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Ecosystem Models of Newfoundland For The Time Periods 1995, 1985, 1900 and 1450

**ECOSYSTEM MODELS OF NEWFOUNDLAND
FOR THE TIME PERIODS 1995, 1985,
1900 AND 1450**

Edited by

*Tony J. Pitcher, Johanna J. (Sheila) Heymans
and Marcelo Vasconcellos*

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Johanna J. (Sheila) Heymans and Tony J. Pitcher

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*A Research Report from
'Back to the Future: the Restoration of Past Ecosystems as Policy Goals for Fisheries'
Supported by the Coasts Under Stress 'Arm 2' Project*



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DIRECTOR'S FOREWORD

MORE THAN ONE ROUTE TO HEAVEN

Imagine a shipwreck after escaping from Moors in Morocco, being rescued by sailors from Sicily, meeting St Francis of Assisi, delivering a brilliant impromptu address, and eventually taking over as head of the new Franciscan order after St Francis' death in 1226. This is the life story of a remarkable Portuguese man, Saint Antony of Padua (1195 - 1231), the Patron Saint of Lisbon, and an excuse for an annual festival in that city every June 13th.

St Antony inherited both the vow of utter poverty, and St Francis' trick of getting animals to listen to him. His logic and style made him particularly effective in converting educated heretics - there were lots of those in 13th century Italy - and in a famous sermon at Rimini he is reputed to have rebuked inattentive heretics by extolling the good behaviour of fishes in schools. In one version, he actually preaches to the fish (Figure 1). In an era where advanced science and technology under Islam were an unspoken challenge to the meager achievements of Christianity at the end of the Dark Ages, many were tempted to experiment with amalgams of the two religions (the Knights Templar is an example of this). St Antony's uncompromising message was that you can only have one religion (i.e. his) if you wanted to reach heaven.

But, as Dr Villy Christensen has pointed out, ECOPATH Models are not like religion; you are allowed to have more than one on your route to mass-balance heaven. Hence, this report, and its companion volume on Northern British Columbia, present four different ECOPATH models for each of the west and east coasts of Canada.

The models describe the state of the marine ecosystem at four snapshots in time, from the present day to a time long past before contact of aboriginal peoples with Europeans. In the case of Newfoundland, these times are 1995-97, representing a post cod-collapse ecosystem; 1985-87, before the cod collapse, 1900, before the



Figure 1. *St Antony of Padua Preaching to the Fishes At Rimini*, a 3m-wide panel of *azulejos*, blue ceramic tiles (Moorish technology) for which the Portuguese are justly famous. The panel is located just behind the main door of the Church of St Antony in Alfama, an old Moorish district of Lisbon. St Antony's skill as a Franciscan preacher is evident from the attentive department of the fishes, compared to the unruly line of Italian heretics on the bridge behind.

major expansion of industrial fisheries and 1450, probably before Cabot and the Europeans arrived.

This material is the culmination of two years of work, and represents our best shot at describing the recent and historical past in these two environments. Doubtless, all of these models can be further improved, but these versions embody our closest approach to the perfection of 'heaven' to date. At a later stage, the more recent of the models can be tuned using their ability to emulate historical estimates of biomass from surveys, VPAs and the like, but this process is unlikely to be possible before such estimates began around 1950. The older ecosystem models have to rely on the constraints imposed by mass-balance itself, and as such, they are less certain than the recent models.

Information used in the models has derived from the workshops reported in Pitcher *et al.* (2002), and on further consultations with experts on each group on both coasts. In addition, a great amount of archival and historical material has been sifted and used wherever possible to improve the biomass. For example, compared to the ancient past, some animals have gone locally extinct (e.g. walrus in Newfoundland). The static mass-balance models reported here will be employed as baselines in dynamic simulations using ECOSIM, aimed at determining what fisheries might be sustained by each of these marine ecosystems

were they to be restored today - part of the *Back to the Future* policy research method.

Further information about *Back to the Future* research may be found on the web site www.fisheries.ubc.ca/projects/btf. This report forms part of the research output from the *Coasts Under Stress* (Arm 2) project, a *Major Collaborative Research Initiative of the Canadian Government*, led by Dr Rosemary Ommer.

The Fisheries Centre Research Reports series publishes results of research work carried out, or workshops held, at the UBC Fisheries Centre. The series focusses on multidisciplinary problems in fisheries management, and aims to provide a synoptic overview of the foundations, themes and prospects of current research. Fisheries Centre Research Reports are distributed to appropriate workshop participants or project partners, and are recorded in the Aquatic Sciences and Fisheries Abstracts. A full list appears on the Fisheries Centre's Web site, www.fisheries.ubc.ca from where copies of most reports may be downloaded free of charge. Paper copies are available on request for a modest cost-recovery charge.

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EXECUTIVE SUMMARY

Papers in this report set out the sources and derivations of parameters for four Ecopath mass-balance models covering Newfoundland and southern Labrador's marine ecosystem (DFO statistical areas 2J3KLNO), referring to the historical times 1985, 1995, 1990 and 1450 (approximated as 3- to 5-year averages). The models have 50 compartments, including linked juvenile and adult life history stages for 6 groups of fish. The models include animals, such as walrus, that are locally extinct today. These models span a Newfoundland marine ecosystem that has changed greatly over the past 500 years. Anthropogenic changes were likely noticeable as soon as Basque whalers arrived, probably before 1450, while mass exploitation of seabirds in the 18th century resulted in extinction of the great auk. For several centuries cod fisheries were seemingly sustainable, but in the late 1980s they collapsed and have failed to recover. The precision of the models changes as we go back in time. While the 1990s and 1980s models, based on many recent scientific surveys and estimates, are likely a good approximation of the true ecosystem, the earlier models have an approximate date of reference, and are less certain, although a great deal of information from historical, archival and archaeological sources was incorporated. These static mass-balance models represent starting values for dynamic ecosystem simulations, which aim to determine sustainable and responsible fisheries that might be operated in ecosystems restored to these past states: part of 'Back to the Future' policy explorations.

A MODEL OF THE MARINE ECOSYSTEM OF NEWFOUNDLAND AND SOUTHERN LABRADOR (2J3KLNO) IN THE TIME PERIODS 1985-1987 AND 1995-1997

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INTRODUCTION

The marine ecosystem of Newfoundland and southern Labrador has changed dramatically from the post World War II period, with the most noticeable change being from the late 1980s onwards. The collapse of groundfish species prior to the closure of the fishery in 1992 spawned a range of descriptions, explanations and theories regarding its origins (Bradbury *et al.* 2000, Hutchings and Myers 1995, Hutchings 1996, Myers and Cadigan 1995, Myers *et al.* 1997b, O'Driscoll *et al.* 2000, Rose *et al.* 2000, Shelton and Stansbury 2000 and Taggart *et al.* 1994). The reduction in the biomass of major species (cod and haddock) fundamentally changed groundfish community structure and reduced the total species biomass by 90% from the 1950s to the 1990s (Casey and Myers 2001). During this decrease in gadoid biomass on the southern Grand Bank, flatfish biomass increased and dominated from the late 1960s into the early 1980s. Biomass of Atlantic cod, haddock and white hake was greatest in the 1950s, with cod and haddock being equally abundant. Redfish biomass increased on the southern Grand Banks in the 1980s, but decreased overall since the 1950s (Casey and Myers 2001).

The objective of this paper is to derive parameters for mass-balance models of the marine ecosystem of Newfoundland and southern Labrador (*DFO statistical areas 2J3KLNO*) for two time periods: 1985-87 and 1995-97. The ecosystem was defined from the coast to the 1,000 m isobath and encompasses a total area of approximately 495,000 km². These models will be used as historical starting points for dynamic policy explorations in the 'Back to the Future' project (Pitcher 2001).

The models consist of 50 compartments: 48 consumers, one primary producer (phytoplankton), and one detritus group. A previous mass-balance model constructed for 1985-87 (Bundy *et al.* 2000) was used as a starting point for both new models, and was adapted by increasing the model compartments to include more linked juvenile-adult stages.

These groups, and the representative species they include, are listed in Appendix A. In some cases groups are locally extinct (walrus and grey whales), but these compartments have been kept in the model (with very low biomass estimates) to facilitate comparison with historical models for 1900 and 1450 constructed by Heymans and Pitcher (*this volume*).

Summary information from earlier reports of workshops with local scientists (Pitcher *et al.* 2002) has been enhanced by further publications and advice from experts cited in the account for each group. In addition, much publicly available data from several sources (notably DFO, NAFO, FAO and ICES) has been taken from the *Sea Around Us Project* (SAUP) database (Watson *et al.* 2000).

MODEL DESCRIPTION BY GROUP

1) Walrus

In the past century only five walruses have been recorded in the area: two in 1949 and three in 1967 (Mercer 1967). In 1904 Ganong (1904) reported that they do not occur further south than Labrador and in 1951 Wright (1951) suggested that they are no longer found south of Hudson Strait. Thus, biomass in the 1980s and 1990s models was assumed to be very low ($1 \times 10^{-6} \text{ t} \cdot \text{km}^{-2}$) in order to include these groups for comparison purposes. The P/B ratio of 6% was obtained from walruses in a Bering Sea mass-balance model (Trites *et al.* 1999). According to FAO (FAO 1978), adult walruses consume 45 kg of food per day, which gives a Q/B of 16.8 year⁻¹. As the species was nearly extinct, they were not hunted off Newfoundland in the late twentieth century.

Walruses feed mostly on invertebrates that live in or on the bottom sediments (Anon. 2001a). Brenton (1979) suggests that 65 species of benthic invertebrates, principally mollusks, echinoderms, tunicates, crustaceans, priapulids and echiuroids are consumed. Allen (1942) reports that their diet occasionally includes seals and rarely fish. The diet of walruses in the Bering Sea model (Trites *et al.* 1999) was adapted as follows: consumption of small flatfish in the Bering Sea was assigned to juvenile American plaice; consumption of large flatfish was assigned to flounders; consumption of adult pollock was assigned to Greenland cod; consumption of juvenile pollock was assigned to demersal benthic-pelagic juveniles. Consumption of pelagics was assigned to capelin, and deepwater fish were broken down into other large demersals and seals (1% each for juvenile

demersals and other small demersal feeders, and 0.1% each for grey, harp and hooded seals). The benthic particulate feeders in the Bering Sea model included snow and tanner crabs, red and blue king crabs, and shrimp (Trites *et al.* 1999), and this was therefore redistributed to small crabs and shrimps (12% each). Infauna in the Bering Sea model consist of clams, polychaetes and other worms (mainly *Echiuridae*) (Trites *et al.* 1999). Thus the consumption of infauna in the Newfoundland model includes 10% polychaetes and 30% bivalves. Epifauna in the Bering Sea model include hermit crabs, snails, brittle stars, and starfish (Trites *et al.* 1999). In the Newfoundland model the consumption of epifauna was split between other benthic invertebrates (20%) and Echinoderms (5%) (Appendix B).

2) Cetaceans

The species of whales that are known to occur in the area include the humpback *Megaptera novaeangliae*, fin *Balaenoptera physalus*, minke *Balaenoptera acutorostrata*, sei *Balaenoptera borealis*, sperm *Physeter catodon*, pilot *Globicephala melaena* and blue whale *Balaenoptera musculus* (Bundy *et al.* 2000). The main porpoise species is the harbour porpoise *Phocoena phocoena*. Stenson *et al.* (2002) assumed that the biomass of whales in the 1990s was similar to that of 1985-1987 ($0.251 \text{ t}\cdot\text{km}^{-2}$ as obtained from Bundy *et al.* 2000). The P/B and Q/B estimates for cetaceans given by Bundy *et al.* (2000) were used in both models. Almost no whales were killed by humans during 1985-1987, but a small catch was recorded by the grappling and wounding fishery ($0.000058 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) in 1995-97 (see Table 7).

Diet estimates for cetaceans made by Bundy *et al.* (2000) were adapted for the new groupings as follows: the proportions of large and small demersals in the diet were broken down into 1.5% each for large and small benthic-pelagic and demersal fish, and 0.6% for lumpfish. Piscivorous and planktivorous pelagic feeders (small) were divided into small pelagics, herring, squid (5.4% each) and mesopelagics (3%) (Appendix B).

3) Grey seals

For the purposes of the Back to the Future project, it was assumed that there were some grey seals in the 2J3KLNO area prior to commercial sealing (Heymans and Pitcher, *this volume*). Therefore grey seals were added, although a very small biomass was assumed ($1\cdot 10^{-6} \text{ t}\cdot\text{km}^{-2}$). The P/B ratio of 6% for seals in the Bering Sea model

(Trites *et al.* 1999) was used for grey seals in all models. Dommasnes *et al.* (2001) and Trites *et al.* (1999) estimate a Q/B ratio for grey seals in the Norwegian and Bering Seas of 15.0 and 15.93 yr^{-1} , respectively. We used 15.0 yr^{-1} as a Q/B ratio for grey seals in Newfoundland. Diets of grey seals (Appendix A) were adapted from diets for areas 4T, 4X and 3Ps obtained by Hammill and Stenson (2000). There were no catches of grey seals in 2J3KLNO in either time periods.

4) Harp seals

The biomass of harp seals in the 1980s was estimated at $0.184 \text{ t}\cdot\text{km}^{-2}$ (Bundy *et al.* 2000), and estimates for the 1990s were based on population size data obtained by Healey and Stenson (2000), Hammill and Stenson (2000) and Stenson and Sjare (1997). To estimate harp seal biomass in the model area it was assumed that 20% of all age groups remain in the Arctic throughout the year and that the residency period in Div. 2J and 3KL is from 21 November to 6 July (Stenson and Sjare 1997). One-third of the adult population and 20% of juveniles (ages 1-4) were assumed to enter the Gulf of St. Lawrence at or around the beginning of December and remain there until the end of May. A small proportion (5%) of the seals that migrated southward were assumed to remain in the study area for the entire year, with the proportion in each area the same as

Table 1. Catch (numbers) of harp seals in the Gulf and Front region of Newfoundland and Labrador (Stenson, *pers. comm.*)

Age	1995	1996	1997
0	34106	184856	220476
1	6750	15052	17730
2	4898	10919	8126
3	4040	4133	2733
4	2995	3146	1920
5	3138	2757	1553
6	1950	2165	1255
7	1950	2067	1106
8	807	1376	739
9	570	981	516
10	332	1376	1330
11	475	1277	962
12	332	789	516
13	190	789	813
14	475	981	297
15	475	981	367
16	237	1474	516
17	285	1474	590
18	380	888	442
19	190	592	297
20	285	592	516
21	285	592	297
22	47	789	223
23	190	493	149
24	47	592	223
25+	332	1771	516

Table 2. Bycatch of pups (= 'beaters') and adult (1+) harp seals in the lumpfish fishery (Walsh *et al.* 2000) and Stenson (*pers. comm.*)

Year	Pups (numbers)	Adults (numbers)	Pups (tonnes)	Adults (tonnes)
1985	6047	3160	197	316
1986	11026	5725	358	573
1987	18559	11135	603	1113
Average			386	667
1995	5210	11736	169	1174
1996	8597	14803	279	1480
1997	12036	5495	391	549
Average			280	1068

for the winter period. The average weight of a harp seal is 100 kg (Hammill and Stenson 2000). Based on the above assumptions and on an average population of 5 million seals the biomass of harp seals in the 1990s is estimated at approximately $0.41 \text{ t}\cdot\text{km}^{-2}$.

The P/B and Q/B ratios of 0.102 and 17.412 yr^{-1} , respectively, were obtained from Bundy *et al.* (2000). Diets of harp seals for 1985-87 and 1995-97 were obtained from Stenson (*pers. comm.*) and adapted to the groups in this model (Appendix B) by assuming that birds in the diet are mostly dovekeys and murre (piscivorous birds). The flounders in the diet were assumed to be mainly witch flounder, and unknown fish was assumed to be yellowtail flounder, as it was a very small proportion of the total diet. Gadoid species (< 35 cm) was assumed to be Arctic cod, and *Gadus* species (\leq and $>$ 35 cm) was divided between Atlantic cod and Greenland cod according to the ratio of their biomass estimates (Appendix B).

The catch of harp seals in the 1980s was estimated at around $0.001 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Bundy *et al.* 2000). Total harp seal catches for the 1995-97 period, in the Gulf and Front areas of Newfoundland and Labrador were obtained from Stenson (*pers. comm.*, Table 1) and adapted for seals caught in 2J3KLNO by assuming that 76% of the 0 age group and 85% of 1+ seals in 1995 were caught in the Front region (obtained from the official catch statistics). In 1996 the proportion of seals caught on the Front was 62% and 86% respectively for 0 and 1+ seals, and in 1997 the proportions were 74% and 83% respectively. The percentage struck-and-lost is only 1% for the 0 group while in 1+ approximately 50% is lost. Thus the total harp seal catch was approximately 3,320 tonnes juveniles (0 group) and 3,830 tonnes adults (1+), when using the average weight obtained from Hammill and Stenson (2000), with the total catch being approximately 7,150 tonnes or $0.014 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$. There was also a very small catch ($2\cdot 10^{-6} \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) of harp seals in 1995-1997 by the grappling and wounding fishery (see Table 7).

Of the six species found in Newfoundland (harp, hooded, grey, harbour, ringed and bearded seals) all are known to occur as bycatch in various types of fishing gear, including trawls, purse seines, gill nets, and hook and line (FAO, 1995 in Walsh *et al.* 2000). Harp seals are the most common bycatch species and are taken primarily by inshore monofilament gill nets set for cod, flounder and lumpfish (Walsh *et al.* 2000). Entrapped seals are usually dumped at sea or used locally for food (Lien *et al.* 1988). The number of beaters (pups) and 1+ (adult) harp seals caught as bycatch in the lumpfish fishery (Walsh *et al.* 2000) are given in Table 2. The total bycatch of harp seals was therefore $1,053 \text{ tonnes}$ ($0.002 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) and $1,348 \text{ tonnes}$ ($0.003 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) in the 1985-1987 and 1995-1997 models, respectively.

5) Hooded seals

There were approximately 600,000 hooded seals in the population in 1995 and 1996 (Hammill and Stenson 2000). Hooded seals have an average weight of 220 kg, and stay in the area for about half the year (Hammill and Stenson 2000). Half the population goes to the Gulf of St. Lawrence, which gives a 1990s biomass of approximately $0.062 \text{ t}\cdot\text{km}^{-2}$. The biomass of hooded seals in 1985-1987 was estimated at $0.034 \text{ t}\cdot\text{km}^{-2}$ (Bundy *et al.* 2000). The P/B and Q/B ratios of 0.109 and 13.1 yr^{-1} , respectively, obtained from Bundy *et al.* (2000) were used in both models. Diets were obtained from Hammill and Stenson (2000) and adapted for the groups in this model (Appendix B).

The catch of hooded seals in the 1980s was estimated at $0.00018 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Bundy *et al.* 2000), while the catch for 1995-97 was obtained from ICES/NAFO (Anon. 2001b). It was assumed that most of these catches (Table 3) were taken from 2J3KLNO and that approximately 25,000 of the hooded seals caught in 1996 were pups, while all the other seals caught in these 3 years were adults (Stenson *pers. comm.*). The average weights of juvenile and adult hooded seals (37.5 kg and 220 kg respectively) were obtained from Hammill and Stenson (2000). Thus the total catch of hooded seals in 1995-1997 was estimated at approximately 950 tonnes (Table 3), or $0.002 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$. No data are available on

Table 3. Number of hooded seals caught for 1995-1997 (ICES/NAFO, Anon. 2001b). *Available statistics not split by age.

Year	Pups	1+	Unknown	Total
1995	0	0	857*	857
1996	0	0	25754*	25754
1997	0	7058	0	7058
Average	8333	2890		
Tonnes	312	636		

Table 4. Estimates of average seabird biomass ($t \cdot km^{-2}$) and catch ($t \cdot km^{-2} \cdot yr^{-1}$) in 1980s and 1990s, with fulmars and shearwaters as piscivores. The average area for 2J3KL is 367,542 km² (Bundy, 2002). * from Bundy *et al.* (2000), t = tonnes.

	Biomass 1990s		Biomass 1980s*	Catch
	t	$t \cdot km^{-2}$	$t \cdot km^{-2}$	$t \cdot km^{-2} \cdot yr^{-1}$
Ducks	83	0.0002	0.0002	0.0001
Piscivores	4,945	0.0135	0.0010	0.0008
Planktivores	1,073	0.0029	0.0022	0.0002

bycatch of hooded seals although they are presumably not caught in large quantities.

6-8) Seabirds

In this model seabirds are partitioned into ducks, planktivorous and piscivorous birds. Ducks include the common eider, scoters and oldsquaws, while planktivorous birds include storm petrels and dovekies. Piscivorous birds include gannets, cormorants, gulls, kittiwakes, terns, guillemots, murre, razorbills and puffins (Burke *et al.* 2002). (*The extinct great auk is included in historical models.*) Fulmars and shearwaters (Brown *et al.* 1981) were at first placed with planktivorous birds, but Montevecchi (Memorial University of Newfoundland, *pers. comm.*) suggested that they should be grouped with piscivorous birds. The average annual biomass of breeding and wintering birds in 2J3KL for 2000 was obtained from Burke *et al.* (2002) and the sum of these two values was used to calculate the biomass assuming that the biomass in 2J3KL and 2J3KLNO would be similar (Table 4). Bird biomass in the 1980s was estimated from average values obtained from Bundy *et al.* (2000), and also includes fulmars and shearwaters as piscivores. The P/B and Q/B ratios

for birds given in Bundy *et al.* (2000) were used for all three of these groups.

