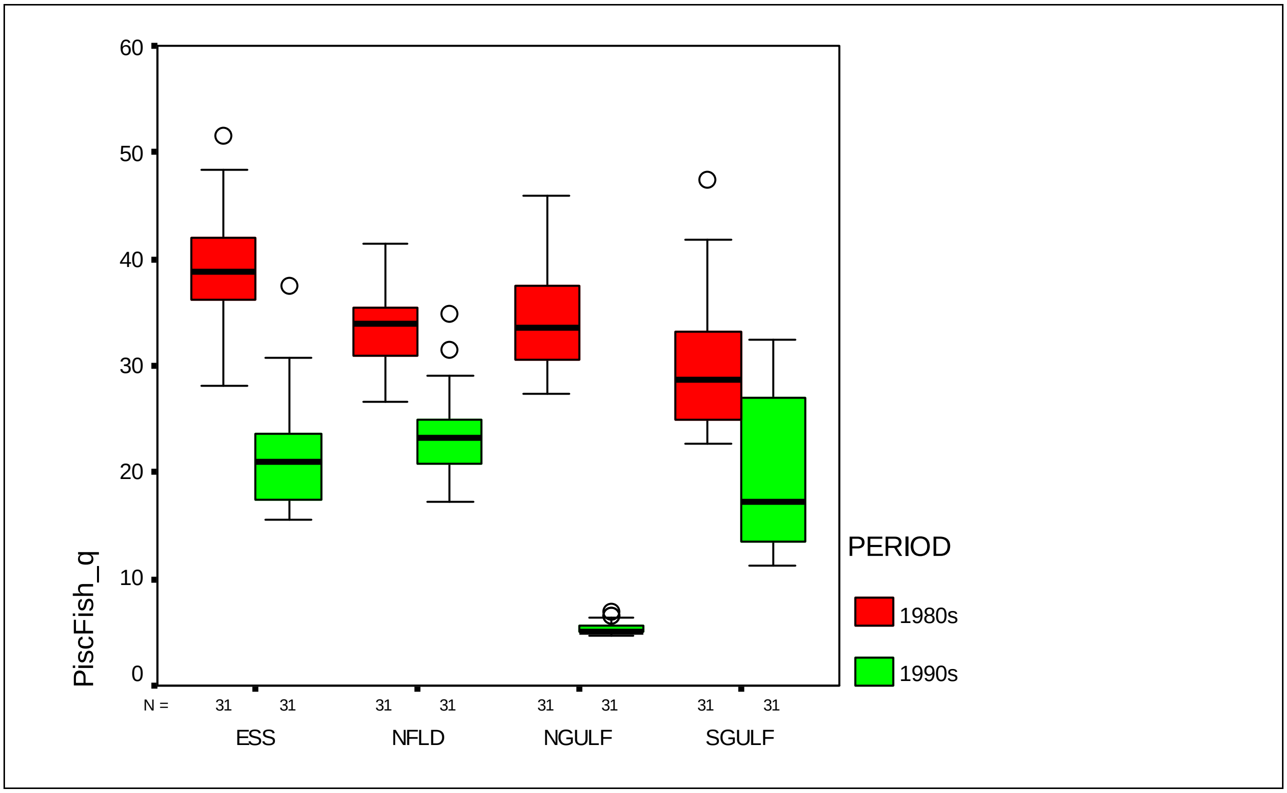


Figure 16. Total consumption by piscivorous fish in the 1980s and 1990s in the 4 NW Atlantic ecosystems.

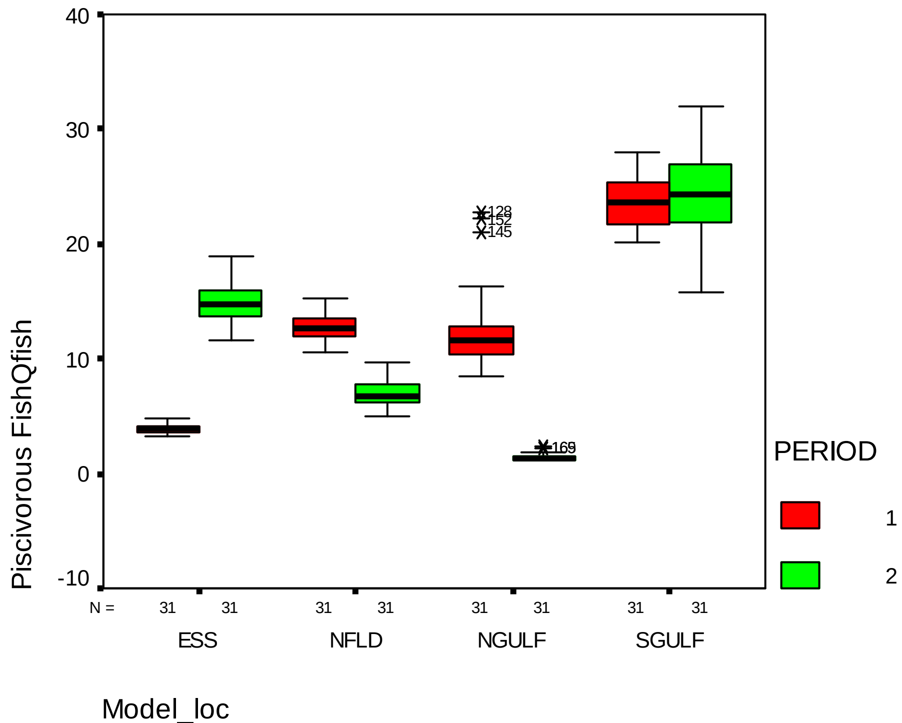


Figure 17. Total fish consumption by piscivorous fish in the 1980s and 1990s in the 4 NW Atlantic ecosystems.

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 6). The global resource overlap index, α, for all four ecosystems, decreased between the two time periods (0.0430 in the 1980s vs 0.0293 in the 1990s). This decrease in overlap was also found in the eastern Scotian Shelf (-26%), Newfoundland (-71%), and the southern Gulf (-37%) ecosystems, but not in the northern Gulf, where the overlap between marine mammals and fisheries increased by 19%. The ecosystem where the highest overlap occurs is the southern Gulf, in the 1980s as in the 1990s. The lowest overlap seems to occur in the eastern Scotian Shelf.

Table 6. Estimated resource overlap index between marine mammals and fisheries from four Nortwest Atlantic ecosystem models.

Ecosystem model	$\alpha_{j,l}$ 1980s	$\alpha_{j,l}$ 1990s
Eastern Scotian Shelf	0.0081	0.0060
Newfoundland	0.0276	0.0081
Northern Gulf of St. Lawrence	0.0307	0.0364
Southern Gulf of St. Lawrence	0.1054	0.0664
GLOBAL (average)	0.0430	0.0292

Whole System Indicators

Summary Statistics.

Total biomass of the ecosystem increased in the eastern Scotian Shelf and southern Gulf, but decreased in the northern Gulf and Newfoundland, Table 7. There was an increase in almost all the metrics related to total flows in the southern Gulf, i.e, total consumption, total respiration, flows to detritus, total production and total system throughput. The reverse occurred in the northern Gulf and in Newfoundland, with the exception of flows to detritus which was not significantly different in Newfoundland. In the eastern Scotian Shelf, total consumption increased, while there was no significant change in total respiration, production or total system throughput. Flow to detritus decreased in eastern Scotian Shelf. Net system production did not change significantly in any of the ecosystems from the 1980s to the 1990s. The ratio of primary production to total biomass decreased in all systems except the southern Gulf where there was no significant change, indicating that the systems have become less mature. 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, where it did not change. The omnivory index did not change in the Gulf models, decreased in eastern Scotian Shelf and increased in Newfoundland.

As might be anticipated, all the catch related indicators (total catch, the mean trophic level of the catch and the gross efficiency of the catch decreased everywhere.

Table 7: Summary of significant changes for summary statistic metrics

	ESS	NFLD	NGULF	SGULF
Total Biomass	+	–	–	+
Total Consumption	+	–	–	+
Total Respiration	~	–	–	+
Flow to detritus	–	~	–	+
TST	~	–	–	+
Total Production	~	–	–	+
NetSysPP	~	~	~	~
PP/B	–	–	–	~
B/TST	+	+	+	~
CI	-	~	–	–
OI	-	+	~	~
Total Catch	–	–	–	–
MeanTL	–	–	–	–
Grosseff	–	–	–	–

Network Indices

Table 8: Summary of significant changes for network indices

	ESS	NFLD	NGULF	SGULF
Entropy	+	~	-	~
AMI	+	~	~	~
A:C	-	~	+	~
Redundancy	+	+	~	~
Finn's Cycling Index	+	+	~	~

Entropy (H):

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). In the eastern Scotian Shelf the 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 (Figure 18). H is very stable in Newfoundland and the southern Gulf, so the flow diversity has not changed over that time, which means that the reduction in flows from groundfish was replaced by flows to invertebrates.