The diet of seabirds used in Bundy *et al.* (2000) was adapted to the new groups (Appendix B) by using the large and small zooplankton for planktivorous birds, and dividing the mollusks in the diet of ducks between bivalves and other benthic invertebrates. Fish species eaten by piscivorous birds were divided as follows: small demersal feeders were partitioned into juvenile demersal feeders and juvenile benthic-pelagic piscivores, lumpfish and Greenland cod. Piscivorous small pelagic feeders were divided between small pelagics, mesopelagics and shortfin squid, while planktivorous small pelagic feeders were divided into herring, mesopelagics and Arctic squid. Large pelagic feeders were divided into salmon, transient pelagics and large transient mackerel. An extra source of food from fishery discards and offal probably have had significant positive effects on birds like the northern fulmar and several species of gulls (Tasker *et al.* 2000). This effect is not yet incorporated in the model, but may be included at a later stage.

Anthropogenic mortality of seabirds includes hunting, bycatch, disturbance and oil pollution, which kill large numbers of ducks and other sea birds (Montevecchi and Tuck 1987). Approximately 500,000 thick billed and common murre are hunted annually (Montevecchi and Tuck 1987), although the hunting pressure decreased during the 1990s, when bag limits were imposed. Pursuit divers, such as auks and shearwaters, are the seabirds most commonly

Table 5. Biomass estimates ($t \cdot km^{-2}$) of groundfish species obtained from Lilly (*pers. comm.*) without adjustments for catchability. Total catch ($t \cdot km^{-2} \cdot yr^{-1}$) from Tables 6 and 7 and P/B (yr^{-1}) calculated from mortality rates ($Z = M + F$) or from Q/B and gross conversion efficiency (see text for details). * biomass estimated assuming ecotrophic efficiency of 95%.

Group	Biomass	Biomass	Catch	Catch	Natural	P/B	P/B
	1985-87	1995-97	1985-87	1995-97	mortality	1985-87	1995-97
Cod > 35 cm	1.8111	0.0799	0.5430	0.0011	0.104	0.404	0.118
Cod ≤ 35 cm	0.3018	0.0133	0.0000	0.0000	0.155	0.155	0.155
American plaice >35 cm	0.7215	0.3396	0.1021	0.0019	0.083	0.224	0.088
American plaice ≤35 cm	0.5802	0.2731	0.0000	0.0000	0.124	0.124	0.124
Greenland halibut > 40 cm	0.3317	0.3657	0.0371	0.0260	0.026	0.138	0.098
Greenland halibut ≤ 40 cm	0.4739	0.5225	0.0000	0.0000	0.040	0.040	0.040
Yellowtail flounder	0.1784	0.3300	0.0387	0.0006	0.317	0.534	0.319
Witch flounder	0.0691	0.0243	0.0244	0.0028	0.235	0.588	0.348
Winter flounder	*	*	0.0026	0.0009	0.267	0.267	0.267
Skates	0.2347	0.2077	0.0300	0.0180	0.233	0.361	0.320
Dogfish	0.0073	0.0065	0.0003	0.0002	0.159	0.193	0.194
Redfish	0.4184	0.3799	0.1576	0.0133	0.113	0.489	0.148
Dem. & BP piscivores > 40 cm	0.0374	0.0152	0.0194	0.0016	0.098	0.617	0.206
Dem. & BP piscivores ≤ 40 cm	*	*	0.0000	0.0000	0.147	0.147	0.147
Large demersals > 30 cm	0.2366	0.1185	0.0276	0.0088	0.155	0.272	0.229
Large demersals ≤ 30 cm	*	*	0.0000	< 0.0001	0.232	0.232	0.232
Small demersals	0.0087	0.1190	0.0000	< 0.0001	0.564	0.564	0.564
Lumpfish	0.0129	0.0194	0.0000	< 0.0001	0.114	0.114	0.116
Greenland cod	0.0003	0.0001	< 0.0001	< 0.0001	0.101	0.166	0.594
Salmon	*	*	0.0019	0.0001	0.279	0.615	0.615

Table 6. Catches ($\text{kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) of all species in the model area during 1985-1987 obtained from the SAUP database.

	Bottom Trawls	Midwater Trawls	Mobile Seine	Surround Nets	Gill & Entangle	Hooks and Lines	Traps and Lift Nets	Dredges	Grappling Wounding	Other Gear	Total
Cod	385.580	0.701	0.560		56.071	37.169	62.787			0.088	542.956
American plaice	95.589	0.086	0.112		5.870	0.276	0.147	0.002		0.007	102.090
Greenland halibut	18.564	0.013			18.409	0.057	0.040			0.001	37.086
Yellowtail flounder	38.566	0.014	0.114			0.017				0.002	38.713
Witch flounder	23.208	0.228	0.017		0.935	0.006	0.002			0.002	24.400
Winter flounder	0.206				2.247	0.042	0.078				2.573
Skates	27.601	2.156			0.246	0.023	0.003				30.030
Dogfish	0.133	0.117									0.251
Redfish	125.189	31.960			0.428	0.001	0.001			0.001	157.579
Mackerel		0.040		15.886	1.385	0.007	0.636				17.956
BP piscivores	10.982	0.374	0.054		2.189	5.811	0.004			0.010	19.426
Large demersals	26.952	0.036	0.048		0.434	0.127	0.030			0.005	27.632
Greenland cod					0.005	0.013	0.002				0.020
Salmon					1.797	0.019	0.040				1.856
Capelin	0.024	44.123		18.483	0.008		35.720				98.358
Sandlance	0.083										0.083
Herring	0.010			11.084	4.314	0.002	0.487				15.898
Transient pelagics						0.708				0.007	0.715
Small pelagics	0.025	0.059			0.018	0.014	0.003				0.118
Shortfin squid	0.763	0.001				0.392	0.006				1.162
Large crabs					0.015		8.839				8.854
Lobster							1.382				1.382
Shrimp	2.345										2.345
Bivalves								0.233			0.233

caught as bycatch in gill nets, while loons, cormorants, puffins and gannets are also caught in high numbers (Montevecchi 2001). The common murre is the species most widely affected by fishing nets (Montevecchi 2001).

Seabirds vulnerable to longline fisheries include petrels, such as northern fulmars, shearwaters,

gulls and skuas (Montevecchi 2001). Estimates of seabird bycatch from gill nets range from 0.25% in Atlantic puffins, to up to 20% in common murre, and virtually all other gear types also catch birds (Tasker *et al.* 2000). We assume that the $0.001\text{t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ estimated as a catch by (Bundy *et al.* 2000) is divided into ducks, piscivorous and planktivorous birds in the ratio of

Table 7. Catches ($\text{kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) of all species in the model area during 1995-1997 obtained from the SAUP database.

	Bottom Trawls	Midwater Trawls	Mobile Seine	Surround Nets	Gill & Entangle	Hooks and Lines	Traps and Lift Nets	Dredges	Grappling Wounding	Other Gear	Total
Cetaceans									0.058		0.058
Harp seals									0.002		0.002
Cod	0.174	0.002			0.711	0.187	0.078				1.152
American plaice	1.784	0.001			0.115	0.003					1.905
Greenland halibut	20.201				5.780	0.046				0.001	26.028
Yellowtail flounder	0.642					0.001					0.644
Witch flounder	2.742	0.001	0.001		0.011	0.001					2.755
Winter flounder					0.888		0.015				0.904
Skates	15.542				1.224	0.593			0.686		18.045
Dogfish	0.228										0.228
Redfish	11.502	1.792			0.023	0.028				0.001	13.346
Mackerel				0.002	0.013		0.001				0.017
BP piscivores	0.481				0.446	0.705					1.633
Large demersals	8.167				0.424	0.152	0.084				8.828
J demersals				0.002			0.001				0.003
Small demersals					0.028		0.003				0.030
Lumpfish							0.026				0.026
Greenland cod					0.006	0.036	0.001				0.043
Salmon					0.105	0.005	0.001				0.111
Capelin				12.475	0.010		11.520				24.005
Herring				5.343	1.603		0.040				6.987
Transient pelagics						0.955					0.956
Small pelagics	0.020				0.007	0.007	0.007		0.222		0.263
Mesopelagics					0.001			0.237	0.006		0.244
SF squid	0.003						0.230				0.233
Large crabs					0.017		65.248				65.265
Small crabs							0.044				0.044
Lobster							0.999				0.999
Shrimp	44.988							0.075			45.063
Bivalves					0.001			32.889		0.001	32.890
Other inverts							0.840	0.654		0.925	2.418

their biomasses (Table 4). This was also used as an estimate of catch (and other anthropogenic mortality) in the 1990s.

Groundfish species

Biomass estimates for all groundfish species were obtained from G. Lilly (Department of Fisheries and Oceans, St. John's, Newfoundland, *pers. comm.*), and were taken from Engels survey trawls for the 1980s and Campelen survey trawl estimates in the 1990s (Table 5). No catchability adjustments were made, as this information was not available at the time the models were constructed. Comparisons to subsequent models that include catchability adjustments will be made later.

Diet estimates for groundfish species were obtained from Lilly (2002). Catches of all species were obtained from the SAUP database (Watson *et al.* 2000) (Tables 6 and 7).

9-10) Cod (adult and juvenile)

Bundy *et al.* (2000) estimated the (catchability adjusted) 1985-87 biomass of adult (> 35 cm) and juvenile cod at $2.04 \text{ t}\cdot\text{km}^{-2}$ and $0.34 \text{ t}\cdot\text{km}^{-2}$ respectively, and the unadjusted adult cod biomasses (Table 5) for both 1985-87 and 1995-97 were obtained from Lilly (*pers. comm.*). The ratio between adult and juvenile biomass obtained from Bundy *et al.* (2000) was used to estimate the biomass of juvenile cod at $0.3 \text{ t}\cdot\text{km}^{-2}$ and $0.013 \text{ t}\cdot\text{km}^{-2}$ respectively for 1985-87 and 1995-97 (Table 5). Q/B estimates calculated for the reconstruction of the 1900 model (Heymans and Pitcher, *this volume*) were in most cases much lower than those used in Bundy *et al.* (2000), probably due to the change in size structure of these species. Thus, the Q/B ratio obtained from Bundy *et al.* (2000) for Atlantic cod (3.24 yr^{-1} for adults and 6.09 yr^{-1} for juveniles) were used in the 1985-87 and 1995-97 models.

Bundy *et al.* (2000) estimated the annual P/B of adult and juvenile Atlantic cod to be 0.65 and 1.6 yr^{-1} respectively in the 1980s. Vasconcellos *et al.* (2002d) quotes Lilly as considering that the P/B of cod would have been higher in the mid-1980s than in the 1990s. Natural mortality is estimated at approximately 0.1 yr^{-1} (Appendix A Table A1 in Heymans and Pitcher, *this volume*). Fishing mortality is added to natural mortality to estimate P/B ratios for adult cod at 0.4 and 0.1 yr^{-1} for 1980s and 1990s respectively (Table 5). The P/B ratio of juvenile cod was assumed to be similar to the natural mortality (0.15 yr^{-1}) for both models. Catches by fishing gears were obtained from the SAUP database (Tables 11 and 12). The diets of

adult and juvenile cod (Appendix B) were obtained from Lilly (2002).

11-12) American plaice (adult and juvenile)

The biomass of adult American plaice (> 35 cm) (Table 5) for both 1985-87 and 1995-97 were obtained from Lilly (*pers. comm.*). The ratio between adult and juvenile biomass obtained from Bundy *et al.* (2000) was used to estimate the biomass of juvenile American plaice at $0.58 \text{ t}\cdot\text{km}^{-2}$ and $0.27 \text{ t}\cdot\text{km}^{-2}$ respectively for 1985-87 and 1995-97 (Table 5). The P/B ratio of adult American plaice was estimated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.22 and 0.08 yr^{-1} for 1980s and 1990s respectively (Table 5). The P/B ratio of juvenile American plaice was assumed to be similar to natural mortality (0.12 yr^{-1}) for both models. The Q/B estimates obtained from Bundy *et al.* (2000) for American plaice (2.0 yr^{-1} for adults and 3.7 yr^{-1} for juveniles) were used in the 1985-87 and 1995-97 models. The diets of adult and juvenile American plaice (Appendix B) were obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

13-14) Greenland halibut (adult and juvenile)

The biomass of adult (> 40 cm) Greenland halibut (= 'turbot'), for both 1985-87 and 1995-97 (Table 5) were obtained from Lilly (*pers. comm.*). The ratio between adult and juvenile biomass obtained from Bundy *et al.* (2000) was used to estimate the biomass of juvenile Greenland halibut as $0.47 \text{ t}\cdot\text{km}^{-2}$ and $0.52 \text{ t}\cdot\text{km}^{-2}$ respectively for 1985-87 and 1995-97 (Table 5). The P/B ratio of adult Greenland halibut was estimated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to fishing mortality, to give P/B ratios of 0.14 and 0.10 yr^{-1} for 1980s and 1990s respectively (Table 5). The P/B ratio of juvenile American plaice was assumed to be similar to natural mortality (0.04 yr^{-1}) for both models. The Q/B estimates obtained from Bundy *et al.* (2000), for Greenland halibut (1.5 yr^{-1} for adults and 4.5 yr^{-1} for juveniles) were used in the 1985-87 and 1995-97 models. The diets of adult and juvenile Greenland halibut (Appendix B) were obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

15-17) Flounders

This group consists of yellowtail flounder *Limanda ferruginea*, witch flounder *Glypto-*

cephalus cynoglossus and winter flounder *Pseudopleuronectes americanus*. Winter flounder is abundant from southern Labrador to Georgia, and is generally not found in depths exceeding 40 m (DFO, Anon. 1996a). Winter flounder is an opportunistic feeder that takes a variety of benthic organisms. They are caught in divisions 3K and 3L with gillnets as lobster bait and for food (DFO, Anon. 1996a). The biomass of yellowtail and witch flounder (Table 5) for 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*), while the biomass of winter flounder was estimated by assuming an ecotrophic efficiency of 95%. P/B ratios of yellowtail and witch flounder were based on estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality. P/B ratios of 0.5 and 0.3 yr⁻¹ were estimated for yellowtail flounder in the 1980s and 1990s respectively. Similarly, the P/B ratios of witch flounder were calculated at 0.6 and 0.3 yr⁻¹ for the 1980s and 1990s respectively (Table 5). The P/B ratio of winter flounder was assumed to be similar to natural mortality (0.27 yr⁻¹) for both models, as the species has been taken in small quantities for many years and no estimate of biomass was available to calculate fishing mortality.

The Q/B estimate (3.6 yr⁻¹) of flounder obtained from Bundy *et al.* (2000) was used for yellowtail flounder in both the 1980s and 1990s models, as it was marginally larger than that calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*). The Q/B estimates calculated for witch (2.3 yr⁻¹) and winter (1.6 yr⁻¹) flounder in the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) were used in both the 1985-87 and 1995-97 models. The diets of all three flounder species (Appendix B) were obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

18) Skates

This group consists of barndoor skates *Dipturus laevis*, thorny skates *Amblyraja radiata*, smooth *Malacoraja senta*, little *Leucoraja erinacea* and winter skates *Leucoraja ocellata*. The biomass of skates (Table 5) for 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*). The P/B ratios of skates in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.36 and 0.32 yr⁻¹ in the 1980s and 1990s respectively. The Q/B estimate (2.9 yr⁻¹) of skates obtained from Bundy *et al.* (2000) was used in

both the 1980s and 1990s models. The diet of skates (Appendix B) was obtained from Lilly (2002) and the catches (Tables 11 and 12) from the SAUP database.

19) Dogfish

Spiny dogfish *Squalus acanthias* was separated from the large pelagic feeders in Bundy *et al.* (2000). The biomass (Table 5) for 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*). The P/B ratio of dogfish in the 1980s and 1990s was calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.193 and 0.194 yr⁻¹ in the 1980s and 1990s respectively. The Q/B estimate (4.8 yr⁻¹) of dogfish in New England, obtained from Bundy *et al.* (2000), was used in both the 1980s and 1990s models. The diet of dogfish (Appendix B) was obtained from Lilly (2002) and the catches (Tables 11 and 12) from the SAUP database.

20) Redfish

The biomass of redfish (= *Sebastes*) for 1985-87 and 1995-97 (Table 5) was obtained from Lilly (*pers. comm.*). The P/B ratios in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.49 yr⁻¹ and 0.15 yr⁻¹ in the 1980s and 1990s respectively. The Q/B estimate (2.0 yr⁻¹) of redfish obtained from Bundy *et al.* (2000) was used in both the 1980s and 1990s models. The diet of redfish (Appendix B) was obtained from Lilly (2002) and the catches (Tables 11 and 12) from the SAUP database.

21) Transient mackerel (> 29 cm)

The biomass of transient (= migratory) mackerel is not well studied. Bundy *et al.* (2000) suggest that the biomass of mackerel in 1985-87 was approximately 184,411 tonnes, or 0.37 t•km⁻². However, no estimate of biomass for transient mackerel is available for 1995-97, and it is estimated by assuming an ecotrophic efficiency of 95%. The natural mortality of mackerel was calculated at 0.5 yr⁻¹ (Appendix A Table A1 in Heymans and Pitcher, *this volume*), while the P/B ratio used in Bundy *et al.* (2000) was only 0.3 yr⁻¹, as it took into account the residence time of the transients. The value obtained from Bundy *et al.* (2000) was used in both the 1985-87 and 1995-97 models. The Q/B ratio (4.4 yr⁻¹) obtained from Bundy *et al.* (2000) for transient mackerel on Georges Bank was used in both models. The

diet of transient mackerel (Appendix B) was obtained from Lilly (2002) and the catches (Tables 11 and 12) from the SAUP database.

22-23) Demersal and benthopelagic piscivores (adult and juvenile)

The demersal and benthopelagic piscivores include white and silver hake (*Urophycis tenuis* and *Merluccius bilinearis*), monkfish *Lophius americanus*, sea ravens *Hemitripterus americanus*, cusk *Brosme brosme* and Atlantic halibut *Hippoglossus hippoglossus*. The biomass (Table 5) of adult (>40 cm) demersal and benthopelagic piscivores in 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*), while that of juveniles was estimated by assuming an ecotrophic efficiency of 95% for both models. The P/B ratios for adults in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.6 and 0.2 yr⁻¹ in the 1980s and 1990s respectively. The P/B ratio for juveniles was assumed to be similar to that of natural mortality (0.15 yr⁻¹) and was used for both models. The Q/B estimates calculated for adults (1.1 yr⁻¹) and juveniles (1.7 yr⁻¹) in the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) were used in both the 1985-87 and 1995-97 models. The diets of both adults and juveniles (Appendix B) were obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

24-25) Large demersal fish (adult and juvenile)

This group consists of a range of species that feed in the demersal domain, including haddock *Melanogrammus aeglefinus*, longfin *Phycis chesteri* and red hake *Urophycis chuss*, wolffish *Anarhichas* spp., grenadiers *Coryphaenoides* spp., eelpouts *Lycodes* spp. and batfishes. The biomass (Table 5) of adult (>40 cm) large demersals in 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*), while that of juveniles was estimated by assuming an ecotrophic efficiency of 95% for both models. The P/B ratios for adults in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.27 and 0.23 yr⁻¹ in the 1980s and 1990s respectively. The P/B ratio for juveniles was assumed to be similar to that of natural mortality (0.23 yr⁻¹) and was used for both models. The Q/B estimates calculated for adults (1.4 yr⁻¹) and juveniles (2.1 yr⁻¹) in the 1900 model (see

Appendix A Table A2 in Heymans and Pitcher, *this volume*) were used in both the 1985-87 and 1995-97 models. The diets of both adults and juveniles (Appendix B) were obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

26) Other small demersals

The other small demersals group consists of rocklings *Enchelyopus* spp., gunnel *Pholis gunnellus*, alligator fishes *Ulcina olriki*, Atlantic poachers *Leptagonus decagonus*, snake blennies *Lumpenus lampretaeformis*, seasnails and shannies *Leptoclinus* spp., sculpin *Myoxocephalus* spp., searobins *Prionotus* spp., eel blennies *Anisarchus* spp., wrymouth etc. The biomass (Table 5) of small demersals in 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*), although without catchability conversions these might be very low estimates. The P/B ratios for small demersals in the 1980s and 1990s were assumed to be similar to natural mortality (0.56 yr⁻¹ from Appendix A Table A1 in Heymans and Pitcher, *this volume*). The Q/B estimate (4.47 yr⁻¹) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of small demersals (Appendix B) was obtained from Lilly (2002) and the catches (Tables 11 and 12) were obtained from the SAUP database.

27) Lumpfish

Lumpfish are found in major concentrations on the St. Pierre bank off the southeast coast of Newfoundland (Garavis, 1985 in Walsh *et al.* 2000). They remain in deep offshore waters from late September to April and then migrate inshore during late April or early May to spawn (Stevenson and Baird 1988 in Walsh *et al.* 2000). The biomass (Table 5) of lumpfish in 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*). The P/B ratio for lumpfish in the 1980s and 1990s was calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.114 and 0.116 yr⁻¹ in the 1980s and 1990s respectively. The Q/B estimate (1.4 yr⁻¹) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of lumpfish (Appendix B) was obtained from Lilly (2002).

Lumpfish fishing started in 1968 and was conducted by inshore fishermen between April and July, using small vessels less than 35 feet

long (Walsh *et al.* 2000). At present the fishery is mainly operated with gill nets while 20% have been longliners since the 1980s (Walsh *et al.* 2000). Lumpfish roe landings increased dramatically from 500 tonnes in 1985 to 3,000 tonnes in 1987 (Walsh *et al.* 2000), and varied between 1,000 and 2,300 tonnes in more recent years. South coast catches made up the greatest proportion of the catches in the 1980s (Walsh *et al.* 2000). Estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

28) Greenland cod

The biomass (Table 5) of Greenland cod in 1985-87 and 1995-97 was obtained from Lilly (*pers. comm.*). The P/B ratios in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.17 and 0.59 yr⁻¹ in the 1980s and 1990s respectively. The Q/B estimate (1.3 yr⁻¹) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of Greenland cod (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

29) Atlantic salmon

No estimates of Atlantic salmon biomass were available for the 1985-87 or 1995-97 models, and it was estimated in both time periods by assuming an ecotrophic efficiency of 95%. The natural mortality of Atlantic salmon is calculated at 0.28 yr⁻¹ (Appendix A Table A1 in Heymans and Pitcher, *this volume*). But with no estimate of fishing mortality, the P/B of Atlantic salmon (0.615 yr⁻¹) was estimated by assuming a gross conversion efficiency of 0.15, and using the Q/B estimate (4.1 yr⁻¹) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*). The diet of Atlantic salmon (Appendix B Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

30) Capelin

The biomass of capelin in the 1980s model was estimated at 13 t•km⁻² (Bundy *et al.* 2000). Anderson *et al.* (2001) estimated that the biomass of capelin in 2J3KLNO in the late 1990s was between 725,000 tonnes and 1,800,000 tonnes

Table 8. Biomass of capelin (from Anderson *et al.* 2001) estimated using three different catchability coefficients.

Year	Q=0.14	Q=0.1	Q=0.25
1995	244,686	342,561	137,024
1996	941,267	1,317,774	527,109
1997	2,702,202	3,783,082	1,513,233
Average (tonnes)	1,296,052	1,814,472	725,789
Biomass (t•km ⁻²)	2.6	3.7	1.5

using catchabilities of 10% - 25% (Table 8). The lower catchability was used as it still estimates a very small biomass (3.7 t•km⁻²) for capelin. However, we used biomass estimates of 0.03 t•km⁻² and 0.1 t•km⁻² for 1985-87 and 1995-97 respectively, made by Lilly (*pers. comm.*), as none of the other biomass estimates that we have at present are adapted for catchability.

The P/B (1.15 yr⁻¹) and Q/B (4.3 yr⁻¹) estimates obtained from Bundy *et al.* (2000) were used in both models. However, when the catchability-adjusted biomass referred to in the previous paragraph was used to calculate F, P/B was subsequently calculated at approximately 0.59 yr⁻¹ for both models. The diet of capelin (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

31) Sandlance

The biomass of sandlance in 1985-87 (0.00007 t•km⁻²) and 1995-97 (0.2 t•km⁻²) was obtained from Lilly (*pers. comm.*). However, the Engels trawl that was used in the 1985-87 period substantially underestimated the biomass of sandlance. Therefore, as in Bundy *et al.* (2000), the biomass was assumed to be similar in the 1985-87 and 1995-97 periods. The P/B (0.62 yr⁻¹) and Q/B (7.7 yr⁻¹) estimates obtained from Bundy *et al.* (2000) were used in both models. The diet of sandlance (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

32) Arctic cod

The biomass of Arctic cod in 1985-87 (0.006 t•km⁻²) and 1995-97 (0.14 t•km⁻²) was obtained from Lilly (*pers. comm.*). However, the Engels trawl that was used in the 1985-87 period substantially underestimated the biomass of Arctic cod, and it is suggested that the biomass (2.7 t•km⁻²) used in Bundy *et al.* (2000) should be used as the biomass of Arctic cod in 1985-87. The P/B (0.4 yr⁻¹) and Q/B (2.6 yr⁻¹) estimates obtained from Bundy *et al.* (2000) were used in both models. The diet of Arctic cod (Appendix B)

was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

33) Herring

The biomass of herring in the 1985-87 model was 235,000 tonnes, or $0.47 \text{ t} \cdot \text{km}^{-2}$ (Bundy *et al.* 2000). DFO (Anon. 2000) suggests that the biomass of mature herring (age 5+) for east and southeast Newfoundland decreased from 89,700 tonnes in 1998 to 83,100 tonnes in 2000. This gives an average biomass of $0.17 \text{ t} \cdot \text{km}^{-2}$, but it could be doubled to include the juveniles. A tentative value of $0.2 \text{ t} \cdot \text{km}^{-2}$ was used in the model for the 1990s. The P/B ratios for herring in the 1980s and 1990s were calculated from estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*) added to that of fishing mortality, to give P/B ratios of 0.54 yr^{-1} in both the 1980s and 1990s. The Q/B estimate (4.1 yr^{-1}) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of herring (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

34) Transient pelagics

Transient pelagics include bluefin tuna *Thunnus thynnus*, swordfish *Xiphias gladius* and sharks. Biomass for transient pelagics was estimated for both models by assuming an ecotrophic efficiency of 95%. The P/B (0.4 yr^{-1}) and Q/B (3.3 yr^{-1}) estimates obtained from Bundy *et al.* (2000) were used in both models. The estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database. The diet of transient pelagics (Appendix B) was not well known, and was adapted from Bundy *et al.* (2000) by assuming that the 0.2% cod was split into Atlantic and Greenland cod (0.1% each), and the small demersal feeders were divided into juvenile benthopelagic piscivores (1.2%), juvenile large demersal feeders (1.2%) and other small demersals (1.1%). Piscivorous and planktivorous pelagic feeders were divided into herring (11.5%), small pelagics (11.5%), small mesopelagics (11.5%) and shortfin and Arctic squid (5.6%).

35) Small pelagics

Small pelagics include shad *Alosa sapidissima*, butterfish *Peprilus triacanthus*, argentine *Argentina silus*, juvenile mackerel and Atlantic rainbow smelt *Osmerus mordax mordax*. Very

little is known about these species, and the biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. The P/B ratios for small pelagics in the 1980s and 1990s were assumed to be similar to estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*), to give a P/B ratio of 0.64 yr^{-1} in both the 1980s and 1990s. The Q/B estimate (5.3 yr^{-1}) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of small pelagics (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

36) Mesopelagics

Mesopelagic species in the 2J3KLNO area include lanternfishes (Myctophidae), pearlides *Maurolicus muelleri* and barracudinas *Paralepis elongata*. Lilly (*pers. comm.*) calculates a biomass of 0.003 and $0.14 \text{ t} \cdot \text{km}^{-2}$ for the 1985-87 and 1995-97 models, respectively. However, this is probably grossly underestimating their biomass, as neither the Engels nor the Campelen sampling trawls catch mesopelagics effectively. Thus, their biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. The P/B ratios for mesopelagics in the 1980s and 1990s were assumed to be similar to estimates of natural mortality (Appendix A Table A1 in Heymans and Pitcher, *this volume*), to give a P/B ratio of 1.4 yr^{-1} in both the 1980s and 1990s. The Q/B estimate (4.8 yr^{-1}) calculated for the 1900 model (see Appendix A Table A2 in Heymans and Pitcher, *this volume*) was used in both the 1985-87 and 1995-97 models. The diet of mesopelagics (Appendix B) was obtained from Lilly (2002) and estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

37-38) Squid (shortfin and Arctic squid)

Two species of squid are present in the area: shortfin squid *Illex illecebrosus* and Arctic squid *Gonatus* spp. Very little is known about Arctic squid aside from the fact that they stay in the area throughout the year, while shortfin squid are highly migratory and spend only part of their time in the area (Bundy *et al.* 2000). The biomass of shortfin squid was probably very low during the 1985-1987 time-period. Bundy *et al.* (2000) and Vasconcellos *et al.* (2002c) suggested that large quantities of squid were last seen 20 years ago, and since 1982 the stock has remained small, indicating low productivity (Dawe *et al.* 2000).

Thus the relative abundance of *Illex sp.* was assumed to be the same between 1985-1987 and 1995-1997 (Bundy 2002). However, no estimates of squid biomass are available for the 1980s model, so the biomasses of both shortfin and Arctic squid were estimated by assuming ecotrophic efficiencies of 95% for both species in all four models.

Bundy *et al.* (2000) estimated P/B ratios for planktivorous and piscivorous small pelagics of 0.5 and 0.6 yr⁻¹, respectively, and used a gross efficiency of 0.15 to calculate their Q/B ratios. Thus, a P/B of 0.5 yr⁻¹ was used for Arctic squid and 0.6 yr⁻¹ for shortfin squid in all four models, with their Q/B ratios calculated by using a GE of 0.15. The diet of shortfin squid was taken from Appendix C Table 16 in Bundy *et al.* (2000) and it was assumed that the diet of Arctic squid consist of large and small zooplankton (Appendix B). Arctic squid are not fished in this system (Bundy *et al.* 2000) and estimates of shortfin squid catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

39-41) Large Crustaceans (large crabs, small crabs, and lobster)

The biomass estimates of large (> 95 mm carapace width) and small snow crabs (Table 9) for 1996-97 were obtained from Dawe *et al.* (2000), while in 1985-87 the biomass of large snow crabs was estimated at 86,345 tonnes or 0.17 t•km⁻² (Bundy *et al.* 2000). No estimates were available for small crabs in the 1980s, and the biomass was left to be estimated by the model assuming an ecotrophic efficiency of 95%. These estimates were taken as the lower limit to the crab (> 95 mm and ≤ 95 mm) biomass. Bundy *et al.* (2000) estimated a biomass of 2,217 tonnes (0.005 t•km⁻²) for lobster in 1985-87 and no new estimate of lobster biomass was available for 1995-97. Therefore the biomass of lobster in the 1990s was left to be estimated by Ecopath assuming an ecotrophic efficiency of 95%. The P/B (0.4 yr⁻¹) and Q/B (4.4 yr⁻¹) estimates obtained from Bundy *et al.* (2000) for large crustaceans were used for all three compartments in both models. Estimates of catch for all three compartments in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

Table 9. Biomass estimates of snow crab obtained from (Dawe *et al.* 2000).

Year	Snow crab > 95mm	Snow crab (≤ 95 mm)
1996	76,673	19,799
1997	100,726	26,876
Average (tonnes)	88,700	23,338
t•km ⁻²	0.179	0.0471

Table 10. Estimates of rock and toad crabs discarded in 2J3KLNO.

	Rock Crab (tonnes)	Toad Crab (tonnes)	Total Discards (t•km ⁻² •yr)
1995	26	352	0.000764
1996	0	0	0.000000
1997	13	17	0.000060
Average	13	123	0.000274

The diet of large and small crabs (Appendix B) were adapted from Lovrich and Sainte-Marie (1997) who suggested that large snow crabs feed on annelids, crustacean decapods and fish. Small snow crabs feed on amphipods and ophiuroids (Lovrich and Sainte-Marie 1997), while rock crabs feed on mussels, snails, brittlestars, amphipods and polychaetes (DFO 1996a) and toad crabs feed on amphipods, polychaetes, bivalves, ophiuroids, gastropods, chitons, sea urchins, small crabs and scavenge fish (DFO 1996b). The diet of lobster was assumed to be similar to that of large snow crabs (Appendix B).

Estimates of catch for all three compartments in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database. Discards of rock and toad crabs (Table 10) were obtained from Earl Dawe and Eric Way (*pers. comm.*).

42) Shrimp

Northern shrimp *Pandalus borealis* are fished from southern Davis Strait (0B) to the northeast Newfoundland Shelf (3K), while *Pandalus montagui* are fished commercially in areas 2, 3 and 4 (Parsons *et al.* 2000). The biomasses of these two species are distributed in the ratio of 9:1 (Parsons *pers. comm.*) and the average biomass of *P. borealis* from 1995-1997 was approximately 497,000 tonnes, or 1.0 t•km⁻² (Table 11) which gives an overall biomass for all shrimp of 1.1 t•km⁻² (Parsons *et al.* 2000). Bundy *et al.* (2000) estimated the biomass of shrimp in the 1980s to be 1.5 t•km⁻², which is marginally larger than that of the 1990s. The P/B (1.45 yr⁻¹) and Q/B (9.7 yr⁻¹) estimates, as well as diet obtained from Bundy *et al.* (2000) for shrimp in 1985-87, were used in both models. Estimates of catch in 1985-87 and 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

Table 11. Biomass of northern shrimp *P. borealis* and total shrimp obtained from Parsons *et al.* (2000), based on a 9:1 biomass ratio of *P. borealis* to *P. montagui*.

Year	3K	2HJ	3LNO	Total
1995	267,000	—	8,002	
1996	501,300	90,480	26,694	
1997	438,500	40,740	52,730	
Average (tonnes)	402,267	65,610	29,142	497,019
Northern shrimp (t•km ⁻²)				1.004
Total shrimp biomass (t•km ⁻²)				1.104

43-46) Benthos

The benthos of the Grand Banks include polychaetes, crustaceans, echinoderms and mollusks, and the undisturbed macrofauna are relatively homogenous (Kenchington *et al.* 2001). We divide benthos into echinoderms, polychaetes, bivalves and other benthic invertebrates. Kenchington *et al.* (2001) suggested that the biomass is dominated by propeller clams *Cyrtodaria siliqua*, and sand dollars *Echinarachnius parma*, while the polychaete *Prionospio steenstrupi* and the mollusk *Macoma calcarea* were the most abundant. The brittlestar *Ophiura sarsi*, the bivalve *Macoma calcarea*, and the sea urchin *Strongylocentrotus pallidus* also contributed substantially to the biomass (Kenchington *et al.* 2001). In general, Kenchington *et al.* (2001) found that the effect of trawling (otter trawling) on the infauna was limited and short term, especially on sandy bottoms where prominent bedforms were lacking. We therefore assume that the biomass of benthos would not have changed dramatically subsequent to the 1980s (Bundy *et al.* 2000). However, as no newer information on these groups is available, the biomass, P/B and Q/B ratios and diets of these groups were assumed to be similar in 1995-97 to 1985-87 (Bundy *et al.* 2000).

A directed fishery for Icelandic scallops started on the Grand Banks only in 1993, while they were caught in the Strait of Belle Isle and on St. Pierre Bank before that time (Anon. 1996b). They are mostly taken in areas 3LNO (Anon. 1996b). Estimates of catch of bivalves only in 1985-87 and bivalves and other invertebrates (probably sea-cucumbers) in 1995-97 (Tables 11 and 12) were obtained from the SAUP database.

47-48) Zooplankton

Zooplankton are divided into two groups, small and large zooplankton: large zooplankton are generally greater than 5 mm in length and include euphausiids, Chaetognaths, hyperiid amphipods, Cnidarians and Ctenophores (jellyfish), mysids, tunicates >5 mm and ichthyoplankton (Bundy *et al.* 2000). The group includes herbivores (some euphausiid species), omnivores (most euphausiids, hyperiid amphipods, mysids and large tunicates) and carnivores (chaetognaths and jellyfish, Cnidarians and Ctenophores) (Bundy *et al.* 2000). Small zooplankton are generally smaller than or equal to 5 mm in length and include mainly copepods, with *Calanus finmarchicus* and *Oithona similis* being the most numerous. Other small plankton include

Table 12. Small zooplankton biomass ($t \cdot km^{-2}$) estimates obtained from Bundy *et al.* (2000).

Year	Small zooplankton biomass	Seasonally adjusted biomass
1995	16.3	23.4
1996	17.3	24.8
1997	30.0	42.9
Average	21.2	30.4

tunicates <5 mm and meroplankton. *C. finmarchicus* and *O. similis* are omnivorous.

Bundy *et al.* (2000) calculated the biomass of large zooplankton in 1996-1997 at $18.3 t \cdot km^{-2}$ and in 1985-87 at $22.5 t \cdot km^{-2}$. For small zooplankton in 1985-87, a value of $33.7 t \cdot km^{-2}$ was used, while for 1995-97 the average seasonally adjusted biomass of $30.4 t \cdot km^{-2}$ (Table 12) obtained from Bundy *et al.* (2000) was used. The P/B and Q/B ratios and diets obtained from Bundy *et al.* (2000) were used in both models and zooplankton were not caught in either time periods.

49) Phytoplankton

The biomass of phytoplankton in 1985-87 was estimated at $26.9 t \cdot km^{-2}$ by Bundy *et al.* (2000), while in 1995-97 the average chlorophyll-*a* concentration ($1.59 \mu g \cdot l^{-1}$, or $0.12 t \cdot km^{-2}$ over an average depth of 67 m) were obtained from the *Ships of Opportunity* and dedicated zonal monitoring cruises (Pepin, *pers. comm.*). The average C:Chl-*a* ratio of 43.9% used in Bundy *et al.* (2000) was used to calculate a phytoplankton biomass of $5.5 t \cdot km^{-2}$, while the C:wet weight ratio of 1:9 (Pauly and Christensen 1995) was used to calculate a biomass of $47.9 t \cdot km^{-2}$ wet weight in 1995-97. The P/B ratio of $93.1 yr^{-1}$ obtained from Bundy *et al.* (2000) was used in both models.

50) Detritus

The detritus pool was recalculated from the formula for detritus obtained from Pauly *et al.* (1993):

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E$$

where D = detritus standing stock in $gC \cdot m^{-2}$ (grams of carbon per square metre), PP = primary productivity in $gC \cdot m^{-2} \cdot yr^{-1}$ and E = euphotic depth (m).

A value of 54.7 m was used for the euphotic zone depth (Bundy *et al.* 2000), and a detritus pool of $412 t \cdot km^{-2}$ was calculated, which is higher than the $389 t \cdot km^{-2}$ calculated by Bundy *et al.* (2000) for 1985-87. However, if the estimate of primary production, or phytoplankton biomass, is

incorrect, this would change the detritus pool substantially.

BALANCING THE MODELS: 1995-1997

The unbalanced model of 1995-97 calculated large discrepancies with the ecotrophic efficiency of most of the fish species (Table 13). The biomass estimates of sandlance, Arctic cod and small mesopelagics were obviously too small, due to the lack of catchability adjustments. Therefore, their biomasses were estimated by assuming an ecotrophic efficiency of 95% each after adjusting the percentage they represented in the diet of other species.

Juvenile cod

The large ecotrophic efficiency of juvenile cod was probably due to the low P/B used in this model. The P/B estimate from Bundy *et al.* (2000) produced an ecotrophic efficiency of 39.7. To reduce the ecotrophic efficiency of juvenile cod, the percentages of juvenile cod in the diet of shortfin squid and juvenile benthopelagic piscivores were reduced to 0.01% each and in the diet of cetaceans and hooded seals it was reduced to 0.1%. The ecotrophic efficiency was still 6.4, and the only other predator taking large proportions of juvenile cod was the harp seal, the diet of which is more certain than the biomass estimate of juvenile cod. Thus, after these changes were made to the predators of juvenile cod, its biomass was estimated by assuming an ecotrophic efficiency of 0.95, giving a biomass of $0.09 \text{ t}\cdot\text{km}^{-2}$, which is similar to that of the biomass of large cod. With the reduction of large cod in the system, this possibility may be assumed.

Greenland cod

The ecotrophic efficiency of Greenland cod was estimated at ca. 333, and was mainly due to large dietary requirements of cetaceans, harp seals, piscivorous birds and adult cod. The percentage that Greenland cod contribute to their diets was reduced to 0.01%, and the diets recalculated. The diet of harp seals is very certain, but the arbitrary division made between Greenland cod and other cod might have overestimated Greenland cod in the diet of harp seals. However, after the diet adjustments were made the ecotrophic efficiency of Greenland cod was still 23. It was therefore decided to have the biomass estimated by assuming an ecotrophic efficiency of 95%, as the biomass of Greenland cod could be severely under-reported by having no catchability adjustment. Thus, the biomass of Greenland cod

is estimated at $0.002 \text{ t}\cdot\text{km}^{-2}$.

Capelin

The ecotrophic efficiency of capelin was estimated at 80, and was mainly due to the high dietary requirements of cetaceans, harp seals, piscivorous birds, shortfin squid, juvenile benthopelagic piscivores and juvenile Greenland halibut.

- Capelin was reduced to 1% in the diet of shortfin squid, and the percentage of small pelagics in the diet of shortfin squid increased to 25.9%, as they were probably part of the diet of squid.
- Capelin was reduced to 10% and small pelagics were increased to 30% in the diet of cetaceans.
- Capelin in the diet of juvenile Greenland halibut was reduced to 5%, and small pelagics were increased to 30%, and the diet of juvenile Greenland halibut was recalculated.
- Capelin in the diet of adult Greenland halibut was reduced to 10% and 20% of the diet was attributed to small pelagics.
- Capelin in the diet of both adult and juvenile cod was reduced to 10% and small pelagics were increased to 23%.
- Capelin in the diet of juvenile American plaice was reduced to 10% and small pelagics were increased to 15%.
- In the diet of piscivorous birds, capelin was reduced to 10% and small pelagics and herring were increased to 20% each.

The ecotrophic efficiency of capelin was still 42.6 and the only two mortalities that were still a problem were harp seals and cetaceans. Thus, the biomass ($4.4 \text{ t}\cdot\text{km}^{-2}$) was estimated by assuming

Table 13. Model compartments that were unbalanced in 1995-97.

#	Group name	Ecotrophic efficiency
10	Juvenile cod $\leq 40 \text{ cm}$	410.1217
28	Greenland cod	333.3397
30	Capelin	79.9645
16	Witch flounder	70.2847
40	Small crabs $\leq 95 \text{ cm}$	65.8388
36	Mesopelagics	36.6623
31	Sandlance	17.9046
22	Dem. ben-pel pisc. $> 40 \text{ cm}$	14.7108
12	Juvenile Am. plaice $\leq 35 \text{ cm}$	12.7039
32	Arctic cod	11.3257
27	Lumpfish	8.8316
33	Herring	8.1190
20	Redfish	7.2716
9	Adult Cod $> 40 \text{ cm}$	6.6873
26	Other small demersals	6.4762
13	Adult G. halibut $> 65 \text{ cm}$	3.8546
19	Dogfish	2.9010
24	Large demersal fish $> 30 \text{ cm}$	2.8904
11	American plaice $> 35 \text{ cm}$	2.5115
14	Juvenile G. halibut $\leq 65 \text{ cm}$	1.8763
42	Shrimp	1.1377

an ecotrophic efficiency of 95%, as the biomass estimates obtained from Lilly (*pers. comm.*) were not adjusted for catchability, and Anderson *et al.* (2001) estimates a biomass of $3.7 \text{ t}\cdot\text{km}^{-2}$.