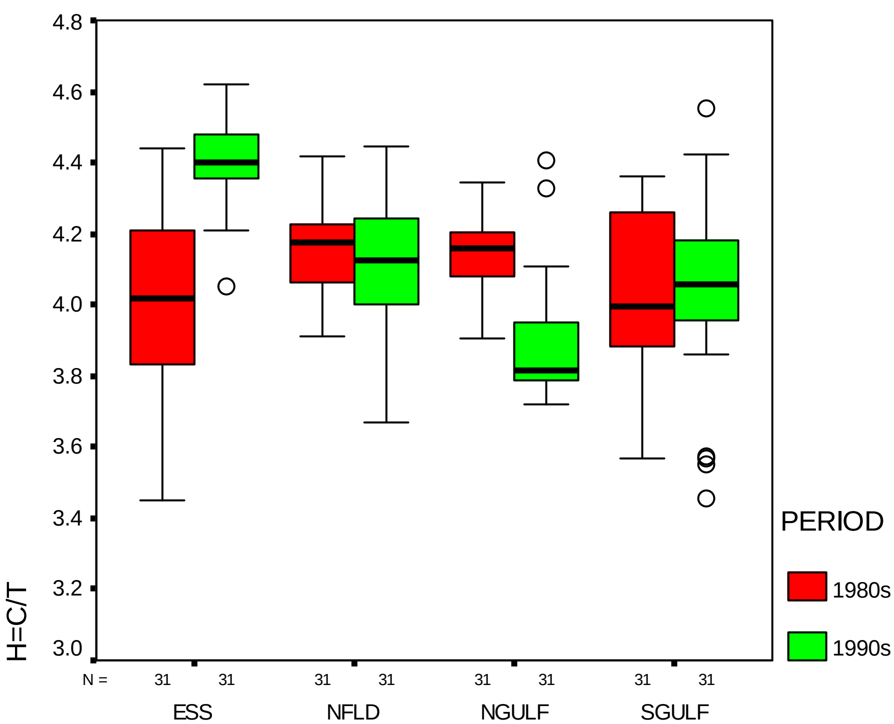


Figure 18. Estimated Statistical Entropy in the 4 NW Atlantic ecosystem in the 1980s and 1990s.

Average Mutual Information measures organization and exchanges among components, and increase in AMI shows that system is becoming more constrained and channeling flows among more specific pathways. The eastern Scotian Shelf was the only ecosystem where this increased (Figure 19). AMI is higher in the eastern Scotian Shelf and Newfoundland higher than in the Gulf models, suggesting that these ecosystems are more constrained.

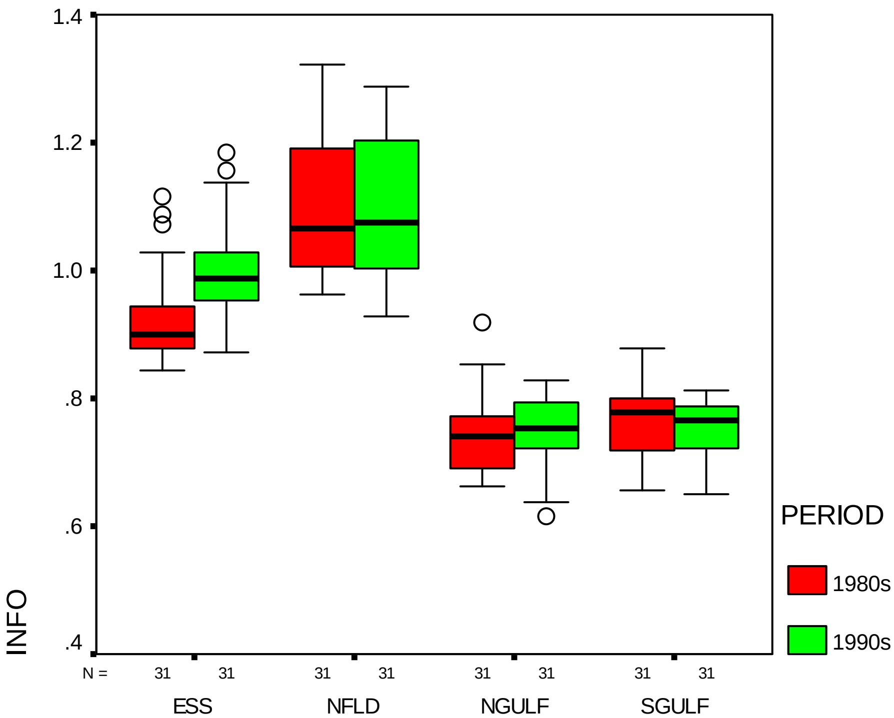


Figure 19. Estimated Average Mutual Information (AMI) in the 4 NW Atlantic ecosystem in the 1980s and 1990s.

The Ascendancy:Capacity ratio increased in the northern Gulf and decreased in the eastern Scotian Shelf (Figure 20). There was no significant different in either Newfoundland or the southern Gulf, However, both the Gulf models have a lower A:C then the eastern Scotian Shelf or Newfoundland. This suggests that the latter ecosystems were more channel like with very little variations in flow.