Witch flounder

The ecotrophic efficiency of witch flounder was estimated at 70.3, and was mainly due to the high dietary requirements of harp and hooded seals. However, flounder in the diet of harp seals was taken to be all witch flounder, thus we reduced the amount of witch flounder in the diet to 2% and increased the winter flounder in the diet of harp seals to 4%, and recalculated the diet of harp seals. The percentage of witch flounder in the diet of hooded seals was also reduced to 0.1% and the diet recalculated. However, this still gave an ecotrophic efficiency of 18.8, and it was decided to estimate the biomass ($0.48 \text{ t}\cdot\text{km}^{-2}$), as the biomass estimates were not adjusted for catchability, by assuming an ecotrophic efficiency of 95%.

Small crabs

The ecotrophic efficiency of small crabs was estimated at 65.8, which could be due to the fact that the P/B ratio of large crustaceans was used for small crabs. It was assumed that the P/B ratio of small crabs would probably be twice as large, which reduced the ecotrophic efficiency to 48.4. The predators that had the largest impact on small crabs were juvenile demersal fish, juvenile planktivorous fish, skates and small cod. The biomass ($0.07 \text{ t}\cdot\text{km}^{-2}$) of small crabs was then estimated by assuming an ecotrophic efficiency of 95%.

The percentage of small crabs in the diet of adult and juvenile cod, adult and juvenile American plaice, adult and juvenile benthopelagic piscivores and adult demersal fish was reduced to 0.1%, while the percentage in the diet of skates was reduced to 0.5%. The percentage of small crabs in the diet of juvenile demersal fish was reduced to 0.01%, and all predator diets were recalculated to balance the small crab group.

Mesopelagics

Mesopelagic ecotrophic efficiency was 36.6 in the unbalanced system, and had risen to 70 with the changes made to the model thus far. However, the biomass estimate of mesopelagics was probably underestimated as no catchability adjustments were made. Thus, the biomass ($2.04 \text{ t}\cdot\text{km}^{-2}$) was estimated by assuming an ecotrophic efficiency of 95%. This value is compatible with density

estimates from a world review of mesopelagics (Gjosæter and Kawaguchi 1980). When mapped into the *Sea Around Us* database of half-degree squares (R. Watson, *pers. comm.*), this source gives a mean biomass for 2J3KLNO of $1.1 \text{ t}\cdot\text{km}^{-2}$, with average offshore densities of $1.7 \text{ t}\cdot\text{km}^{-2}$.

Sandlance

Sandlance ecotrophic efficiency was estimated at 17.9, and had risen to 30.2 with the changes made to the model thus far. The main predators of sandlance were shortfin squid, juvenile benthopelagic piscivores, juvenile demersal fish, adult and juvenile American plaice, harp seals, cetaceans and adult and juvenile American plaice. The percentage of sandlance in the diet of shortfin squid was reduced to 1%, while in the diet of juvenile benthopelagic piscivores it was reduced to 0.5% and in the diet of juvenile demersal fish it was reduced to 0.1%. In the diet of adult and juvenile American plaice the percentages of sandlance were reduced to 10% each and in the diet of cetaceans the sandlance was reduced to 1%. All predator diets were recalculated, and the ecotrophic efficiency of sandlance was still 15.1. As the diet of harp seals was well established it was decided to estimate the biomass ($3.6 \text{ t}\cdot\text{km}^{-2}$) of sandlance by assuming an ecotrophic efficiency of 95%.

Adult benthopelagic piscivores

The ecotrophic efficiency of adult benthopelagic piscivores was 14.7 in the unbalanced model, and 21.5 after the balancing of the above groups. The only predator of this species in the model is cetaceans, and we reduced the percentage it contributes to the diet of cetaceans to 0.1%, which calculates an ecotrophic efficiency of 1.5. The biomass was subsequently estimated by assuming an ecotrophic efficiency of 95% at $0.024 \text{ t}\cdot\text{km}^{-2}$, or double that given by the biomass estimates that were not adjusted for catchability.

Juvenile American plaice

The ecotrophic efficiency of juvenile American plaice was 12.7 in the unbalanced model, and had increased to 38.5 after the balancing of the previous groups. The P/B ratio of juvenile American plaice was assumed to be similar to their natural mortality (0.12 yr^{-1}), but in the 1985-87 model (Bundy *et al.* 2000) it was estimated at 0.63 yr^{-1} . It is assumed that the fishing mortality of juvenile American plaice was much reduced in 1995-97, but the P/B ratio was probably still higher than 0.1 yr^{-1} , and a P/B of 0.4 yr^{-1} was assumed. The main predators of juvenile

American plaice were harp seals and juvenile benthic-pelagic piscivores, and the juvenile plaice in the diet of juvenile benthic-pelagic piscivores was reduced to 0.1% to give an ecotrophic efficiency of 2.6. The biomass of juvenile American plaice ($0.8 \text{ t}\cdot\text{km}^{-2}$) was then estimated by assuming an ecotrophic efficiency of 95% to take into consideration the lack of catchability adjustment in the biomass estimates.

At this stage, it was found that the cannibalism in juvenile benthic-pelagic piscivores was driving the ecotrophic efficiency of all other unbalanced compartments higher, while it caused previously balanced compartments to become unbalanced. The cannibalism in this group was therefore reduced to 0.01%.

Arctic cod

Arctic cod had an ecotrophic efficiency of 11.3, when using the P/B obtained from Bundy *et al.* (2000). However, using the natural mortality (0.57 yr^{-1}) calculated for the 1900 model (Heymans *this volume*, Appendix A, Table A1), reduced the ecotrophic efficiency. The main predators of Arctic cod were harp seals and juvenile Greenland halibut. The percentage of Arctic cod in the diet of Greenland halibut was reduced to 0.1%, which reduces the ecotrophic efficiency to 7.7. As the diet of harp seals is relatively well known, and catchability was not included in the biomass estimates, the biomass ($1.1 \text{ t}\cdot\text{km}^{-2}$) is estimated by assuming an ecotrophic efficiency of 95%.

Lumpfish

The ecotrophic efficiency of lumpfish was estimated at 8.8 in the unbalanced model, and increased to 14.5 after balancing the previous groups. Their main predators are cetaceans and piscivorous birds, and the percentage that lumpfish contribute to both their diets was reduced to 0.1%, which reduced the ecotrophic efficiency to 1.7. The biomass ($0.034 \text{ t}\cdot\text{km}^{-2}$) was subsequently estimated by assuming an ecotrophic efficiency of 95%.

Herring

The ecotrophic efficiency of herring was estimated at 8.1 in the unbalanced model, and increased to 11.5 after balancing the previous groups. The main predators of herring are cetaceans and harp seals, and the percentage of herring in the diet of cetaceans was reduced to 0.1%, which reduced the ecotrophic efficiency of herring to 9.6. The biomass of herring was then

estimated at $2.2 \text{ t}\cdot\text{km}^{-2}$ assuming an ecotrophic efficiency of 95% (an order of magnitude higher than estimated by DFO (Anon. 2000)).

Redfish

The ecotrophic efficiency of redfish was estimated at 7.3 in the unbalanced model, and increased to 8.0 after balancing the previous groups. The main predators of redfish are juvenile demersal fish, juvenile Greenland halibut, skates and hooded seals. The percentages of redfish in the diet of juvenile Greenland halibut and skates were reduced to 5% each, while the percentage in the diet of juvenile demersal fish was reduced to 0.1% and the percentage in the diet of hooded seals was reduced to 1%. The biomass was then estimated by assuming an ecotrophic efficiency of 95% at $0.99 \text{ t}\cdot\text{km}^{-2}$, which more than doubles the $0.37 \text{ t}\cdot\text{km}^{-2}$ estimated by the Campelen trawl survey (unadjusted for catchability).

Adult cod

The ecotrophic efficiency of adult cod was estimated at 6.7 in the unbalanced model, and increased to 7.0 after balancing the previous groups. The main predators of adult cod are harp and hooded seals. Reducing the percentage of adult cod in the diet of hooded seals to 0.1% reduced the ecotrophic efficiency to 5.5. The P/B ratio used for adult cod (0.11 yr^{-1}) in the 1995-97 model was much lower than the 0.65 yr^{-1} estimated by Bundy *et al.* (2000). It was assumed that the P/B ratio was higher than that estimated by adding natural mortality to fishing mortality, and a value of 0.3 yr^{-1} was used, which reduced the ecotrophic efficiency to 2.2. The biomass of adult cod was then estimated at $0.18 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Other small demersals

The ecotrophic efficiency of small demersals was estimated at 6.5 in the unbalanced model, and increased to 9.0 after balancing the previous groups. The main predators of small demersals include juvenile benthic-pelagic piscivores, winter flounder, juvenile Greenland halibut, juvenile American plaice and harp seals. The percentage of small demersals in the diets of all these species (except for harp seal) was reduced to 0.5%. The biomass was then estimated at $0.5 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Adult Greenland halibut

The ecotrophic efficiency of adult Greenland halibut was estimated at 3.8 in the unbalanced

model, and increased to 4.5 after balancing the previous groups. The main predators of adult Greenland halibut are harp and hooded seals, and the percentage of this group in the diet of hooded seals was reduced to 1%, which decreased the ecotrophic efficiency to 2.0. The biomass ($0.77 \text{ t}\cdot\text{km}^{-2}$) was then estimated by assuming an ecotrophic efficiency of 95%.

Dogfish

The ecotrophic efficiency of dogfish was estimated at 2.9 in the unbalanced model, and increased to 4.2 after balancing the previous groups. The main predators of dogfish are cetaceans, and reducing the percentage of dogfish in the diet of cetaceans to 0.1% reduced the ecotrophic efficiency to 2.5. The biomass was then calculated at $0.02 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Large demersal fish

The ecotrophic efficiency of large demersal fish was estimated at 2.9 in the unbalanced model, and increased to 4.4 after balancing the previous groups. The main predators of large demersal fish are cetaceans, and the percentage of large demersal fish in the diet of cetaceans was reduced to 0.1%, which reduced the ecotrophic efficiency to 1.8. The biomass was then estimated at $0.23 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%, which is double the biomass estimated from the Campelen trawl (unadjusted for catchability).

Adult American plaice

The ecotrophic efficiency of adult American plaice was estimated at 2.5 in the unbalanced model, and increased to 2.6 after balancing the previous groups. The main predators of adult American plaice are harp seals. As the diet of harp seals is well studied, the biomass was re-estimated at $0.9 \text{ t}\cdot\text{km}^{-2}$, by assuming an ecotrophic efficiency of 95%.

Juvenile Greenland halibut

The ecotrophic efficiency of juvenile Greenland halibut was estimated at 1.9 in the unbalanced model, and increased to 2.8 after balancing the previous groups. The main predators of juvenile Greenland halibut are hooded seals, and reducing the percentage of juvenile Greenland halibut in the diet of hooded seals to 10% reduced the ecotrophic efficiency to 1.7. The biomass was then calculated at $1.0 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Shrimp

The ecotrophic efficiency of shrimp was estimated at 1.1 in the unbalanced model, and increased to 2.0 after balancing the previous groups. The main predators of shrimp are juvenile Greenland halibut and juvenile demersal fish, and by reducing the percentage of shrimp in their diets to 1%, the ecotrophic efficiency of shrimp was reduced to 0.9.

Large zooplankton

After balancing the previous compartments the ecotrophic efficiency of large zooplankton was 1.7. The main predators of large zooplankton are small pelagic fish, mesopelagics, Arctic squid and cannibals. Cannibalism was reduced to 1%, with the percentage of small zooplankton in the diet of large zooplankton decreasing to 30% and phytoplankton increasing to 59%. The percentage of large zooplankton in the diet of small pelagic fish was reduced to 60%, while its contribution to the diet of Arctic squid and mesopelagics was reduced to 30% each. The percentage of large zooplankton in the diet of shortfin squid was reduced to 25%, and in the diet of herring it was reduced to 0.45%. This still calculated an ecotrophic efficiency of 1.3, and the biomass of large zooplankton was then estimated at $25.4 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Final changes to the model in balancing

We opted to balance the model from the top-down, i.e., making the biomass of prey match the demand of predators by setting EE to 0.95. The alternative method (bottom-up) would be to reduce the predation pressure by decreasing the biomass or consumption rates of predators so that the total consumption matches the production of preys. One obvious consequence of using a top-down balancing is the tendency to estimate lower Fs using the ratio between catches and the new (increased) biomasses. To see which balancing method is the better assumption, the Fs estimated by Ecopath for the 1990s could be compared to the Fs estimated by DFO for the key demersal species (cod, American plaice, Greenland halibut, Greenland cod, redfish and witch flounder). [This will be done at a later stage, ED.]

Subsequent to the balancing of this model, changes were made to the bird compartments as given by Burke *et al.* (2002). These changes were the inclusion of fulmars and shearwaters into the piscivorous birds compartment (Montevecchi,

Table 14. Recreational catches ($t/km^2 \cdot yr^{-1}$) in Newfoundland and Labrador for 1985 and 1995.

Species	1985	1995
Salmon	0.0017	0.0005
Cod	0.0082	0.1920
Mackerel	0.0003	0.2670
Smelts (small pelagics)	0.0016	0.0010
Tomcod (small demersals)		0.000007

Memorial University of Newfoundland, *pers. comm.*), and the addition of the wintering and breeding birds vs. taking the average of the two groups.

Additional information on recreational catches (Table 14) became available from the 1985 and 1995 surveys of recreational fishing in Canada (Robyn Forrest, Fisheries Centre, UBC *pers. comm.*¹).

Finally, the predators of three other species were also expanded, as they were under-represented in the model:

- The predators of salmon were expanded to include cetaceans, grey seals, piscivorous birds, skates and transient pelagics.
- The predators of large crabs were expanded to include grey, harp and hooded seals as well as large cod.
- The predators of lobster were expanded to include walrus, large cod, skates, large demersal piscivores and other large demersal species.

The new biomass estimates were put into the previously balanced model, and the new balanced model parameters given in Appendix C.

BALANCING THE MODELS: 1985-1987

The unbalanced model of 1985-87 calculated large discrepancies with the ecotrophic efficiency of most of the fish species (Table 15). The estimates of sandlance, Arctic cod and small mesopelagics, capelin and Greenland cod were obviously too small, due to the lack of catchability adjustments, so their biomasses were estimated by assuming an ecotrophic efficiency of 95% each after adjusting the percentage that they contribute to their predators.

Sandlance

The ecotrophic efficiency of sandlance was estimated at 30,412. The fishing mortality rate of $1.17 yr^{-1}$ indicates that the biomass of sandlance

Table 15. Model compartments that were unbalanced in 1985-87.

#	Group name	Ecotrophic efficiency
31	Sand lance	30411.81
36	Mesopelagics	1462.53
30	Capelin	396.67
32	Arctic cod	363.52
28	Greenland cod	257.73
26	Other small demersals	86.17
14	G.halibut<=40cm	15.87
10	Cod <= 35 cm	15.04
27	Lumpfish	14.56
16	Witch flounder	7.45
12	Am. plaice<=35cm	5.34
20	Redfish	2.90
22	Large Dem. BP	2.76
19	Dogfish	2.61
13	G.halibut>40cm	2.25
33	Herring	1.87
24	L.dem. feeders	1.53
42	Shrimp	1.13

was unrealistically small. The biomass of sandlance, calculated by Lilly (*pers. comm.*) was not adjusted for catchability, and therefore it was estimated ($2.26 t \cdot km^{-2}$) by assuming an ecotrophic efficiency of 95%. This estimate of sandlance biomass is comparable to the $2.7 t \cdot km^{-2}$ estimated by Bundy *et al.* (2000).

Mesopelagics

Similar to sandlance, the biomass of mesopelagics was not adjusted for catchability, and the large ecotrophic efficiency (1463) calculated for mesopelagics indicates that the biomass was heavily underestimated. The biomass estimated by Lilly (*pers. comm.*) was $0.0003 t \cdot km^{-2}$, but Ecopath estimated a value of $1.16 t \cdot km^{-2}$ when taking into consideration the predator requirements in the ecosystem using an ecotrophic efficiency of 95%. This value is compatible with density estimates from a world review of mesopelagics (Gjosaeter and Kawaguchi 1980). When mapped into the Sea Around Us database of half-degree squares (R. Watson, *pers. comm.*), this source gives a mean biomass for 2J3KLNO of $1.1 t \cdot km^{-2}$ with average offshore densities of $1.7 t \cdot km^{-2}$.

Capelin

The ecotrophic efficiency of capelin was calculated at 397, and the fishing mortality was estimated at $3.5 yr^{-1}$, which indicates the underestimation of capelin biomass. The biomass of capelin was therefore estimated by assuming an ecotrophic efficiency of 95%, which estimated a biomass of $11.5 t \cdot km^{-2}$, similar to the $13 t \cdot km^{-2}$ estimated by Bundy *et al.* (2000) on which this model is based.

¹ <http://www.dfo-mpo.gc.ca/communic/statistics/recfsh95/content3.htm>.
http://www.dfo-mpo.gc.ca/communic/statistics/Historic/RECFISH/Index_85.htm

Arctic cod

Arctic cod ecotrophic efficiency was estimated at 363, and the biomass was estimated at $2.23 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%, which is comparable to the $3.0 \text{ t}\cdot\text{km}^{-2}$ estimated by Bundy *et al.* (2000).

Greenland cod

Greenland cod ecotrophic efficiency was estimated at 258, and the biomass was estimated at $0.1 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Other small demersals

Small demersal ecotrophic efficiency was estimated at 86, and the biomass was estimated at $0.9 \text{ t}\cdot\text{km}^{-2}$ by assuming an ecotrophic efficiency of 95%.

Juvenile cod

Juvenile cod ecotrophic efficiency was estimated at 15.04, and if the biomass was calculated by assuming an ecotrophic efficiency of 95%, the biomass of juvenile cod would have to be $7.6 \text{ t}\cdot\text{km}^{-2}$. This value is not realistic, and parameters of juvenile cod were examined. Bundy *et al.* (2000) estimates a P/B of juvenile cod of 1.6 yr^{-1} , which is an order of magnitude larger than the 0.115 yr^{-1} calculated by assuming that $P/B = Z = F + M$. As the calculation of F is dependent on the biomass, which is uncertain as discards are not well known, the 1.6 yr^{-1} calculated by Bundy *et al.* (2000) was used, calculating an ecotrophic efficiency of 0.8.

Juvenile Greenland halibut

Juvenile Greenland halibut ecotrophic efficiency was estimated at 15.8, and if the biomass was calculated by assuming an ecotrophic efficiency of 95%, the biomass would have to be $22.0 \text{ t}\cdot\text{km}^{-2}$. This value is not realistic, and parameters of juvenile Greenland halibut were examined. Bundy *et al.* (2000) estimated a P/B of 0.87 yr^{-1} , which is an order of magnitude larger than the 0.04 yr^{-1} calculated by assuming that $P/B = Z = F + M$. As the calculation of F is dependent on the biomass, which is uncertain as discards are not well known, the 0.87 yr^{-1} calculated by Bundy *et al.* (2000) was used, leading to an estimated ecotrophic efficiency of 0.7.

Lumpfish, adult benthopelagic piscivores and adult demersal feeders

Lumpfish ecotrophic efficiency was estimated at 14.6, and the biomass is calculated at $0.23 \text{ t}\cdot\text{km}^{-2}$ if an ecotrophic efficiency of 95% is assumed. Lumpfish, Greenland cod, adult benthopelagic piscivores and large demersal fish were all combined in the large demersal feeders group in Bundy *et al.* (2000), thus the sum of the biomass of lumpfish ($0.23 \text{ t}\cdot\text{km}^{-2}$), Greenland cod ($0.1 \text{ t}\cdot\text{km}^{-2}$), adult benthopelagic piscivores ($0.04 \text{ t}\cdot\text{km}^{-2}$) and adult demersal feeders ($0.24 \text{ t}\cdot\text{km}^{-2}$) is still less than the $0.85 \text{ t}\cdot\text{km}^{-2}$ estimated by Bundy *et al.* (2000).

The ecotrophic efficiency of adult benthopelagic piscivores was calculated at 2.8, and estimating their biomass by assuming an ecotrophic efficiency of 95% gives a biomass of $0.12 \text{ t}\cdot\text{km}^{-2}$, which, added to the biomass of adult demersal feeders, Greenland cod and lumpfish, approaches the $0.85 \text{ t}\cdot\text{km}^{-2}$ of large demersal estimated by Bundy *et al.* (2000). Similarly, the ecotrophic efficiency of adult demersal feeders was calculated at 1.5, and assuming an ecotrophic efficiency of 95%, calculates a biomass of $0.4 \text{ t}\cdot\text{km}^{-2}$, which, added to the $0.23 \text{ t}\cdot\text{km}^{-2}$ of lumpfish, $0.1 \text{ t}\cdot\text{km}^{-2}$ of Greenland cod and $0.12 \text{ t}\cdot\text{km}^{-2}$ of adult benthopelagic piscivores, approaches the $0.85 \text{ t}\cdot\text{km}^{-2}$ estimated by Bundy *et al.* (2000).

Juvenile American plaice

The ecotrophic efficiency of juvenile American plaice was calculated at 5.3, and assuming an ecotrophic efficiency of 95% calculates a biomass of $8.8 \text{ t}\cdot\text{km}^{-2}$, which is an order of magnitude higher than the $0.8 \text{ t}\cdot\text{km}^{-2}$ calculated by Bundy *et al.* (2000). Bundy *et al.* (2000) estimates a P/B of 0.63 yr^{-1} , which is three times larger than the 0.12 yr^{-1} calculated by assuming that $P/B = Z = F + M$. As the calculation of F is dependent on the biomass, which is uncertain as discards are not well known, the 0.63 yr^{-1} calculated by Bundy *et al.* (2000) was used, calculating a biomass of $0.77 \text{ t}\cdot\text{km}^{-2}$. This value is similar to the $0.78 \text{ t}\cdot\text{km}^{-2}$ calculated by Bundy *et al.* (2000), but larger than the $0.72 \text{ t}\cdot\text{km}^{-2}$ estimated for adult American plaice, which were obtained from Lilly (*pers. comm.*) and not adjusted for catchability yet.

Redfish

Lilly (*pers. comm.*) estimated redfish biomass (not adjusted for catchability) at $0.4 \text{ t}\cdot\text{km}^{-2}$, which is much lower than the biomass of $1.88 \text{ t}\cdot\text{km}^{-2}$ estimated by Bundy *et al.* (2000), and which calculates an ecotrophic efficiency of 2.9.

Assuming an ecotrophic efficiency of 95% calculates a biomass of $1.4 \text{ t}\cdot\text{km}^{-2}$, which is closer to that estimated by Bundy *et al* (2000).

Herring

The ecotrophic efficiency of herring was calculated at 1.87, and assuming an ecotrophic efficiency of 95% calculates a biomass of herring of $1.24 \text{ t}\cdot\text{km}^{-2}$, which is nearly three times the (catchability unadjusted) biomass estimated by Lilly (*pers. comm.*). However, the biomass of herring, mackerel, squid, small pelagics and mesopelagics (as calculated by Ecopath) sums to $4.6 \text{ t}\cdot\text{km}^{-2}$, which is lower than the $5.1 \text{ t}\cdot\text{km}^{-2}$ estimated by Bundy *et al* (2000) for small piscivorous and planktivorous feeders.

Dogfish

Dogfish ecotrophic efficiency was calculated at 2.6, using the biomass estimate (unadjusted for catchability) obtained from Lilly (*pers. comm.*). Assuming an ecotrophic efficiency of 95% estimates a biomass of $0.018 \text{ t}\cdot\text{km}^{-2}$. Dogfish, together with other sharks, tuna, swordfish and Atlantic salmon, were classified as large pelagic feeders by Bundy *et al* (2000), with a biomass of $0.03 \text{ t}\cdot\text{km}^{-2}$, which is similar to their sum total in this model.

Adult Greenland halibut

The ecotrophic efficiency of Adult Greenland halibut was calculated at 2.25 when using the biomass estimate (unadjusted for catchability) obtained from Lilly (*pers. comm.*). Conversely, assuming an ecotrophic efficiency of 95% calculates a biomass of $0.78 \text{ t}\cdot\text{km}^{-2}$, which is higher than the biomass estimated for juvenile Greenland halibut, and higher than the biomass estimated for adult Greenland halibut in Bundy *et al* (2000).

Bundy *et al* (2000) estimated a P/B of 0.3 yr^{-1} , which is double the 0.14 yr^{-1} calculated by assuming $P/B = Z = F + M$. Since the calculation of F is dependent on the biomass, which is uncertain as discards and catchability are not well known, the 0.3 yr^{-1} calculated by Bundy *et al* (2000) was used, calculating an ecotrophic efficiency of 1.04. Subsequently, the biomass of adult Greenland halibut was estimated ($0.36 \text{ t}\cdot\text{km}^{-2}$) by assuming an ecotrophic efficiency of 95%.

Witch and yellowtail flounders

The ecotrophic efficiency of witch flounder was

calculated at 7.5, and assuming an ecotrophic efficiency of 95%, calculates a biomass of $0.54 \text{ t}\cdot\text{km}^{-2}$. Similarly, the ecotrophic efficiency of yellowtail flounder increased to 1.14 after balancing the above compartments, thus assuming an ecotrophic efficiency of 95% estimates a biomass of $0.21 \text{ t}\cdot\text{km}^{-2}$. The biomass of all flounders (yellowtail = $0.21 \text{ t}\cdot\text{km}^{-2}$, witch = $0.54 \text{ t}\cdot\text{km}^{-2}$ and winter = $0.05 \text{ t}\cdot\text{km}^{-2}$) is still lower than the $1.11 \text{ t}\cdot\text{km}^{-2}$ estimated for all flounders in Bundy *et al.* (2000).

Shrimp

Shrimp ecotrophic efficiency was estimated at 1.13 when using the biomass, P/B and Q/B estimates obtained from Bundy *et al.* (2000), thus assuming an ecotrophic efficiency of 95% estimates a biomass of $2.36 \text{ t}\cdot\text{km}^{-2}$, which is nearly double the $1.5 \text{ t}\cdot\text{km}^{-2}$ obtained from Bundy *et al.* (2000). However, as the biomass estimated by Bundy *et al* (2000) was adapted from later data, we will keep the new estimate of shrimp biomass.

Large and small zooplankton

The ecotrophic efficiency of large zooplankton increased to above 100% after balancing the compartments above, and assuming an ecotrophic efficiency of 95% the biomass of large zooplankton increased to $24.8 \text{ t}\cdot\text{km}^{-2}$. This value is higher than, but comparable to, the $22.5 \text{ t}\cdot\text{km}^{-2}$ estimated in Bundy *et al* (2000).

A higher biomass of large zooplankton would need to be sustained by a larger biomass of small zooplankton, and the balancing of large zooplankton therefore increased the ecotrophic efficiency of small zooplankton to 104%. Thus assuming an ecotrophic efficiency of small zooplankton of 95% estimates a biomass of $37 \text{ t}\cdot\text{km}^{-2}$, which is larger than, but comparable to, the biomass of small zooplankton estimated in Bundy *et al* (2000).

Final changes to the model

Additional information on recreational catches (Table 14) became available from the 1985 and 1995 surveys of recreational fishing in Canada (Robyn Forrest, Fisheries Centre, UBC *pers. comm.*)

The predators of three species were also expanded, as they were under-represented in the model:

- i. The predators of salmon were expanded to

- include cetaceans, grey seals, piscivorous birds, skates and transient pelagics.
- ii. The predators of large crabs were expanded to include grey, harp and hooded seals as well as large cod.
 - iii. The predators of lobster were expanded to include walrus, large cod, skates, large demersal piscivores and other large demersal species.

The new biomass estimates were entered into the previously balanced model, and the new balanced model's parameters are listed in Appendix D.

CONCLUSIONS

These models were adapted from Bundy *et al.* (2000), with an increase in the number of compartments, as well as a redistribution of species amongst compartments. In the 1985-87 model, the biomass estimates obtained from Lilly (*pers. comm.*) were mostly disregarded as they were not adjusted for catchability, and it was assumed that the estimates obtained by Bundy *et al.* (2000) were a truer representation of the biomass of these species. In the 1995-97 model no such guidelines were available, and in balancing that model the diets of the various fish species were changed more dramatically than in the 1985-87 model. This report gives a preliminary view of the ecosystem in 1995-97, and will be rebalanced when data on catchability coefficients for the Campelen trawl biomass estimates become available.

In subsequent work, time-series biomass data from 1985 to 1997 will be fitted, and the effects of climatic change, (i.e. North Atlantic Oscillation Index) on the model groups will be investigated.

These static mass-balance ECOPATH models will be used as baselines for dynamic exploration using ECOSIM. Policy explorations in *Back to the Future* aim to determine what fisheries could be sustained by the Newfoundland marine ecosystem if it were restored to its state in 1985 or 1995. Fishery options will be explored for sustainably managing each of these ecosystems in future, so that the value of each system, if restored and sustainably fished, can be compared using the *Back to the Future* technique (Sumaila *et al.* 2001).

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REFERENCES

- Ancellin, J., 1954. Observations sur la morue de Terre-Neuve et du Labrador. Rapp. P.-v. Réun. CIEM 136:72-76.
- Allen, G. M. 1942. Family Odobenidae: Walruses. Pages 469-477 in *Extinct and vanishing mammals of the Western Hemisphere with Marine Species of all the oceans*. American Committee for International Wild Life Protection Special Publication No. 11. Cooper Sq. Publishers, Inc., New York, N.Y.
- Anderson, J. T., Davis, D. J., Dalley, E. L. and Carscadden, J. E. 2001. Abundance and Biomass of Juvenile and Adult Capelin in the Newfoundland Region (NAFO 2J3KL) Estimated from the Pelagic Juvenile Fish Surveys, 1994-1999. Pages 1-12 in DFO Research Document, St. John's, Newfoundland.
- Anon. 1996a. Blackback (Winter) Flounder in Divisions 3K, 3L and 3Ps. Stock Status Report 96/92, DFO.
- Anon. 1996b. Grand Banks of Newfoundland (NAFO Div. 3LN) Iceland Scallops. Stock Status Report DFO.
- Anon. 2000. East and Southeast Newfoundland Atlantic Herring. Draft Report. Stock Status Report B2-01 (2000), DFO.
- Anon. 2001a. Walrus (*Odobenus rosmarus*). in Seal Conservation Society webpage (<http://www.pinnipeds.fsnet.co.uk/species/walrus.htm>).
- Anon. 2001b. Report Of The Joint ICES/NAFO Working Group On Harp And Hooded Seals. ICES CM 2001/ACFM:08.
- Beattie, A. I. 2001. A New Model for Evaluating the Optimal Size, Placement and Configuration of Marine Protected Areas. Unpublished Master's Thesis, University of British Columbia.
- Beverton, R.J.H. and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. Pages 142-180 in Wolstenholme, G.E.W. and O'Connor, M. (eds) CIBA Foundation colloquia on ageing: the lifespan of animals. Volume 5. J & A Churchill Ltd, London.
- Bradbury, I. R., Lawson, G. L., Robichaud, D., Rose, G. A. and Snelgrove, P. V. R. 2000. Success and failure of Atlantic cod, *Gadus morhua*: a case study from coastal Newfoundland. Research

- Document 2000/022, DFO, Canadian Science Advisory Secretariat, St. John's, Newfoundland.
- Brenton, C. 1979. Walrus. Pages 55-57 in Mammals in the seas. Volume II Pinniped Species Summaries and Report on Sirenians. FAO, Rome.
- Brown, R.G.B., Barker, S.P., Gaskin, D.E. and Sandeman, M.R. 1981. The Foods Of Great And Sooty Shearwaters *Puffinus gravis* And *Puffinus griseus* In Eastern Canadian Waters. Ibis 123 (1): 19-30.
- Bundy, A., Lilly, G. R. and Shelton, P. A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Canadian Technical Report of Fisheries and Aquatic Sciences 2310, 157 pp.
- Bundy, A. 2002. Adaptations of a Newfoundland-Labrador Ecopath model for 1985-1987 in statistical area 2J3KLNO to the area 2J3KL. Pages 13-21 in Pitcher, T.J., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1): 116 pp.
- Burke, C., Davoren, G.K., Montevecchi, W.A. and Stenhouse, I.J. 2002. Winging back to the future: An historic reconstruction of seabird diversity, distribution and abundance in the northwest Atlantic, 1500-2000. Pages 27-37 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Casey, J. M. and Myers, R. A. 2001. Community Changes in an Exploited Marine Ecosystem: Newfoundland Southern Grand Bank and St. Pierre Bank, 1951-1995. in ref??
- Christensen, V. and Pauly, D. 1992. A guide to the Ecopath II software system (version 2.1) ICLARM Software 6. 72 pp.
- Clay, D. and Clay, H. 1991. Determination of age and growth of white hake (*Urophycis tenuis* Mitchell) from the southern Gulf of St. Lawrence, Canada (including techniques for commercial sampling). Can. Tech. Rep. Fish. Aquat. Sci. 1828. 29pp.
- Dawe, E. G., Drew, H.J., Beck, P.C. and Veitch, P.J. 2000. Status of the Newfoundland and Labrador Snow Crab Resource in 1999. Stock Assessment Report 2000/121, Science, Oceans and Environment, DFO, Ottawa.
- Dawe, E. G., Hendrickson, L.C. and Showell, M.A. 2000. An update to commercial catch and survey indices for shortfinned squid (*Illex illecebrosus*) in the Northwest Atlantic for 1999. NAFO SCR Doc. 00/37.
- DFO. 1996a. Coastal Zone Species Profile Series No. 2 Rock Crab. in DFO Fisheries and Oceans Canada.
- DFO. 1996b. Coastal Zone Species Profile Series No. 3: Toad Crab. in DFO Fisheries and Oceans Canada.
- Dommasnes, A., Christensen, V., Ellertsen, B., Kvamme, C., Melle, W., Nøttestad, L., Pedersen, T., Tjelmeland, S. and Zeller, D. 2001. Ecosystem model for the Norwegian and Barents Seas. Pages 213-241 in S. Guénette, S., Christensen, V. and Pauly, D. (eds) Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4).
- Dorel, D. 1985. Poissons de l'Atlantique nord-est relations taille-poids. Institut Français de Recherche pour l'Exploitation de la Mer.
- Elvertowsky, J. 1964. Observations sur les poissons du genre *Sebastes* (Campagne océanographique de la 'Thalassa' en Juillet-Août 1962 dans l'Atlantique Nord-Ouest). Rev. Trav. Inst. Pêch. marit. 28(4):427-435.
- FAO. 1978. Mammals in the seas. Volume I: Report on the FAO Advisory Committee on Marine Resources Research. FAO Advisory Committee on Marine Resources Research Working Party on Marine Mammals, Rome.
- Ganong, W. F. 1904. The walrus in New Brunswick. Bulletin of the Natural History Society of New Brunswick II 5:240-241.
- Garavis, S. 1985. Lumpfish. Underwater World, Department of Fisheries and Oceans, St. John's Newfoundland, 4 pp.
- Gjosæter, J. and Kawaguchi, K. 1980. A review of the world resources of mesopelagic fish. FAO Fish. Tech. Pap. 193: 151 pp.
- Grant, R.F. 1934. The Canadian Atlantic Fishery. Ryerson Press, Toronto, 147 pp.
- Gosling, W.G. 1910. Labrador: its discovery, exploration and development. Alston Rivers Ltd., London.
- Grieve, S. 1885. The Great Auk or Garefowl. Jack, London.
- Hammill, M. O. and Stenson, G. B. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fisheries Science 26:1-23.
- Healey, B. P. and Stenson, G. B. 2000. Estimating pup production and population size of the Northwest Atlantic harp seal (*Phoca groenlandica*). Research Document 2000/081, Canadian Stock Assessment Secretariat, Ottawa.
- Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Science 53:943-962.
- Hutchings, J. A. and Myers, R. A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: An exploration of historical changes in exploitation, harvesting technology, and management. Pages 39-92 in Arnason, R. and Felt, L. (eds) The North Atlantic Fisheries: Successes, failures and challenges. The Institute of Island Studies, Charlottetown, Prince Edward Island.
- Kenchington, E. L. R., Prena, J., Gilkinson, K. D., Gordon, D. C. J., MacIsaac, K., Bourdonnais, C., Schwinghamer, P. J., Rowell, T. W., McKeown, D. L. and Vass, W. P. 2001. Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Canadian Journal of Fisheries and Aquatic Science 58: 1043-1057.
- Lien, J., Stenson, G. B. and Ni, H.I. 1988. A review of incidental entrapment of seabirds, seals, and whales in inshore fishing gear in Newfoundland and Labrador: A problem for fishermen and

- fishing gear designers. Pages 67-71 in World Symposium on Fishing Gear and Fishing Vessel Design. Marine Institute, St. John's, Newfoundland.
- Lilly, G. R. 2002. Swept area biomass estimates and diets of fish on the Newfoundland Shelf (NAFO Div. 2J3KLNO): inputs for bulk (Ecopath) modelling of the mid-1980s and late 1990s. Canadian Technical Report of Fisheries and Aquatic Sciences (in prep).
- Lovrich, G. A. and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *Journal of Experimental Marine Biology and Ecology* 211:225-245.
- Mari, A. and Dominguez, R. 1979. Distribucion, edad y crecimiento de la merluza plateada (*Merluccius bilinearis*) en la plataforma de Nueva Escocia. *Rev. Cub. Inv. Pesq.* 4:78-106.
- Masters, D.C. 1969. Reciprocity, 1846-1911. Historical Booklet No. 12, The Canadian Historical Association, Ottawa.
- Mercer, M. C. 1967. Records of the Atlantic Walrus, *Odobenus rosmarus rosmarus*, from Newfoundland. *Journal of the Fisheries Research Board of Canada* 24:2631-2635.
- Montevecchi, W. A. 2001. Interactions between fisheries and seabirds. Pages 527-557 in Schreiber, E.A. and Burger, J. (eds) *Biology of Marine Birds*. CRC Press, Boca Ranton.
- Montevecchi, W. A. and Tuck, L. M. 1987. Newfoundland Birds: Exploitation, study, conservation. Nuttall Ornithological Club, Cambridge, Massachusetts.
- Myers, R. A. and Cadigan, N. G. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? *Canadian Journal of Fisheries and Aquatic Science* 52:1274-1285.
- Myers, R. A., Hutchings, J. A. and Barrowman, N. J. 1997b. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7:91-106.
- Nammack, M.J., Musick, J.A. and Colvocoresses, J.A. 1985. Life history of spiny dogfish off the northeastern United States. *Trans. Am. Fish. Soc.* 114:367-376.
- O'Driscoll, R. L., Schneider, D. C., Rose, G. A. and Lilly, G. R. 2000. Potential contact statistics for measuring scale-dependent spatial pattern and association: an example of northern cod (*Gadus morhua*) and capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Science* 57:1355-1368.
- Parsons, D. G., Veitch, P. J., Orr, D. and Evans, G. T. 2000. Assessment of northern shrimp (*Pandalus borealis*) off Baffin Island, Labrador and northeastern Newfoundland. Research Document 2000/069, Canadian Stock Assessment Secretariat, Ottawa.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39: 175-192.
- Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature* 374: 255-257.
- Pitcher, T. J. 2001. Rebuilding ecosystems as a new goal for fisheries Management: Reconstructing the past to salvage the future. *Ecological Applications* 11(2): 601-617.
- Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) 2002. Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Pauly, D., Soriano-Bartz, M.L. and Palomares, M.L.D. 1993. Improved construction, parameterisation and interpretation of steady-state ecosystem models. Pages 1-13 in Christensen, V. and Pauly, D. (eds.) *Trophic models of aquatic ecosystems*. ICLARM Conf. Proc. 26.
- Pitt, T.K. 1975. Changes in the abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. *J. Fish. Res. Board Can.* 32(8):1383-1398.
- Prowse, D.W. 1972. A history of Newfoundland. Mika Studio Belleville, originally published by MacMillan and Co. London, 1895.
- Rose, G. A., deYoung, B., Kulka, D. W., Goddard, S. V. and Fletcher, G. L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. *Canadian Journal of Fisheries and Aquatic Science* 57:644-663.
- Rostlund, E. 1952. Freshwater fish and fishing in native North America. University of California Publications in Geography, Vol. 9. University of California Press, Berkeley.
- Shelton, P. A. and Stansbury, D. E. 2000. Northern cod recruitment before, during and after collapse. Research Document 2000/089, DFO, Canadian Science Advisory Secretariat, St. John's, Newfoundland.
- Stenson, G. and Hammill, M. 2002a. Harp seals, Page 40 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stenson, G. and Hammill, M. 2002b. Hooded seals, Pages 40-41 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stenson, G.B. and Sjare, B. 1997. Newfoundland hooded seal tag returns in the Northeast Atlantic. *Sci. Coun. Stud. NAFO.* 26: 115-118, Dec 1996.
- Stenson, G., Sjare, B. and Hammill, M. 2002. Whales and Porpoises. Page 39 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stevenson, S.C. and Baird, J.W. 1988. The fishery for lumpfish (*Cyclopterus lumpus*) in Newfoundland waters. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1595, 26 pp.
- Sumaila, R.S., Pitcher, T.J., Haggan, N. and Jones, R. 2001. Evaluating the Benefits from Restored

- Ecosystems: A Back to the Future Approach. Pages 1-7, Chapter 18 in Shriver, A.L. and Johnston, R.S. (eds) Proceedings of the 10th International Conference of the International Institute of Fisheries Economics and Trade, Corvallis, Oregon, USA, July, 2000. (on CD-ROM)
- Taggart, C. G., Anderson, J. T., Bishop, C. A., Colbourne, E. B., Hutchings, J. A., Lilly, G. R., Morgan, J., Murphy, E. F., Myers, R. A., Rose, G. A. and Shelton, P. A. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES marine Science Symposium 198: 140-157.
- Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A. and Blaber, S. J. M. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science 57: 531-547.
- Trites, A. W., Livingston, P. A., Mackinson, S., Vasconcellos, M., Springer, A. M. and Pauly, D. 1999. Ecosystem Changes and the Decline of Marine Mammals in the Eastern Bering Sea. Testing the Ecosystem Shift and Commercial Whaling Hypotheses. Fisheries Centre Research Reports 7(1), 106 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002a. Workshop notes on seabirds. Page 42 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Heymans, J.J. and Pitcher, T. 2002b. Historic reference points for models of past ecosystems in Newfoundland. Pages 7-13 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002c. Workshop notes on small piscivorous pelagic fish. Pages 54-55 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002d. Workshop notes on Northern Cod. Pages 43-45 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Walsh, D., Sjure, B. and Stenson, G. B. 2000. Preliminary estimates of Harp Seal by-catch in the Newfoundland Lumpfish fishery. Research Document 2000/078, Department of Fisheries and Oceans, Ottawa, 16 pp.
- Waring, G.T. 1984. Age, growth, and mortality of the little skate off the northeast coast of the United States. Trans. Am. Fish. Soc. 113: 314-321.
- Watson, R., Guénette, S., Fanning, P. and Pitcher, T.J. 2000. The Basis for Change 1: Reconstructing Fisheries Catch and Catch and Effort Ddata. Pages 23-39 in Pauly, D. and Pitcher, T.J. (eds) Methods for Evaluating the Impacts of Fisheries on North Atlantic Ecosystems. Fisheries Centre Research Reports 8(2), 195 pp.
- Wright, B. S. 1951. A walrus in the Bay of Fundy; the first record. The Canadian Field-Naturalist 65: 61-63.
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APPENDICES