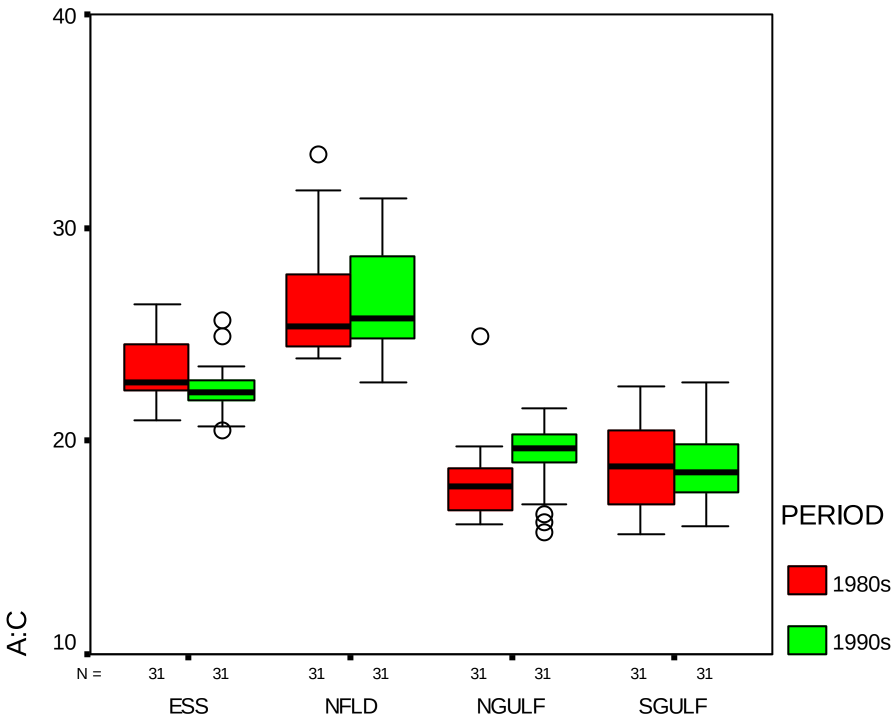


Figure 20. Estimated Ascendancy:Capacity (A:C) in the 4 NW Atlantic ecosystem in the 1980s and 1990s.

Redundancy (R or overhead on internal flows, in % flowbits) increased in the eastern Scotian Shelf and Newfoundland but did not significantly change in the Gulf models (Figure 21). A high R indicates that 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.

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 (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.

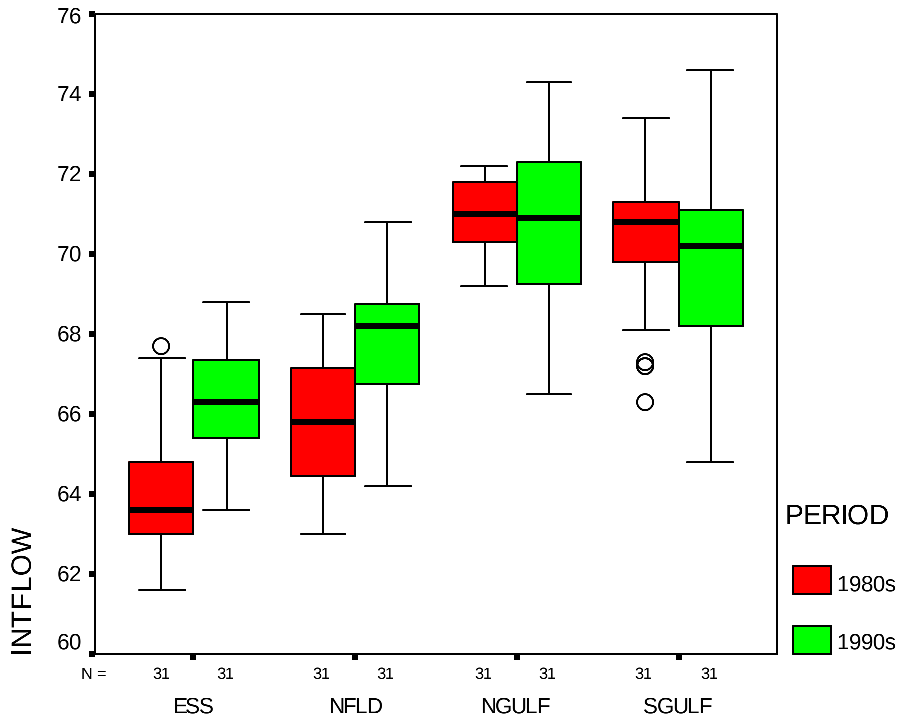


Figure 21. Estimated Redundancy in the 4 NW Atlantic ecosystem in the 1980s and 1990s.

Finn's cycling index (%) increased in the eastern Scotian Shelf and Newfoundland but did not change in the Gulf models (Figure 22). However, Finn's cycling index is much higher in the Gulf models than in Newfoundland or the eastern Scotian Shelf.

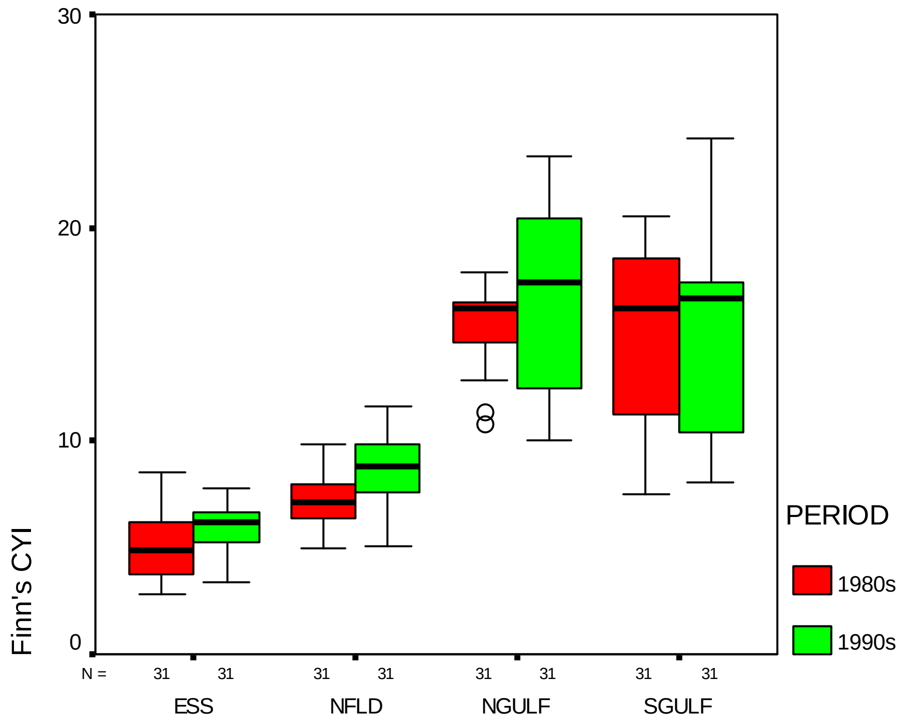


Figure 22. Estimated Finn's Cycling Index in the 4 NW Atlantic ecosystem in the 1980s and 1990s.

Discussion

As might be expected the four NW Atlantic ecosystems follow similar broad trends in the eight ecological indicators that assess the general state of an ecosystem. Although we were not able to examine mean length or weight of fish, the changes in total landings, demersal fish and flatfish biomass, and pelagic or commercial invertebrate to demersals fish biomass ratios indicate the all four systems have switched from a long-lived demersal, commercial fish dominated ecosystem to a shorter lived pelagic and invertebrate dominated ecosystem. The mean trophic level of landings declined in all systems, which was 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, in the southern Gulf, landing are around twice as high as in the other ecosystems. The lower decline in total landings in the southern Gulf than in the northern Gulf, may have occurred because the fishery in the southern Gulf was more diverse (37 species versus 25) during the mid-1980s. However, landings in Newfoundland and eastern Scotian Shelf were also diverse (42 and 32 respectively).

The northern Gulf of St. Lawrence appears to have suffered the greatest decline in finfish biomass, while in the eastern Scotian Shelf total fish biomass increased due to an increase in pelagic fish biomass (which decreased elsewhere). Thus this first set of analyses comparing the 4 ecosystems indicates that the biomass structure has dramatically changed from one dominated by long-lived demersal fish to a shorter lived, small bodied forage species dominated ecosystem.

The 12 keystone species identified from this analysis were mostly composed of species at the top and bottom of the trophic spectrum. The commonality in keystone species among the four NW Atlantic ecosystems was striking, as was the similarity in their biomass trends: cetaceans, seals, cod, forage species, zooplankton and phytoplankton species. However, despite modeling efforts and scientific surveys, there is still great uncertainty over the abundance estimates for some of these species, such as cetaceans. Little is know about the abundance trends of cetaceans in any of these ecosystems: surveys are few or non-existent. We do have some estimates for the 1990s (Heymans 2003, Morissette et al. 2003, Bundy 2004, Savenkoff et al. 2006), but there are no estimates of biomass from the 1980s.

While there was a great deal of consistency in the response of keystone species to ecosystem change since the 1980s, changes in the abundance of forage species differed in the four systems. The only region where small planktivorous pelagics increased was the eastern Scotian Shelf, due to increases in sand lance and herring. While we are confident of these increases, the absolute biomass is uncertain. Small planktivores do not increase elsewhere. One explanation maybe that other than in Chedabucto Bay, small pelagics (herring and sand lance) have not been exploited in the eastern Scotian Shelf, whereas there have been herring and capelin fisheries in Newfoundland, and the northern Gulf. In the southern Gulf, small planktivores decrease. However, taking the longer term perspective, herring has increased since the mid 1990s in the southern (DFO 2005) and so it too has seen an increase in forage fish in general, since capelin also increased. In the Northern Gulf, capelin do not appear to have increased, although there has been a range extension (DFO 2001).

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 support this since, 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 are no time series data for either zooplankton or phytoplankton in the Gulf of St. Lawrence, so we cannot say what is occurring at the lowest trophic levels, but we do see an increase in seals, decrease cod and skates, an increase in forage species (shrimp, herring and capelin) 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 (Savenkoff et al. 2006, Bourdages et al. 2007).