APPENDIX A: MODEL GROUPS AND SPECIES IN NEWFOUNDLAND

#	Ecopath Group	Species
1	Walrus	<i>Odobenus rosmarus</i>
2	Cetaceans	Humpback whale (<i>Megaptera novaeangliae</i>), fin whale (<i>Balaenoptera physalus</i>), minke whale (<i>B. acutorostrata</i>), sei whale (<i>B. borealis</i>), blue whale (<i>B. musculus</i>) sperm whale (<i>Physeter catodon</i>), pilot whale (<i>Globicephala melaena</i>) and harbour porpoise (<i>Phocoena phocoena</i>)
3	Grey seals	<i>Halichoerus grypus</i>
4	Harp Seals	<i>Phoca groenlandica</i>
5	Hooded Seals	<i>Cystophora cristata</i>
6	Ducks	Common eider (<i>Somateria mollissima</i>), scoters (<i>Melanitta</i> spp.) and oldsquaws (<i>Clangula hyemalis</i>)
7	Piscivorous birds	Great auk (<i>Pinguinus impennis</i>), northern gannet (<i>Sula bassana</i>), great cormorants (<i>Phalacrocorax carbo</i>), double crested cormorant (<i>P. auritus</i>), herring gull (<i>Larus argentatus</i>) ring-billed gull (<i>L. delawarensis</i>) common black-headed gull (<i>L. ridibundus</i>), black-legged kittiwakes (<i>Rissa tridactyla</i>), common tern (<i>Sterna hirundo</i>), arctic tern (<i>S. paradisaea</i>), Caspian tern (<i>Sterna caspia</i>), common murre (<i>Uria aalge</i>), thick-billed murre (<i>U. lomvia</i>), black guillemot (<i>Cephus grylle</i>), razorbill (<i>Alca torda</i>) and Atlantic puffins (<i>Fratercula arctica</i>), northern fulmar (<i>Fulmarus glacialis</i>), Manx shearwater (<i>Puffinus puffinus</i>) greater shearwater (<i>Puffinus gravis</i>) and sooty shearwater (<i>P. griseus</i>)
8	Planktivorous birds	Leach's storm petrel (<i>Oceanodroma leucorhoa</i>) and dovekies (<i>Alle alle</i>)
9	Juvenile Cod > 35 cm	<i>Gadus morhua</i>
10	Adult Cod ≤ 35 cm	
11	American Plaice >35 cm	
12	American Plaice ≤35 cm	<i>Hippoglossoides platessoides</i>
13	Greenland Halibut > 40 cm	
14	Greenland Halibut ≤ 40 cm	<i>Reinhardtius hippoglossoides</i>
15	Yellowtail flounder	<i>Limanda ferruginea</i>
16	Witch flounder	<i>Glyptodentophalus cynoglossus</i>
17	Winter flounder	<i>Pseudopleuronectes americanus</i>
18	Skates	Barndoor (<i>Raja laevis</i>), thorny (<i>R. radiata</i>), smooth (<i>R. senta</i>), winter (<i>R. ocellata</i>) and little skate (<i>Leucoraja erinacea</i>)
19	Dogfish	<i>Squalus acanthias</i>
20	Redfish	Deepwater redfish (<i>Sebastes mentella</i>) and Acadian redfish (<i>S. fasciatus</i>)
21	Transient mackerel > 29cm	<i>Scomber scombrus</i>
22	Demersal and benthopelagic piscivores > 40 cm	White hake (<i>Urophycis tenuis</i>) silver hake (<i>Merluccius bilinearis</i>), monkfish (<i>Lophius americanus</i>), sea raven (<i>Hemitripterus americanus</i>), cusk (<i>Brosme brosme</i>) and Atlantic halibut (<i>Hippoglossus hippoglossus</i>)
23	Demersal and benthopelagic piscivores ≤ 40 cm	
24	Other large demersals > 30 cm	Haddock (<i>Melanogrammus aeglefinus</i>), longfin hake (<i>Phycis chesteri</i>) and red hake (<i>Urophycis chuss</i>), wolffish (<i>Anarhichas</i> spp.), grenadiers (<i>Coryphaenoides</i> spp.), eelpouts (<i>Lycodes</i> spp.) and batfishes (Ogcocephalidae)
25	Other large demersals ≤ 30 cm	
26	Small demersals	Rocklings (<i>Enchelyopus</i> spp.), gunnel (<i>Pholis gunnellus</i>), alligator fishes (<i>Ulcina olrikii</i>), Atlantic poachers (<i>Leptagonus decagonus</i>), snakeblennies (<i>Lumpenus lampretiformis</i>), shannies (<i>Leptoclinus</i> spp.), sculpin (<i>Myoxocephalus</i> spp.), searobins (<i>Prionotus</i> spp.), eelblennies (<i>Anisarchus</i> spp.)
27	Lumpfish	Lumpsuckers (<i>Cyclopterus lumpus</i>)
28	Greenland cod	<i>Gadus opac</i>
29	Atlantic salmon	<i>Salmo salar</i>
30	Capelin	<i>Mallotus villosus</i>
31	Sandlance	<i>Ammodytes dubius</i>
32	Arctic cod	<i>Boreogadus saida</i>
33	Herring	<i>Clupea harengus harengus</i>
34	Transient pelagics	Bluefin tuna (<i>Thunnus thynnus</i>), swordfish (<i>Xiphias gladius</i>), porbeagle (<i>Lamna nasus</i>), basking shark (<i>Cetorhinus maximus</i>) and other sharks (Elasmobranchii).
35	Small pelagics	Shad (<i>Alosa sapidissima</i>), butterfish (<i>Peprilus triacanthus</i>), argentine (<i>Argentina silus</i>), juvenile mackerel (<i>Scomber scombrus</i>) and Atlantic rainbow smelt (<i>Osmerus mordax mordax</i>)
36	Small mesopelagics	Laternfishes (Myctophidae), pearlsides (<i>Maurollicus muelleri</i>) and barracudinas (<i>Paralepis elongata</i>)

#	Ecopath Group	Species
37	Shortfin squid	<i>Illex illecebrosus</i>
38	Arctic squid	<i>Gonatus</i> spp.
39	Large crabs (> 95 mm CW)	Snow crab (<i>Chionoecetes opilio</i>), jonah crabs (<i>Cancer borealis</i>), red crabs (<i>Chaceon quinque-dens</i>) and northern stone crabs (<i>Lithodes maia</i>)
40	Small crabs (≤ 95 mm)	Toad crabs (<i>Hyas areneus</i> and <i>H. coarctatus</i>), hermit crabs (<i>Pagurus</i> spp.), rock crabs (<i>Cancer irroratus</i>) and juveniles of large crabs
41	American lobster	<i>Lomarus americanus</i>
42	Shrimps	Northern shrimp (<i>Pandalus borealis</i>) and deep water shrimp (<i>Pandalus montagui</i>)
43	Echinoderms	Sea urchin (<i>Strongylocentrotus pallidus</i>), sand dollars (<i>Echinarachnius parma</i>) and others
44	Polycheates	<i>Prionospio steenstrupi</i> and others
45	Bivalves	Sea scallops (<i>Placopecten magellanicus</i>), Icelandic scallop (<i>Chlamys islandicus</i>), propeller clams (<i>Cyrtodaria siliqua</i>), chalky macoma (<i>Macoma calcarea</i>) and others
46	Other benthic invertebrates	Brittlestar (<i>Ophiura sarsi</i>) and others
47	Large zooplankton	Euphausiids, Chaetognaths, hyperiid amphipods, Cnidarians and Ctenophores (jellyfish), mysids, tunicates >5 mm and ichthyoplankton
48	Small zooplankton	Copepods (<i>Calanus finmarchicus</i> and <i>Oithona similis</i>), tunicates < 5 mm and meroplankton
49	Phytoplankton	Diatoms (<i>Cahetoceros decipiens</i> , <i>Thalassiosira</i> spp.) and others
50	Detritus	

Appendix B, Table 1. (continued)

	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
1																
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10		0.0010			0.2150											
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17																
18																
19																
20		0.0020														
21																
22																
23		0.0120			0.0003											
24																
25		0.0120			0.0003											
26		0.0110			0.0003											
27		0.0000														
28		0.0010														
29																
30		0.0750		0.0100	0.3590											
31		0.0860			0.1260											
32					0.0030											
33		0.1150			0.0580											
34																
35		0.1150														
36		0.1150		0.0500	0.0290											
37		0.0565														
38		0.0565		0.0400	0.0290											
39																
40							0.0010		0.0100							
41																
42		0.0120					0.0200	0.0500	0.0200							
43							0.3030	0.0500	0.3000							
44		0.0030					0.3030	0.1000	0.3000	0.0150						
45							0.1200	0.2500	0.1200							
46	0.1000	0.0190					0.1200	0.1500	0.1200	0.0150						
47	0.5130	0.2950	0.7500	0.4500	0.1800	0.5000	0.0200	0.2000	0.0200	0.1200					0.0500	
48	0.3870	0.0130	0.2500	0.4500		0.5000	0.0100	0.1500	0.0100	0.2400					0.4800	
49										0.0850					0.3700	1.0000
50							0.1030	0.0500	0.1000	0.5250	1.0000	1.0000	1.0000	1.0000	0.1000	

APPENDIX C: BALANCED MODEL AND DIET MATRIX 1995-1997*Input parameters of the balanced 1995-1997 model (values in bold are estimated by Ecopath).*

Group name	Trophic level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.30	0.000001	0.060	16.846	0.000	0.004
Cetaceans	3.86	0.251	0.100	11.742	0.002	0.009
Grey seals	4.34	0.000001	0.060	15.000	0.281	0.004
Harp Seals	4.13	0.405	0.102	17.412	0.432	0.006
Hooded Seals	4.39	0.062	0.109	13.100	0.283	0.008
Ducks	3.00	0.000227	0.250	54.750	0.247	0.005
Piscivorous Birds	4.19	0.013	0.250	54.750	0.352	0.005
Planktivorous Birds	3.30	0.003	0.250	54.750	0.241	0.005
Adult Cod > 40cm	4.04	0.181	0.300	3.240	0.950	0.093
Juv Cod ≤ 40 cm	3.73	0.198	1.600	6.090	0.950	0.263
American plaice >35cm	3.38	0.954	0.088	2.000	0.950	0.044
American plaice ≤35cm	3.54	0.850	0.400	3.736	0.950	0.107
Greenland halibut >65cm	4.28	0.750	0.098	1.478	0.950	0.066
Greenland halibut ≤ 65 cm	4.11	1.082	0.397	4.480	0.950	0.089
Yellowtail Flounders	3.10	0.330	0.319	3.600	0.507	0.089
Witch flounder	3.02	0.471	0.348	2.304	0.950	0.151
Winter flounder	3.01	1.302	0.267	1.644	0.950	0.163
Skates	4.11	0.208	0.320	2.878	0.424	0.111
Dogfish	3.87	0.017	0.194	4.770	0.950	0.041
Redfish	3.51	1.472	0.148	2.000	0.950	0.074
Transient Mackerel (>29cm)	3.77	0.004	0.290	4.400	0.950	0.066
Large demersal piscivores (> 40 cm)	4.20	0.023	0.206	1.107	0.950	0.186
Large demersal piscivores (≤ 40cm)	3.63	0.968	0.147	1.660	0.950	0.088
Large Demersal Feeders (> 30cm)	3.24	0.265	0.229	1.386	0.950	0.166
Small demersal feeders	3.12	8.381	0.232	2.079	0.950	0.112
Other small demersals	3.09	0.580	0.564	4.474	0.950	0.126
Lumpfish	3.38	0.039	0.116	1.374	0.950	0.084
Greenland cod	3.96	0.002	0.594	1.265	0.950	0.470
Salmon	4.14	0.009	0.614	4.093	0.950	0.150
Capelin	3.15	5.443	1.150	4.300	0.950	0.267
Sandlance	3.13	4.302	0.620	7.670	0.950	0.081
Arctic cod	3.25	1.408	0.573	2.633	0.950	0.218
Herring	3.14	3.365	0.541	4.131	0.950	0.131
Transient Pelagics	3.91	0.041	0.400	3.333	0.950	0.120
Small Pelagics	3.19	9.688	0.638	5.291	0.950	0.121
Small Mesopelagics	3.21	2.036	1.422	4.789	0.950	0.297
Shortfin squid	3.95	1.101	0.600	4.000	0.950	0.150
Arctic Squid	3.09	4.127	0.500	3.333	0.950	0.150
Large Crabs (>95 cm)	2.91	0.179	0.380	4.420	0.989	0.086
Small Crabs (≤ 95 cm)	3.03	0.081	0.630	4.420	0.950	0.143
Lobster	2.93	0.003	0.380	4.420	0.950	0.086
Shrimp	2.43	1.104	1.450	9.670	0.914	0.150
Echinoderms	2.00	112.300	0.600	6.670	0.140	0.090
Polychaetes	2.00	10.500	2.000	6.330	0.236	0.316
Bivalves	2.00	42.100	0.570	22.220	0.066	0.026
Other benthic invertebrates	2.00	7.800	2.500	12.500	0.552	0.200
Large zooplankton	2.31	25.722	3.433	19.500	0.950	0.176
Small zooplankton	2.00	30.367	8.400	20.670	0.903	0.406
Phytoplankton	1.00	47.887	93.100	-	0.207	-
Detritus	1.00	412.176	-	-	0.420	-

1995-1997 diet continued...

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	
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23					0.0120			0.0008												
24																				
25					0.0120			0.0008												
26					0.0110			0.0008												
27																				
28					0.0010															
29					0.0010															
30	0.005		0.038		0.0749		0.01	0.0101												
31	0.005				0.0859			0.0101												
32			0.002					0.0093												
33					0.1149			0.1717												
34																				
35					0.1149			0.3673												
36					0.1149		0.05	0.0859												
37					0.0569															
38					0.0569		0.04	0.0859												
39																				
40										0.001		0.01								
41																				
42					0.0120					0.020	0.05	0.02								
43										0.303	0.05	0.30								
44					0.0030					0.303	0.10	0.30	0.015							
45										0.120	0.25	0.12								
46				0.1127	0.0190					0.120	0.15	0.12	0.015							
47	0.439	0.4	0.640	0.4510	0.2947	0.6	0.30	0.2572	0.3	0.020	0.20	0.02	0.120						0.01	
48	0.551	0.6	0.320	0.4363	0.0130	0.4	0.60		0.7	0.010	0.15	0.01	0.240						0.30	
49													0.085						0.59	1.0
50										0.103	0.05	0.10	0.525	1.0	1.0	1.0	1.0	0.10		

APPENDIX D: BALANCED MODEL AND DIET MATRIX 1985-1987*Input parameters of the balanced 1985-87 model (values in bold are estimated by Ecopath).*

Group name	Trophic level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.32	0.000001	0.060	16.846	0.000	0.004
Cetaceans	4.11	0.251	0.100	11.794	0.000	0.009
Grey seals	4.45	0.000001	0.060	16.000	0.281	0.004
Harp Seals	4.24	0.184	0.102	17.412	0.161	0.006
Hooded Seals	4.78	0.034	0.109	13.100	0.048	0.008
Ducks	3.00	0.0002	0.250	54.750	0.333	0.005
Piscivorous Birds	4.28	0.010	0.250	54.750	0.409	0.005
Planktivorous Birds	3.53	0.002	0.250	54.750	0.325	0.005
Adult Cod > 40cm	4.16	1.811	0.404	3.240	0.777	0.125
Juv Cod ≤ 40 cm	3.86	0.302	1.600	6.090	0.943	0.263
American plaice >35cm	3.66	0.722	0.224	2.000	0.844	0.112
American plaice ≤35cm	3.68	0.773	0.630	3.740	0.950	0.168
Greenland halibut >65cm	4.53	0.361	0.300	1.480	0.950	0.203
Greenland halibut ≤ 65 cm	4.23	0.474	0.870	4.480	0.746	0.194
Yellowtail Flounders	3.12	0.214	0.534	3.600	0.950	0.148
Witch flounder	3.02	0.550	0.588	2.305	0.950	0.255
Winter flounder	3.08	0.048	0.267	1.644	0.950	0.163
Skates	4.24	0.235	0.361	2.878	0.520	0.125
Dogfish	4.01	0.018	0.193	4.770	0.950	0.041
Redfish	3.68	1.450	0.489	2.000	0.950	0.245
Transient Mackerel (>29cm)	3.85	0.373	0.300	4.400	0.166	0.068
Large demersal piscivores (> 40 cm)	4.34	0.124	0.617	4.111	0.950	0.150
Large demersal piscivores (≤ 40cm)	3.97	3.257	0.147	1.400	0.950	0.105
Large Demersal Feeders (> 30cm)	3.36	0.416	0.272	1.747	0.950	0.156
Small demersal feeders	3.28	3.698	0.232	2.000	0.950	0.116
Other small demersals	3.11	1.189	0.564	4.500	0.950	0.125
Lumpfish	3.59	0.225	0.114	1.400	0.950	0.082
Greenland cod	4.04	0.103	0.166	1.300	0.950	0.128
Salmon	4.26	0.013	0.614	4.093	0.950	0.150
Capelin	3.26	12.977	1.150	4.300	0.950	0.267
Sandlance	3.20	2.614	1.150	7.667	0.950	0.150
Arctic cod	3.41	2.319	0.400	2.633	0.950	0.152
Herring	3.29	1.254	0.544	4.100	0.950	0.133
Transient Pelagics	4.08	0.012	0.400	1.990	0.950	0.201
Small Pelagics	3.42	0.521	0.638	1.767	0.950	0.361
Small Mesopelagics	3.38	1.164	1.422	4.789	0.950	0.297
Shortfin squid	4.06	0.519	0.600	4.000	0.950	0.150
Arctic Squid	3.28	1.507	0.500	3.333	0.950	0.150
Large Crabs (>95 cm)	2.92	0.174	0.380	4.420	0.277	0.086
Small Crabs (≤ 95 cm)	3.08	4.758	0.380	4.420	0.950	0.086
Lobster	2.93	0.005	0.380	4.420	0.959	0.086
Shrimp	2.46	2.363	1.450	9.667	0.950	0.150
Echinoderms	2.00	112.300	0.600	6.667	0.082	0.090
Polychaetes	2.00	10.500	2.000	22.222	0.296	0.090
Bivalves	2.00	42.100	0.570	6.333	0.258	0.090
Other benthic invertebrates	2.00	7.800	2.500	12.500	0.543	0.200
Large zooplankton	2.56	24.834	3.433	19.500	0.950	0.176
Small zooplankton	2.00	36.997	8.400	20.667	0.950	0.406
Phytoplankton	1.00	26.860	93.100	-	0.378	-
Detritus	1.00	389.000	-	-	0.629	-

1985-1987 diet continued...

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	
1																				
2																				
3																				
4																				
5																				
6																				
7																				
8																				
9																				
10					0.001			0.001												
11																				
12																				
13																				
14																				
15																				
16																				
17																				
18																				
19																				
20					0.002															
21																				
22																				
23					0.012			0.001												
24																				
25					0.012			0.001												
26					0.011			0.001												
27																				
28					0.001															
29					0.001															
30	0.01		0.04		0.075		0.010	0.478												
31	0.01				0.086			0.016												
32			0.00					0.004												
33					0.115			0.098												
34																				
35					0.115															
36					0.115		0.050	0.049												
37					0.056															
38					0.056		0.040	0.049												
39																				
40										0.001		0.01								
41																				
42					0.012					0.020	0.05	0.02								
43										0.303	0.05	0.30								
44					0.003					0.303	0.10	0.30	0.02							
45										0.120	0.25	0.12								
46				0.10	0.019					0.120	0.15	0.12	0.02							
47	0.44	0.35	0.64	0.51	0.295	0.750	0.450	0.304	0.500	0.020	0.20	0.02	0.12						0.05	
48	0.55	0.65	0.32	0.39	0.013	0.250	0.450		0.500	0.010	0.15	0.01	0.24						0.48	
49													0.09						0.37	1.00
50										0.103	0.05	0.10	0.53	1.00	1.00	1.00	1.00	0.10		

A PICASSO-ESQUE VIEW OF THE MARINE ECOSYSTEM OF NEWFOUNDLAND AND SOUTHERN LABRADOR: MODELS FOR THE TIME PERIODS 1450 AND 1900

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INTRODUCTION

The marine ecosystem of Newfoundland and southern Labrador (2J3KLNO) has probably changed more over the past 500 years than can ever be captured. This description of the Newfoundland system therefore becomes more abstract (i.e. more like a Picasso painting) as we go back in time. One could expect that the 1990s and 1980s models described in Heymans and Pitcher (*this volume*) would be a close proximity to the true ecosystem. The 1900s and 1450s models, however, are less certain, although a great deal of information from historical, archival and archaeological sources has been incorporated in as objective a fashion as possible. As one would expect, scientific information available for constructing the 1900 and 1450 models was not forthcoming, and it was therefore necessary to use any historical information available to us, even if it was taken from secondary sources. We did not have resources to use professional help from historians or archivists to verify material from secondary sources.

The effect of anthropogenic changes on this ecosystem was probably noticeable as soon as the Basque whalers arrived (Dunfield 1985). Before the early 1900s, represented by the second model, 1900-1905, the great auk, walrus and grey seals were effectively extinct, with many cetaceans also following the same path. The effects of the cod fishery were noticeable from around the early 1700s with local extinctions of the inshore stocks (Dunfield 1985), when the English bank fishery started (Anon. 2000a). However, the most noticeable changes were probably seen subsequent to the start of the trawl fishery on the Grand Banks in 1948 (Andersen 1998). The changes in the ecosystem over the past fifty year period, which is probably known better than any time, are myriad: large changes in the groundfish community occurred from the 1950s to the 1970s on the Grand Banks (Casey and Myers 2001). The reduction in the biomass of major species (cod and haddock) fundamentally changed the groundfish community structure and reduced the total species biomass by 90% from the 1950s to the 1990s (Casey and Myers 2001). During this

decrease in gadoid biomass on the southern Grand Bank, flatfish biomass increased and dominated from the late 1960s into the early 1980s. Biomass of Atlantic cod, haddock and white hake was greatest in the 1950s, with cod and haddock being equally abundant. Redfish biomass has increased on the southern Grand Banks in the 1980s, but decreased overall since the 1950s (Casey and Myers 2001).