Keystone species had similar predators in the 4 NW Atlantic systems, although there were differences in total predation mortality and the proportion of mortality due to predation. There are a few key differences. In the eastern Scotian Shelf, large cod have few predators whereas in the other 3 ecosystems, they are preyed on by seals, and this accounts for up to 70% of mortality in the 1990s. Predation mortality on small cod in the 1990s was higher in the eastern Scotian Shelf and Newfoundland 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 has 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.

When aggregated to larger functional groups, it is clear that piscivorous fish have been replaced by marine mammals (seals) as the top predator (piscivorous fish consumption decreased everywhere, while marine mammal consumption increased). However, though marine mammal consumption has increased, the marine mammal overlap index, indicates that in general, marine mammals consume food resources that are not the main target of fisheries. In areas where competition between marine mammals and fisheries is higher (Southern Gulf of St. Lawrence), the results indicate that the resource overlap is higher than the global average presented in Morissette (in prep.). Most overlap appears to occur between fisheries and seals. Cetaceans included in the models preyed mainly on krill, so when all marine mammals are analyzed as a whole, their overlap is not as strong as may be expected.

In the eastern Scotian Shelf, Newfoundland and southern Gulf models, the overlap of marine mammals versus fisheries for food resources decreased from the 1980s to the 1990s. This change is associated with an increase in marine mammals consumption of fish in all ecosystems, but because there is no groundfish species to prey on, seals species seem to have shifted their consumptions towards lower trophic level species, which are not the main target of fisheries. Furthermore, since landings (fishing) has decreased in all systems, this will lower the index.

The overlap with the fishery increased from the 1980s to the 1990s in the northern Gulf. This may be due to increased consumption by marine mammals. Furthermore, in the 1980s, marine mammals were consuming more capelin, small piscivorous pelagics and krill (cetaceans), species that were not the main targets of the Fishery in the 1980s. However, in the 1990s, marine mammals were eating more capelin, krill (cetaceans) and most importantly small planktivorous pelagics (herring), which represented the most important part of the catch at that time.

Based on the ecological indicators, keystone species and functional species analyses, we see both broad similarities in trends among the four NW Atlantic ecosystems, but also differences. The northern Gulf stands out because of the intensity of the decrease in fish landings and fish biomass, the decline or stasis in forage fish, and the large impact that seals have on the ecosystem. Newfoundland falls into a similar category. Alternatively, the southern Gulf is potentially the least affected: it has twice the landings per unit area as the other ecosystems. The eastern Scotian Shelf is also highly impacted, but has large increases in forage species abundance and little seal predation of cod by seals. The summary statistics and network analyses largely confirm these observations.

The eastern Scotian Shelf stands out because total biomass and total consumption increased, although total system throughput remained the same (due to a decrease in flows to detritus). In Newfoundland and the northern Gulf virtually all these statistic decrease, indicating that the whole systems have decreased in size. Although it appears that in the southern Gulf, most of the summary flow statistic increased, this model is in the process of being updated, and indications are that the results for the southern Gulf are more like the Northern Gulf.

The Connectance Index decreased in all ecosystems except in Newfoundland, where it did not change, where as the system ommnivory index increases in Newfoundland, decreased in the eastern Scotian Shelf and remained the same in the two Gulf models, The connectance index represents the number of trophic links in the food web. If we just examine this index, we would tend to think that the there was a decreased in complexity in all ecosystems except for Newfoundland. However, connectance is only based on linking, and thus can be erroneous. 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). With this index, we see that complexity probably increased in the NFLD, while it stayed approximately the same in the NGSL and SGSL and decreased in the ESS.

The network indicators require some explanation and should be interpreted as a group for each ecosystem. On the eastern Scotian Shelf, H, or systems entropy increases, indicating that the systems flows have become more diverse, signifying increased resilience, which is mirrored by the low A:C, showing that the system became less organized. However, the increase in AMI is a sign that pathways are getting more channeled (in contradiction to the increase in entropy described above). 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.

Newfoundland appears to be a very stable system since neither H, AMI or A:C changed much from the 80s to the 90s, perhaps because the decline in cod and other flatfish was replaced by an increase in shrimp and harp seals in the total biomass and flows of the system. 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 gone to a new stable state. The lack of change in A:C indicates that the reduction in flows from groundfish were likely replaced by flows to invertebrates, but without the large pelagic increase observed in the eastern Scotian Shelf.

In the northern Gulf, the only significant changes were a decrease in entropy and a small increase in A:C. This indicates a decrease in uncertainty, and reduced 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 none of the network characteristics changed, so the flow diversity has not changed over that time, which means that the reduction in flows from groundfish was replaced by flows to 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 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 little redundancy in the system. Given earlier similarities between Newfoundland

and the northern Gulf, one would have expected the Northern Gulf to be similar to Newfoundland but it isn't. This might be due to differences in the model construction between the inverse modeling methodology and the Ecopath methodology.