The objective of this paper is to attempt to give a quantitative description of the marine ecosystem of Newfoundland and southern Labrador (2J3KLNO) as it was in 1900 and in 1450. These models will be used in simulations of the ecosystem over time and exploration of alternative sustainable fisheries options for the *Back to the Future* project (Pitcher 2001).

The models consist of 50 compartments: 48 consumers, one primary producer (phytoplankton) and one detritus group. In some cases, groups have gone extinct (walrus and grey whales), and we have kept these compartments in the models (with very low biomass estimates) for comparison between them. In most compartments the diet composition was taken to be the same as the 1980s diet composition given in Heymans and Pitcher (*this volume*).

MODEL DESCRIPTION BY GROUP

1) Walrus

In glacial times the walrus was found as far south as the coast of Virginia, while at the time of the discovery of America by Europeans, their distribution did not come further south than Massachusetts Bay and in colonial times their most southern breeding ground was Sable Island off Nova Scotia (Allen 1942). According to Mowat (1984 p. 308) walrus existed in untold numbers as far south as Cape Cod on the Atlantic shores prior to European contact. Loring (1992) suggested that walrus were once fairly prolific along the Labrador coast and were present in small sociable groups concentrated at favored hauling-out places. In the past century only five walrus (*Odobenus rosmarus*, Linnaeus) have been recorded in the 2J3KLNO area: two in 1949 and three in 1967 (Mercer 1967). In 1904 Ganong (Ganong 1904) reported that they do not occur further south than Labrador and in 1951 (Wright 1951) suggested that they are not found south of Hudson Strait anymore. However, Reeks (1871 p. 2550) found that:

From the quantity of "tusks" picked up on the coasts of Newfoundland, the walrus must

have been an inhabitant of the island, or perhaps, like the harp seal, migrated thither on the drift-ice.

Mowat (1984 p. 311) suggested that the Central Gulf herd numbered at least a quarter of a million individuals (300,000 tonnes of wet mass) when Europeans first came upon it. Additionally, the Seal Conservation Society reports that the Atlantic walrus has not been able to recover and is still well below its pre-exploitation level of several hundred thousand (Anon. 2001a).

For our pre-contact model it was assumed that the Atlantic herd was something more than that of the Sable Island herd (100,000 as reported by Mowat 1984 p. 304) and less than the Central Gulf herd (1/4 million as reported by Mowat 1984 p. 311). An abundance of 125,000 walrus was therefore estimated. Brenton (1979) estimated the average weight for male and female walrus to be 1,200 kg and 750 kg respectively. With an average weight of 750 kg the biomass of walrus in 2J3KLNO was estimated at $0.25 \text{ t}\cdot\text{km}^{-2}$. Biomass in the 1900 model was assumed to be very low ($0.000001 \text{ t}\cdot\text{km}^{-2}$) as we had to have some estimate of biomass in the model even though they were not really present. The P/B ratio of 0.06 yr^{-1} , obtained from walrus in the Bering Sea model (Trites *et al.* 1999) was used. According to FAO (1978) they consume 45 kg of food per day, which gives a Q/B of 16.8 yr^{-1} . First Nations were assumed to have caught walrus; it was assumed that part of the 20% of First Nations diet attributed to seals consisted of walrus (Heymans 2002). Thus we assume that $0.020 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ was caught by First Nations. Catches of walrus were not made in any of the subsequent time periods.

Walrus live to be at least 40 years of age and are preyed upon by polar bears and killer whales (Anon. 2001a). They are mostly found in shallow continental shelf waters, usually less than 100m deep, and they feed mostly on invertebrates that live in or on the bottom sediments (Anon. 2001a). Brenton (1979) suggests that 65 species of benthic invertebrates, principally mollusks, echinoderms, tunicates, crustaceans, priapulids and echiuroids are consumed, and the Seal Conservation Society and Allen (1942) report that their diet occasionally includes seals and rarely fish. In the Bering Sea, seal eating was 10 to 100 times more common during the 1970s and early 1980s than during the previous three decades, due to the greater overlap in their distribution during that time (Lowry and Fay 1984). The diet of walrus in the Bering Sea model (Trites *et al.* 1999) was adapted for this ecosystem in the 1980s and 1990s models.

2) Cetaceans

Cetaceans were the main draw to the coasts of Newfoundland for Basque fishermen. By the mid-1500s most of the train oil extracted from seals, walrus, whales and seabirds was used as fuel for lamps and as sources for lubricants, leather and jute processing, while cooking oil came from right whales harvested in Newfoundland, Labrador and the Gulf of St. Lawrence (Vasconcellos *et al.* 2002b). Cartier (Dunfield 1985) reported on the abundance of porpoises in the Gulf in the mid-1530s and, as long as the First Nations and Europeans only used them for food, their populations remained unaffected. In one of the notes on the drawings made by Shanawdithit, written by Mr. W.E. Cormack in 1829, reference was made to the bottlenose whales that frequented the Northern Bays, and how it was considered good luck for them to be killed by "Red Indians" (Howley 1915).

Stenson *et al.* (2002) suggest that the biomass of whales in the 1900s was probably twice that of the present time period, or $0.502 \text{ t}\cdot\text{km}^{-2}$. For the 1500s model, the biomass of whales was estimated by assuming an ecotrophic efficiency of 95%. The P/B and Q/B estimates for cetaceans given by Bundy *et al.* (2000) were used in both models, although the P/B of the 1900s should probably be higher (whaling pressure was high) and the Q/B could be lower in the 1500s and 1900s models due to the larger individuals present in the populations at that time. The diet estimates made for the 1985-87 model by Bundy *et al.* (2000) were adapted for the new model groupings in Heymans and Pitcher (*this volume*).

Cushing (1988) suggested that the early settlers probably observed Indian methods of whaling. They attacked right whales from small boats close to shore, dragged them ashore and cut them up there, although some initial cutting was done at sea (Cushing 1988 p. 138). Sixteenth-century records showed that the combined Basque whaling fleet consisted of between 40 and 120 vessels in any given year and the fleet landed about 2,300 whales annually (Mowat 1984 p. 216). Add 20% to incorporate struck-and-lost mortality and calves that starved to death, and an estimate of 2,500 whales a year is reached for the time period 1515-1560 (Mowat 1984 p. 216). The average weight of adult black right whales was about 80-100 tonnes (FAO 1978). If we assume that the catch on the east coast was small compared to that of the Gulf of St. Lawrence (ca. 10% of the catch from 2J3KLNO), and if the lower end of the weight range (80 tonnes) is used, the catch in the 1500s is estimated at $0.04 \text{ t}\cdot\text{km}^{-2}$.

$2 \cdot \text{yr}^{-1}$. This is similar to the total North Atlantic Basque catch of 300-500 right whales ($0.06 \text{ t} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) estimated for 1530-1610 by Reeves *et al.* (1999). However, the pre-contact catch by Basque fishermen was probably much smaller and here it is assumed that catches were 10% of the estimated catch in 1515-1560, or $0.004 \text{ t} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$. The catch of whales by First Nations was estimated at $0.001 \text{ kg} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$ (Heymans 2002). The catch of whales from 1900 to 1905 ($0.04 \text{ t} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) was estimated from numbers given by Sanger *et al.* (1998) (Table 1) and using average mean body weight (32 tonnes) for rorquals (humpbacks, fin, minke, sei and blue whales) given in Bundy *et al.* (2000).

Table 1: Catch estimates of whales in Newfoundland from 1900-1905 (source: Sanger *et al.* 1998).

Year	Number of rorquals caught
1900	200
1901	250
1902	450
1903	850
1904	1300
1905	900
Average	658

3-5) Seals

Several kinds of seals frequented the northwestern approaches when the European invasion began. Four were pre-eminent: hood, harp, harbour and grey seals. Hoods and harps were the most numerous, but were only present during the winter and early spring, when the Europeans were not there. Grey and harbour seals were available year round (Mowat 1984 p. 325). Grey seals were abundant along the Atlantic coast of North America at first contact (Mowat 1984 p. 328) and gathered in January and February in enormous numbers on the islands and mainland beaches from Labrador to Cape Hatteras to whelp and breed. During the rest of the year they stayed together in inshore waters to fish together and hauled out to sun themselves on bars in salt-water lagoons and river mouths (Mowat 1984 p. 325).

3) Grey seals

Over 200 grey seal whelping rookeries originally existed between Cape Hatteras and Hamilton Inlet on the Labrador coast (NAFO area 2J) and that the total population probably totaled between 750,000 and 1,000,000 seals. Some of these rookeries were still producing 2,000 pups a year as late as the 1850s (Mowat 1984 p. 331). The average weight of a grey seal is about 220 kg (Hammill and Stenson 2000). The study area (2J3KLNO) is approximately a third of the total

area of the population, but there were probably not as many rookeries on the Atlantic coast as in the Gulf of St. Lawrence. Thus we assumed that about $1/5^{\text{th}}$ of the population, or $0.08 \text{ t} \cdot \text{km}^{-2}$, was in 2J3KLNO. For the 1900s a very small biomass of $0.000001 \text{ t} \cdot \text{km}^{-2}$ was assumed.

The P/B ratio of 0.06 yr^{-1} for seals in the Bering Sea model (Trites *et al.* 1999) was used for grey seals in all four models. Dommasnes *et al.* (2001) and Trites *et al.* (1999) estimated a Q/B ratio for grey seals in the Norwegian and Bering Seas of 15.0 and 15.93 yr^{-1} respectively. We used 15.0 yr^{-1} as a Q/B ratio for grey seals in Newfoundland. The diet of grey seals was adapted from Hammill and Stenson (2000) by Heymans and Pitcher (*this volume*).

4) Harp Seals

Mowat (1984 p. 347) records that a whelping patch off the southeast coast of Labrador in 1844 was estimated to be at least 50 miles long and 20 miles broad, and contained about 5 million seals. If we assume that this patch was similar to the whelping patch of Newfoundland in pre-contact times, we could use this as an estimate of harp seals in 2J3KLNO. However, by 1844 between 100,000 and 500,000 seals had been exported from Newfoundland annually (Sanger 1998) thus the biomass was probably much larger, and it was assumed that the biomass was double that in pre-contact times. Using an average weight of 130 kg (Anon. 2000b) and assuming that they only stay in the area $1/2$ the time, the pre-contact biomass was estimated at $1.3 \text{ t} \cdot \text{km}^{-2}$. Stenson and Hammill (2002a) suggest that the total harp seal population in the North Atlantic was probably between 6 and 12 million animals in the early 1900s. At an average weight of 130 kg (Anon. 2000b), assuming that the population in the Newfoundland-Labrador area is $1/4$ of the total population gives a biomass of $0.591 \text{ t} \cdot \text{km}^{-2}$. The P/B and Q/B ratios of 0.102 and 17.412 yr^{-1} , respectively, were obtained from Bundy *et al.* (2000). Diet of harp seals obtained from Stenson (*pers. comm.*, see Heymans and Pitcher, *this volume*) for 1985-1987 was used as the diet of seals in both 1900s and 1500s models.

5) Hooded Seals

Stenson and Hammill (2002b) suggest the biomass of hooded seals in the early 1900s was probably approximately 3 times the mid-1980s value, or $0.102 \text{ t} \cdot \text{km}^{-2}$. Mowat (1984 p.359) suggested that although hooded seals were never as abundant as harps, they may not have been far inferior in terms of biomass. It was assumed that

the pre-contact biomass of hooded seals was in the same ratio as that of the 1900s, thus the biomass of hooded seals pre-contact was approximately $0.26 \text{ t}\cdot\text{km}^{-2}$. The P/B and Q/B ratios of 0.109 and 13.1 yr^{-1} , respectively, obtained from Bundy *et al.* (2000) were used in both models. Diets were obtained from Hammill and Stenson (2000) and adapted for the groups in this model in the 1980s and 1990s (see Heymans and Pitcher, *this volume*).

Seal catches

All of the First Nations that lived in Newfoundland and Labrador relied on seals to a greater or lesser extent. To the Labrador Inuit in particular, the seal was until recently a staple component of a way of life largely adapted to local resources. The meat was eaten or fed to the dogs; the fat was rendered into oil for light and food; the skin was used for clothing, boots and a myriad of other purposes besides trade with European merchants (Hiller 2001). Natives used salmon nets with every other mesh cut away to catch seals (Dunfield 1985). Marshall (*pers. comm.*) suggests that seals probably made up 10% of the diet of Beothuk (or 20% of the diet of Beothuk and Inuit, both present in the area in pre-contact times). Thus, First Nations catches of seals in pre-contact times were estimated at $0.010 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ of grey seals and $0.120 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ of harp seals, based on their biomass ratio (Heymans 2002).

There is less traditional knowledge available for hooded seals as compared to harps because hooded seals are distributed further offshore and are not seen as often by coastal fishermen. This is also why it is assumed that there was no catch of hooded seals by First Nations. The catch statistics for hooded seals have been comprehensive since the 1950s. However, historic data from 1900 to 1950 are not as good as for harp seals, and the information available is summarized with harp seal data (Stenson and Hammill 2002b). The main problem is that for these early time periods hooded seals were not separated from harps in the statistics. According to Mowat (1984 p. 359), sealers took few hooded seals until well into the 19th century. The animals were too big and powerful to be held by nets and too tough to kill in open water with the firearms available.

Ryan (1994) gave the total number of seals exported from Newfoundland from 1861 to 1914. The average number exported from 1900 to 1905 was 326,648 and includes harp and hooded seals, of which both adults and juveniles were taken. Of the total catch, approximately 75% were probably taken from the 2J3KLNO population (Stenson,

pers. comm.). Estimates of the proportion of harp and hooded seal adults and juveniles in the catches were obtained from Anon (1970) for 1937 to 1947 (Table 2), and used to calculate the proportions of adults and young seals caught in the 1900s. The average weights of juvenile and adult harp seals are approximately 32.5 kg and 100 kg respectively, and those of hooded seals are approximately 37.5 kg and 220 kg respectively (Hammill and Stenson 2000). Thus, the total catches of harp and hooded seals in 1900-1905 were probably around $0.017 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ and $0.002 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$, respectively.

Table 2. Numbers of adult and juvenile harp and hooded seals caught from 1937 to 1947 (source: Anon. 1970).

Year	Young Harps	Adult Harps	Young Hoods	Adult Hoods
1937	2796	898	6	15
1938	221297	21341	300	116
1939	102109	25798	2308	315
1940	132360	26188	961	178
1941	16636	25654	272	104
1942	1723	2032	927	16
1943	?	?	?	?
1944	6360	25693	167	92
1945	9516	35432	4	8
1946	73000	29562	5171	734
1947	102294	74215	1851	2784
Average (%) Catch	56.8	39.9	2.9	0.4
($\text{t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$)	0.0091	0.0074	0.0015	0.0004

6-8) Seabirds

Mowat (1984 p. 75) suggested that two dozen species of ducks originally lived in or migrated through the northeastern region and were found in astounding numbers. Most species remained relatively numerous until the beginning of the 19th century after which they were over-exploited for market hunting. Canada, snow and brant geese abounded along the northeastern coasts (Mowat 1984 p. 75). Great auk rookeries were likely few in number, as with current auks, and at times huge (e.g. Funk Island) (Montevicchi and Kirk 1996). The Atlantic coast of Labrador was probably not favored for great auk breeding grounds as it had too much pack ice during the summer season (Mowat 1984 p. 26).

The common and thick-billed murre combined were probably the most numerous seabirds in North America when Europeans first arrived (Mowat 1984 p. 47). Two species of cormorant, the great and the double-crested, formerly bred along the coast from mid-Labrador southward and beside freshwater lakes and rivers (Mowat 1984 p. 45). They were exceedingly abundant and remained so into the 17th century because

Europeans considered them unfit for food, but the bait fishery put an end to their protection (Mowat 1984 p. 45). Four species of terns once bred in colonies on islands, beaches and sandbars in both fresh and salt water throughout the Atlantic seaboard. Terns were only utilized from the middle of the 19th century when feather hunters started exploiting their colonies (Mowat 1984 p. 46). Of the planktivorous species, Leach's storm petrels once bred in enormous numbers on islands and headlands south at least to Cape Cod, but the encroachments of modern man and his associated animals have deprived them of most of their one-time rookeries (Mowat 1984 p. 44), except in Newfoundland where the world's largest colonies are located (Montevecchi and Tuck 1987; Cairns *et al.* 1989).

In contrast to cormorants, storm-petrels, terns and the auk, most gull species benefited enormously from recent human activity, especially during the 20th century (Kadlec and Drury 1968). Herring, ring-billed and black-backed gulls and kittiwakes have staged a remarkable comeback from a centuries-long decline during which they and their eggs were taken in enormous numbers for human food. Their population increases are largely due to garbage generation and fishery offal and discards (Montevecchi, *pers comm.*). During pre-contact times, large seabird colonies were present off the east coast of Newfoundland, including Funk Island, situated approximately 50 kilometers offshore and known as the Isle of Birds in 1505. Funk Island was probably the site of the largest great auk colony in the world (Grieve 1885), where there may have been more than 100,000 nesting pairs (Nettleship and Birkhead 1985; Montevecchi and Tuck 1987; Montevecchi and Kirk 1996).

Surveys of coastal headlands, beaches, reefs, islands and islets from mid Labrador to Florida show that only about 3 out of every 100 suitable sites for seabird colonies are still occupied, even by vestigial populations (Mowat 1984 p. 50). If this ratio is used, the population of seabirds is now probably only 3% of what it was pre-contact. The biomass of the 1990s model was therefore increased ca. 33 times for the pre-contact model (Table 3). This value is probably a gross overestimation, as not all suitable sites would be used at all times, but it was used here as the upper estimate of what seabird numbers could have been in the pre-contact period until a better result is obtained. Vasconcellos *et al.* (2002a) suggest that the biomass of birds in 1900 was probably double what it is today (Table 3). The P/B and Q/B ratios for birds given in Bundy *et al.*

Table 3. Estimates of seabird biomass ($\text{kg}\cdot\text{km}^{-2}$) in the 1990s, 1900, and 1450 models (assuming that only 3% of the colonies are presently still occupied).

	1990s (tonnes)	1990s ($\text{kg}\cdot\text{km}^{-2}$)	1900 ($\text{kg}\cdot\text{km}^{-2}$)	1450 ($\text{kg}\cdot\text{km}^{-2}$)	First Nations catch ($\text{kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$)
Ducks	83	0.227	0.453	7.554	0.001
Piscivores	4945	13.453	26.906	448.429	0.060
Planktivores	1073	2.921	5.841	97.353	0.013

(2000) were used for all three of these groups. The diet of seabirds used in Bundy *et al.* (2000) was adapted to the new groups by Heymans and Pitcher (*this volume*).

First Nations and early European settlers exploited many species of seabirds along the coast of Newfoundland as sources of food, bait, oil and feathers for bedding. One of the most affected species was the great auk (Montevecchi and Tuck, 1987; Vasconcellos *et al.* 2002b). The significance of great auks for First Nations is revealed by the number of their beaks uncovered in graves (Tuck 1975; Montevecchi and Tuck 1987; Montevecchi and Kirk 1996). They provided the Beothuk with eggs and meat. The Beothuks ground the dried contents of great auk eggs into a kind of flour with which they made puddings (Montevecchi and Tuck 1987). Marshall (1996) suggests that the Beothuk utilized ducks, murrelets, puffins, kittiwakes, gulls, guillemots, gannets, cormorants, dovekeys, geese and ducks, and all bird eggs. Marshall (*pers. comm.*) suggests that the diet of Beothuk and Inuit probably consisted of 10% birds (36.5 tonnes or $0.074 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) (Heymans 2002). To estimate catches of each compartment, the total First Nations catch was divided by the biomass ratio of the bird compartments (Table 3). We also assume a similar catch made by First Nations and European settlers for the 1900s model, as fishermen used birds to bait their cod hooks from early in the 19th century (Tasker *et al.* 2000).

9-10) Cod

In 1497, Milan's envoy to London, Raimondo di Soncino, reported that Cabot found the sea swarming with fish which can be taken not only with the net but also in a basket let down with a stone, so that it sinks in the water (Kurlansky 1997 p. 48). On the Newfoundland shore the cod were reported to be so thick that one was hardly able to row a boat through them (Mowat 1984 p. 168). Estimates of harvestable Northern cod biomass (2J3KL) prior to the offshore-dominated catches of the 1960s are given by Hutchings and Myers (1995) as 3,000,000 tonnes. This calculates a biomass of $8.2 \text{ t}\cdot\text{km}^{-2}$ using the area of $367,542 \text{ km}^2$ given by Bundy (2002) for 2J3KL. We assumed this value as the overall biomass for

Table 4. Catch of various species during 1903 in Atlantic Canada and estimates of catches in 2J3KLNO using assumptions of distribution for all species (see text).

Species	Catch in Atlantic Canada (tonnes)	% of population in 2J3KLNO	Catch (kg•km ⁻² •yr ⁻¹)
Haddock (Large Demersal)	7000	10%	1.414
Greenland halibut	2400	75%	3.636
Pollock			
(Bentho-pelagic piscivore)	10000	1%	0.202
Mackerel	5000	1%	0.101
Capelin	10000	80%	16.162
Herring	4000	25%	2.020

the area 2J3KLNO for both the 1900s and 1500s models. To calculate the biomass of juvenile cod in the past models we assumed that the same rate of change of adult biomass applies to juveniles, i.e. historic biomass is 4 times the biomass in the mid-1980s (0.34 t•km⁻²) (Bundy *et al.* 2000). Therefore, the biomass of juvenile cod in the 1900s and 1500s models was estimated at 1.36 t•km⁻². However, this might have to be estimated by ECOPATH to balance the model.