The redundancy is one part of the overhead (which is the compliment to the A:C), with internal respiration, export and import also playing a part in the overhead of the system. Thus with a lower A:C in eastern Scotian Shelf compared to Newfoundland you would expect the R to be higher in that system, but this is not the case. Thus, the increase in overhead in this system over time must be made up by an increase in the other parts of the overhead (internal respiration, export, import) perhaps due to the large change from the groundfish dominated system to a pelagic and invertebrate system, with pelagics and inverts being dependent on other parts of the ecosystem.

Despite best attempts to use a standard approach to modeling (Ecopath estimates of network and summary statistics, models of same size and structure), the results indicate that for several indicators the two Gulf models are different from the Newfoundland and eastern Scotian Shelf 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 4 systems. A:C is also a ratio, but the two Gulf models have much lower values than the eastern Scotian Shelf and Newfoundland 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. Until we can resolve whether these differences are model derived or real, we cannot make robust conclusions about differences between ecosystem network indices.

Within each ecosystem, we can conclude that in eastern Scotian Shelf and Newfoundland 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 ESS seeming to do better than Newfoundland (bigger increase in R than Newfoundland). The two Gulf systems on the other hand have not changed. Since the southern Gulf did not have such a large collapse in ground fish as the other systems, it does not appear to have changed as dramatically as the other ecosystems.

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 4 ecosystems. This decline has left marine mammals such as seals as top predators of many species (especially fishes) during the mid-1990s and had profound effects over all trophic levels (top down effects) in Newfoundland, 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 prey to forage fish. This a variant of the cultivation-depensation hypothesis suggested by Bundy and

Fanning (2005), where cod where 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 or the northern Gulf since the forage fish biomass did not increased. There is scope for further investigation in the southern Gulf.

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

Acknowledgments

This work was originally supported by the DFO funded project "Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic", a program supported by the Canadian Department of Fisheries and Oceans Science Strategic Fund. Thanks to the organisers of the ICES Theme Session D, Comparative marine ecosystem structure and function: Descriptors and characteristics for the invitation and support to attend the 2007 ICES Conference.

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Appendix 1

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

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

	Small mesopelagics	Myctophidae, Sternoptychidae
Squid	Squid	*Illex illecebrosus, Loligo pealeii*
Large crustaceans	Large crabs (> 50 mm CW)	*Chionoecetes opilio, Cancer borealis, Chaceon quinquedens, Lithodes maia, Cancer borealis*
	Small crabs (< 50 mm)	*Hyas areneus, H. coarctatus, Pagurus spp., Cancer irroratus,* juveniles of large crabs
Shrimp	Shrimp	*Pandalus spp Pasiphaea sp., Crangon sp., Spirontocaris sp., Eualus sp., Sabinea sp., Argis Sp., Lebbeus sp.,*
Echinoderms	Echinoderms	*Strongylocentrotus palliddus, Echinarachnius parma*
Polychaetes	Polycheates	*Prionospio steenstrupi* and others
Bivalves	Bivalves	*Placopecten magellanicus, Chlamys islandicus, Cyrtodaria siliqua, Macoma calcarea*
Other benthic invertebrates	Other benthic invertebrates	*Ophiura sarsi* and others
Large zooplankton	Zooplankton (large)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians, ctenophores, mysids, tunicates >5 mm and icthyoplankton
Small zooplankton	Zooplankton (small)	Copepods (mainly Calanus finmarchicus, C. hyperboreus, and Oithona similis), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates) and meroplankton
Phytoplankton	Phytoplankton	Diatoms *(Cahetoceros decipiens, Thalassiosira* 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 2. Functional groups used in modelling in the Newfoundland Shelf for the two time periods.

30 Groups	50 Groups	Species
	Walrus	*Odobenus rosmarus*
Cetaceans	Cetaceans	*Megaptera novaeangliae, Balaenoptera physalus, B. acutorostrata, B. borealis, B. musculus, Physeter catodon, Globicephala melaena, Phocoena phocoena*
	Grey seals	*Halichoerus grypus*
Harp seals	Harp Seals	*Phoca groenlandica*
Hooded seals	Hooded Seals	*Cystophora cristata*
	Ducks	*Somateria mollissima), Melanitta* sp.*, Clangula hyemalis*
Birds	Piscivorous birds	*Pinguinus impennis, Sula bassana, Phalacrocorax carbo, P. auritus, Larus argentatus, L. delawarensis, L. ridibundus, Rissa tridactyla, Sterna hirundo, S. paradisaea, Sterna caspia, Uria aalge, U. lomvia, Cepphus grille, Alca torda, Fratercula arctica, Fulmarus glacialis, Puffinus puffinus, P. gravis, P. griseus.*
	Planktivorous birds	*Oceanodroma leucorhoa, Alle alle*
Large cod	Cod > 35 cm	*Gadus morhua*
Small cod	Cod < 35 cm	Juveniles of above
Large plaice	American Plaice >35 cm	*Hippoglossoides platessoides*
Small plaice	American Plaice <35 cm	Juveniles of above
Large G halibut	Greenland Halibut > 40 cm	*Reinhardtius hippoglossoides*
Small G halibut	Greenland Halibut < 40 cm	Juveniles of above
Yellowtail flounder	Yellowtail flounder	*Limanda ferruginea*
Other flounders	Witch flounder	*Glyptodephalus cynoglossus*
	Winter flounder	*Pseudopleuronectes americanus*
Skates	Skates	*Raja laevis, R. radiate, R. senta, R. ocellata, Leucoraja erinacea*
	Dogfish	*Squalus acanthias*
Large pelagics	Mackerel (> 29cm)	*Scomber scombrus*
	Transient pelagics	*Thunnus thynnus, Xiphias gladius, Lamna nasus, Cetorhinus maximus,* Elasmobranchii
Redfish	Redfish	*Sebastes mentella, S. fasciatus*
Large demersals	Dem. & BP > 40 cm	*Urophycis tenuis, Merluccius bilinearis, Lophius americanus, Hemitripterus americanus, Brosme brosme, Hippoglossus hippoglossus*
	Other Dem. > 30 cm	*Melanogrammus aeglefinus, Phycis chesteri, Urophycis chuss, Anarhichas* sp., *Coryphaenoides* sp., *Lycodes* sp., Ogcocephalidae
	Lumpfish	*Cyclopterus lumpus*
	Greenland cod	*Gadus opac*
	Salmon	*Salmo salar*
Small demersals	Dem. & BP < 40 cm	Juveniles of *Urophycis tenuis, Merluccius bilinearis, Lophius americanus, Hemitripterus americanus, Brosme brosme, Hippoglossus hippoglossus*
	Other Dem. < 30 cm	Juveniles of *Melanogrammus aeglefinus, Phycis chesteri, Urophycis chuss, Anarhichas* sp.,

	Small Dem.	*Coryphaenoides* sp., *Lycodes* sp., Ogcocephalidae *Enchelyopus* sp., *Pholis gunnellus, Ulcina olriki, Leptagonus decagonus, Lumpenus lampretaeformis, Leptoclinus* sp., *Myoxocephalus* sp., *Prionotus* sp., *Anisarchus* sp.
Forage fish	Capelin	*Mallotus villosus*
	Arctic cod	*Boreogadus saida*
	Sand lance	*Ammodytes dubius*
	Herring	*Clupea harengus harengus*
Small pelagics	Small Pelagics	*Alosa sapidissima, Peprilus triacanthus, Argentina silus,* juvenile *Scomber scombrus, Osmerus mordax mordax*
	Small mesopelagics	Myctophidae*, Maurolicus muelleri, Paralepis elongata*
Squid	Arctic Squid	*Gonatus* sp.
	Shortfinned squid	*Illex illecebrosus*
Large crustaceans	Large crabs (> 50 mm CW)	*Chionoecetes opilio, Cancer borealis, Chaceon quinquedens, Lithodes maia*
	Small crabs (< 50 mm)	*Hyas areneus, H. coarctatus, Pagurus spp., Cancer irroratus,* juveniles of large crabs
	American lobster	*Lomarus americanus*
Shrimp	Shrimps	*Pandalus borealis, P. montagui*
Echinoderms	Echinoderms	*Strongylocentrotus palliddus, Echinarachnius parma*
Polychaetes	Polycheates	*Prionospio steenstrupi* and others
Bivalves	Bivalves	*Placopecten magellanicus, Chlamys islandicus, Cyrtodaria siliqua, Macoma calcarea*
Other inverts	Other benthic inverts.	*Ophiura sarsi* and others
Large zooplankton	Zooplankton (large)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians, ctenophores, mysids, tunicates >5 mm and icthyoplankton
Small zooplankton	Zooplankton (small)	Copepods *(Calanus finmarchicus, Oithona similis),* tunicates < 5 mm and meroplankton
Phytoplankton	Phytoplankton	Diatoms *(Cahetoceros decipiens, Thalassiosira* sp.*)*
Detritus	Detritus	

Table 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	*Balaenoptera physalus*, *B. acutorostrata*, *Megaptera novaeangliae*, *Phocoena phocoena*, *Lagenorhynchus acutus*, *L. albirostris*
Harp seals	*Phoca groenlandica*
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delwarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)[a]	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)[a]	*Reinhardtius hippoglossoides*
Large American plaice (> 35 cm)[b]	*Hippoglossoides platessoides*
Small American plaice (≤ 35 cm)[b]	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleureonectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinnus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[c]	*Ammodytes* spp.
Arctic cod[d]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp	*Pandalus borealis*, *P. montagui, Argis dentata*, *Eualus macilentus*, *E. gaimardi*
Large crustaceans	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Stronglyocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogene hebes*
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 *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiiosira nordenskioldii*, *T.* spp., *Fragilariopsis* 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)

[a]: Aggregated as Greenland halibut for the southern Gulf models.

[b]: Aggregated as American plaice for the northern Gulf models.

[c]: Included in the planktivorous small pelagic feeders for the southern Gulf models.

[d]: Included in the capelin group for the southern Gulf models.