The natural mortality and Q/B ratios of all fish species were calculated by using empirical formulas obtained from Pauly (1980) and Palomares and Pauly (1998), respectively (Appendix A Table A1 and A2). For species such as cod, where fishing mortality was available or calculable, the sum of F and M was used to estimate P/B. Thus natural mortality of adult cod was estimated at 0.1 yr⁻¹, and fishing mortality was 0.4 * 10⁻⁸ yr⁻¹ in 1450 and 0.09 yr⁻¹ in 1900, which calculates P/B ratios of approximately 0.104 and 0.198 yr⁻¹ for 1450 and 1900, respectively. The natural mortality of juvenile cod was estimated at 0.155 yr⁻¹ and was used as P/B ratio for both time periods (Appendix A Table A1). The Q/B ratios for adult and juvenile cod were estimated at 1.1 and 1.6 yr⁻¹ respectively (Appendix A Table A2). Diet estimates obtained from Lilly (2002) for 1985-87 were used for juvenile and adult cod in both 1450 and 1900.

The average annual production of dried cod declined from about 791,000 quintals annually for 1884-1888 to about 486,000 quintals for the years 1909-1913 (Lear (1998) quoting Grant (1934)). Thus the catch of cod around 1900 was probably approximately 500,000 quintals. Myers (2001) suggests that 1 tonne of cod produces 4.2 quintals, which calculates a catch of approximately 120,000 tonnes for 1900, or 0.24 t•km⁻²•yr⁻¹. However, Hutchings and Myers (1995) estimated a catch of approximately 280,000 tonnes (*pers comm.* for raw data), or 0.77 t•km⁻²•yr⁻¹ for 2J3KL from 1900-1905, which was used here in the 1900s model.

11-12) American plaice

Estimates of biomass for American plaice, *Hippoglossoides platessoides*, were not available for the pre-contact model and were made by using ecotrophic efficiency values of 0.95 for both adult and juvenile American plaice. Natural mortality estimates (Appendix A Table A1) for adult and juvenile American plaice (0.08 and 0.12 yr⁻¹, respectively) were used to estimate P/B ratios, and the Q/B ratios were calculated at 1.7 and 2.5 yr⁻¹, respectively (Appendix A Table A2). Diet estimates for 1985-87, obtained from Lilly (2002), were used for American plaice in both 1900 and 1450. There was no reported commercial catch of American plaice before 1950 (Morgan *et al.* 2000) and therefore no catch estimates or fishing mortality were entered for American plaice in 1900. However, flounders are reported to have been part of the Beothuk diet (Marshall 1996), and the American plaice catch by First Nations is calculated at approximately 0.003 kg•km⁻²•yr⁻¹ (Heymans 2002).

13-14) Greenland halibut

Greenland halibut occur in NAFO areas 2G, 2H, 2J, 3K, 3L and 3N, and during the 1970s they were abundant in 2G, 2H and 2J, while they were reduced in those areas in the 1990s and increased in 3K, 3L and 3N (Bowering 2001). The biomass in 2J3K at the beginning of the time series (1978) was approximately 300,000 tonnes (Bowering 2001, Figure 7), ca. 230,000 tonnes of adults (> 35 cm), and 70,000 tonnes of juveniles (≤ 35 cm). These figures are used as a lower estimate of the biomass of Greenland halibut prior to the commercial fishery, which started in the 19th century (Table 4). Vasconcellos *et al.* (2002d p. 45) quote Barb Neis:

a fishery for Greenland halibut began in Trinity Bay during the 1960s, but the area was fished out within a year and then the fishery moved offshore.

Thus the biomass of Greenland halibut was probably already much lower by 1978. We therefore assume that the 1900 and 1450 biomasses were double the initial stock biomass estimated from the VPA (Bowering 2001), or 0.93 t•km⁻² and 0.28 t•km⁻² respectively for adult and juvenile Greenland halibut.

Natural mortality of adult Greenland halibut was calculated using an equation from Pauly (1980) with L_∞ and K estimates for the northwest Atlantic (Bowering and Nedreaas 2001) and an average temperature of 2°C. The average M

calculated was 0.026 yr^{-1} and if it is assumed that the juvenile natural mortality is 1.5 times that of adults, the M for juveniles is estimated at 0.04 yr^{-1} (Appendix A Table A1). Halibut was caught commercially at the turn of the 20th century (Table 4), thus a small fishing mortality of 0.004 yr^{-1} is added to the natural mortality of adults to calculate a P/B of 0.03 yr^{-1} . P/B of juveniles was assumed the same as the natural mortality rate of 0.04 yr^{-1} . The Q/B ratios for adults and juveniles were calculated at 1.2 and 1.8 yr^{-1} , respectively (Appendix A Table A2) and the diet obtained from Lilly (2002) for 1985-87 was used for both models. It was assumed that the catch (if any) of Greenland halibut made by First Nations in both time periods was too small for the models. A catch estimate of Greenland halibut in Atlantic Canada in 1903 was obtained from Regier and McCracken (1975) (Table 4). The distributions of haddock, Greenland halibut and pollock in 2J3KLNO (compared to the rest of Atlantic Canada) were estimated from the East Coast of North America Strategic Assessment Project website². Based on the above information it was assumed that 10% of haddock, 75% of Greenland halibut and 1% of pollock caught were caught in 2J3KLNO.

15-17) Flounders (yellowtail, witch, winter)

Yellowtail flounder, *Limanda ferruginea*, are mainly located on Grand and St. Pierre Banks, although they do occur up to the Strait of Belle Isle, and prefer temperatures of 3.1-4.8°C (Pitt 1970). Yellowtail flounder abundance increased from 1961-1968 coincident with higher bottom temperatures. The close association between the species distribution and bottom temperatures could be explored in a future work as a way to estimate historical trends in relative abundance of the species in the study area. However, in the present work, the biomass in 1900 and 1450 was estimated by assuming an ecotrophic efficiency of 95%. Yellowtail flounder was caught commercially from 1965, when 1,800 tons were landed from the Grand Bank. However, no catches were made around 1900 or pre-contact.

Witch flounder *Glyptocephalus cynoglossus* reaches its northern limits near Hamilton Bank off southern Labrador (Anon. 1996b). The fishery began in the 1960s and the peak catch in 2J3KL was 24,000 metric tonnes in 1973 (Bowering 2000). However, no catches were made around 1900 or pre-contact.

Winter flounder *Pseudopleuronectes americanus* is a shallow water species that occurs around the coast of Newfoundland (Anon. 1996a). Winter flounder has been taken in 3K and 3L with gillnets and as lobster bait for years, and the gillnet fishery supported limited food markets since the 1970s (Anon. 1996a). However, no catches were made around 1900 or pre-contact.

The diets of all three species were assumed to be similar to their diet in 1985-1987 (Lilly 2002). The natural mortalities of yellowtail, witch and winter flounder were estimated in Appendix A Table A1 and used as P/B ratios for three species in both 1900 and 1450. The Q/B ratios calculated in Appendix A Table A2 for witch and winter flounder were also used for both models. It was not possible to estimate the Q/B of yellowtail flounder due to the lack of parameters for the L-W relationship. Instead the Q/B of the species was calculated as the average Q/B ratio of yellowtail flounder on the Georges Bank (3.271 yr^{-1}) obtained from Sissenwine (1987). However, this ratio is probably too high, as the 1900 and 1450 population would probably have a higher proportion of old animals.

Flatfishes formed part of the diet of First Nations (Marshall 1996), although it was probably only the inshore species. Thus, the pre-contact catch of yellowtail and winter flounder by First Nations is calculated at $0.002 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ and $0.001 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ respectively (Heymans 2002). No known catches of flounders are available for 1900-1905.

18) Skates

This group consists of barndoor skates, *Dipturus laevis*, thorny skates *Amblyraja radiata*, smooth *Malacoraja senta*, little *Leucoraja erinacea* and winter skates *Leucoraja ocellata*. Thorny skates are the dominant species in the area and George Lilly was quoted by Vasconcellos *et al.* (2002e p. 48) as saying that

although some references say barn door skates have largely disappeared, they are still caught in commercial fisheries.

Vasconcellos *et al.* (2002e) suggest that the biomass in the early 1900s was probably higher than in the mid-1980s considering that large quantities of skates were discarded since the beginning of trawling, and proposed that the biomass of skates in the 1900s should be twice the number estimated for the mid-1980s. A biomass of $0.47 \text{ t}\cdot\text{km}^{-2}$ was therefore estimated for 1900. Biomass of skates in 1450 was estimated by assuming an ecotrophic efficiency of 95% and

² <http://www-orca.nos.noaa.gov/projects/ecnasap/appendix1.html>

their diet in both models was assumed to be similar to their diet in 1985-1987 (Lilly 2002). The natural mortality estimated in Appendix A Table A1 for little skates was used as P/B ratio in both 1900 and 1450 and their Q/B ratio calculated in Appendix A Table A2 was also used for both models. Skates were not caught in 1900 or 1450.

19) Dogfish

Spiny dogfish, *Squalus acanthias*, was separated from the large pelagic feeders in Bundy *et al.* (2000). No estimates were available for 1900 or pre-contact dogfish biomass, and it was therefore estimated by ECOPATH using an ecotrophic efficiency of 0.95. The P/B ratio was taken to be similar to natural mortality (0.16 yr⁻¹ in Appendix A Table A1) and the Q/B ratio of 2.2 yr⁻¹ was estimated in Appendix A Table A2. The diet of dogfish in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). Dogfish was not caught in 1900 or pre-contact.

20) Redfish

Species of redfish, (= ocean perch, rosefish) in the study area include deep-water redfish *Sebastes mentella*, and Acadian redfish *S. fasciatus* (Anon. 1996d). Biomass was estimated for both models by assuming an ecotrophic efficiency of 95% each, and natural mortality (0.11 yr⁻¹) was assumed to be the same as P/B, while the Q/B ratio (1.7 yr⁻¹) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002), and redfish was not caught in 1900 or pre-contact.

21) Transient mackerel (> 29 cm)

Mackerel, *Scomber scombrus*, comprise a single stock in the study area and in some years they are present in large quantities, while in other years they are virtually absent (Vasconcellos *et al.* 2002c). Adult transient mackerel larger than 29 cm were therefore split from the small pelagic group. Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%, and natural mortality (0.007 yr⁻¹, obtained using the equation of Pauly, 1980 [this value might be too low, and should be revised in later versions of the model- Ed]) was assumed to be the same as P/B, as no estimate of biomass was available to calculate fishing mortality. The Q/B ratio (5.9 yr⁻¹) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). A catch of 5,000

tonnes was estimated for mackerel in Atlantic Canada in the early 1900s (Regier and McCracken 1975), and it was assumed that only about 1% of that catch was made in 2J3KLNO, as they are transient and mainly occur in the Gulf of St. Lawrence. Thus the catch in 1900 was estimated at 0.1 kg•km⁻²•yr⁻¹ (Regier and McCracken 1975) (Table 4). Mackerel also formed part of the diet of First Nations (Marshall 1996). Pre-contact catch of mackerel by First Nations is calculated at 0.004 kg•km⁻²•yr⁻¹ (Heymans 2002).

22-23) Demersal and benthopelagic piscivores (adult and juvenile)

The demersal and benthopelagic piscivores include white hake *Urophycis tenuis*, silver hake *Merluccius bilinearis*, monkfish *Lophius americanus*, sea ravens *Hemitripterus americanus*, cusk *Brosme brosme*, Atlantic halibut *Hippoglossus hippoglossus*, and saithe ('pollock') *Pollachius virens*. Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.1 yr⁻¹ for adults and 0.15 yr⁻¹ for juveniles) was assumed to be the same as P/B, as no estimate of biomass was available to calculate fishing mortality. Q/B ratios (1.1 yr⁻¹ for adults and 1.7 yr⁻¹ for juveniles) calculated in Appendix A Table A2 were assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). Ten thousand tonnes of pollock were caught in 1903 in Atlantic Canada (Regier and McCracken 1975) and we assume that 1% (0.2 kg•km⁻²•yr⁻¹, Table 4) of this catch was made in 2J3KLNO. It was assumed that, if any of the demersal and benthopelagic piscivores were caught by First Nations, that catch was too small to be represented in this model.

24-25) Large demersal feeders (adult and juvenile)

This group consists of a range of species that feed in the demersal domain, including haddock *Melanogrammus aeglefinus*, longfin hake *Phycis chesteri*, red hake *Urophycis chuss*, wolffish *Anarhichas* sp., grenadiers *Coryphaenoides* sp., eelpouts *Lycodes* sp., and batfishes. Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.009 yr⁻¹ for adults, obtained using the equation of Pauly, 1980 [this value may be too low and require future revision, Ed], and 0.15 yr⁻¹ for juveniles) was assumed to be the same as P/B, as no estimate of biomass was available to calculate fishing mortality. Q/B ratio (1.4 yr⁻¹ for adults and 2.1 yr⁻¹ for juveniles) calculated in Appendix A

Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). The haddock fishery prior to 1945 was very low, but increased rapidly in the late 1940s in divisions 3NO (Anon. 1996b). The catch of haddock in 1903 was estimated at 7,000 tonnes (Regier and McCracken 1975), and it was assumed that only 10% of the haddock catches were made in 2J3KLNO ($1.0 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$, Table 4). It was also assumed that if any of the demersal and benthopelagic piscivores were caught by First Nations that catch was too small to be represented in this model.

26) Other small demersals

The other small demersals group includes rocklings *Enchelyopus* sp., gunnel *Pholis gunnellus*, alligator fishes *Ulcina olriki*, Atlantic poachers *Leptagonus decagonus*, snakeblennies *Lumpenus lampretæformis*, seasnails and shannies *Leptoclinus* sp., sculpin *Myoxocephalus* sp., searobins *Prionotus* sp., eelblennies *Anisarchus* sp., and wrymouth. Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.56 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (4.5 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). None of these species were reported in the diet of pre-contact First Nations or caught in 1900 and 1450.

27) Lumpfish

Lumpfish, *Cyclopterus lumpus*, are found in major concentrations on the St. Pierre bank off the southeast coast of Newfoundland (Garavis 1985 in Walsh *et al.* 2000). Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.1 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (1.4 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002) and lumpfish was not reported in the diet of pre-contact First Nations or caught in 1900 and 1450.

28) Greenland cod

Greenland cod, *Gadus ogac*, is more closely related to Pacific cod than it is to Atlantic cod and is purported to be a northward and eastward extension of Pacific cod (Carr *et al.* 1999).

Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.1 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (1.3 yr^{-1}) calculated in Appendix A, Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar their diet in the 1985-87 model (Lilly 2002) and Greenland cod was probably part of the diet of pre-contact First Nations. The catch by First Nations is calculated at $0.001 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Heymans 2002).

29) Atlantic salmon

The earliest reference to Atlantic salmon in the Northeast Atlantic was made by Leif Ericson in 995 who suggested (Mowat 1984 p. 181) that on the coast of Newfoundland

There was no shortage of salmon there and these were larger salmon than they had ever seen before.

The rivers that were known to historically contain salmon in the study area include the Hamilton, Kenamu, North, Eagle, Paradise, Alexis, and Pinware Rivers in Labrador, and the Cloud, Cat Arm, Exploits, Gander, Southwest, Northeast, and Salmonier Rivers in Newfoundland (Dunfield 1985). The Exploits River was reported to provide good catches for First Nations despite the fact that only about 20% or no more than 850 square miles of its watershed was accessible (Dunfield 1985).

Although at least one researcher, Gordon W. Hewes, has claimed that the Amerindian salmon fishery was intense enough in some locations to depress the original stock of fish (Rostlund 1952), it is generally believed that native North Americans had no deleterious impact on the resource as a whole. There is even the suggestion that they may have enhanced it by inadvertently and unconsciously practicing good fishery management (Dunfield 1985).

Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.1 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (1.3 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002).

The catch of salmon around 1900 is not known, but Dunfield (1985) gave catches between 1800 and 1867 of approximately $1.3 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$, which we use as an approximation of the catch in 1900 (Appendix B). The total accessible watershed area

in North America over which salmon were distributed in pre-contact times comprised no less than a quarter of a million square miles of primeval territory, untouched by human influences except for the Amerindian who lived in harmony with it (Dunfield 1985). Rostlund (1952) calculated the aboriginal production of Atlantic salmon in the United States to be between 14 and 15 million pounds a year, or an average of 580 pounds per square mile in the occurrence area. Applying Rostlund's base calculation to the total area of salmon occurrence in eastern North America, an estimated 145 million pounds per year is obtained (Dunfield 1985). Marshall (1996) suggested that salmon formed part of the Beothuk diet, and Marshall (*pers. comm.*) indicated that approximately 15% of their diet was comprised of salmon. Based on the above information Heymans (2002) estimated the salmon catch in pre-contact times at 55 tonnes or $0.1 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$.

30) Capelin

Carscadden *et al.* (2001) suggest that prior to 1970 capelin annually contributed in excess of 4.6 million tonnes to the diets of cod, seals and whales, while seabirds and finfish also forage extensively on capelin. Thus, at least 4.6 million tonnes of capelin is a lower limit to their annual production, and using their natural mortality of 0.6 yr^{-1} as an estimate of P/B in pre-contact times, we calculate a biomass of $16 \text{ t}\cdot\text{km}^{-2}$. This estimate would be a lower limit to the biomass of capelin, as it only included the consumption by cod, seals and whales, and not consumption by finfish, seabirds or other predators. This estimate, which we acknowledge to be very uncertain, was used for capelin biomass in the 1900s and 1500s models.

Carscadden *et al.* (2001) suggest that prior to the 1950s, 20-25,000 tonnes of capelin were taken annually in Newfoundland as bait, fertilizer and dog food. Inshore landings declined considerably until the early 1970s, when a directed offshore foreign fishery began. This fishery declined in the late 1970s and an inshore fishery for roe-bearing females started inshore again (Carscadden *et al.* 2001). In contrast, Vasconcellos *et al.* (2002b) suggest that the fishery prior to the 1960s, when the Japanese seiners arrived, was less than 10,000 tonnes per year. Regier and McCracken (1975) suggest a catch of 10,000 tonnes for the whole of Atlantic Canada. Considering that historically most of the distribution of capelin was in areas 2J3KLNO (Carscadden *et al.* 2001), we assume that approximately 80% of the Atlantic catch was made in 2J3KLNO. A catch of $0.016 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ was therefore estimated for

1900, while the catch during pre-contact was estimated at $0.017 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Heymans 2002).

31) Sandlance

Sandlance *Ammodytes dubius* are abundant in coastal regions and over the shallow sandy areas of the continental shelf of the North Atlantic (Winters and Dalley 1988). In Newfoundland and Labrador waters, most sandlance occur on the plateau of Grand Bank, thus sandlance in 2J3KL are at the northerly end of their distribution (Bundy 2002). Sandlance was never commercially exploited and there are no catches or biomass estimates for the 1900 or pre-contact models. Thus biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. The natural mortality of sandlance could not be calculated and was estimated by assuming a gross growth efficiency of 20%, while the Q/B ratio (4.9 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002).

32) Arctic cod

Arctic cod *Boreogadus saida* is an important forage species on the Labrador shelf and northeastern Newfoundland (Vasconcellos *et al.* 2002f). It was also never commercially exploited, although there has been a bycatch of Arctic cod (Lilly *et al.* 1994). There are no reported catches or biomass estimates for the 1900 or pre-contact models, thus biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. The natural mortality of sandlance could not be calculated, therefore P/B ratio was estimated from Q/B assuming a gross growth efficiency of 20%. Q/B ratio (4.9 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002).

33) Herring

Herring *Clupea harengus*, capelin, and mackerel were the traditional bait species for the cod fishery (Vasconcellos *et al.* 2002b), but herring landings rapidly increased from less than 4,000 tonnes a year to 140,000 tonnes after 1969 when a BC seiner was introduced to the fishery (Vasconcellos *et al.* 2002b). Biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.5 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (4.1 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was

assumed to be similar to the 1985-87 diet (Lilly 2002). Regier and McCracken (1975) reported a catch of 4,000 tonnes of herring in Atlantic Canada in the early 1900s. Herring in Newfoundland is at the northern limit of its range, thus it was assumed that only about 25% (or $0.002 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$, see Table 4) of the 4,000 tonnes caught in Atlantic Canada were taken in 2J3KLNO, while the catch during pre-contact was estimated at $0.004 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Heymans 2002).

34) Transient pelagics

Transient pelagics include bluefin tuna *Thunnus thynnus*, swordfish *Xiphias gladius*, and sharks. Biomass for transient pelagics was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.18 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (1.99 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet of transient pelagics was not well known, and was adapted from Bundy *et al.* (2000) by Heymans and Pitcher (*this volume*).

35) Small pelagics

Small pelagics were defined to include shad *Alosa sapidissima*, butterfish *Peprilus triacanthus*, argentine *Argentina silus*, juvenile mackerel, and Atlantic rainbow smelt *Osmerus mordax mordax*. Very little is known about these species, and the biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (0.6 yr^{-1}) was assumed to be the same as P/B, while the Q/B ratio (5.3 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). Smelts were important in the diet of the First Nations during pre-contact times. In Notre Dame Bay, the hundreds of tiny smelt bones found at Boyd's Cove indicate that its inhabitants ate them regularly. The bones were preserved by the large quantities of clam and mussel shells that were discarded by the Beothuks at the same site making the soil less acidic (Pastore 1997). The catch of smelts by First Nations was assumed to be $0.001 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Heymans 2002).

36) Mesopelagics

Mesopelagic species in the 2J3KLNO area include lanternfishes *Myctophidae*, pearlsides *Maurollicus muelleri*, and barracudinas *Paralepis elongata*. This group is very poorly known and their biomass was estimated for both models by assuming an ecotrophic efficiency of 95%. Natural mortality (1.4 yr^{-1}) was assumed to be the same as

P/B, while the Q/B ratio (4.8 yr^{-1}) calculated in Appendix A Table A2 was assumed to be similar for both models. The diet in 1900 and 1450 was assumed to be similar to the 1985-87 diet (Lilly 2002). Mesopelagics were not fished in 1900 or during pre-contact. Biomass estimates from ECOPATH balancing of $10.3 \text{ t}\cdot\text{km}^{-2}$ in 1900 and $11.1 \text{ t}\cdot\text{km}^{-2}$ in 1450 seem very high compared to the present day average biomass in this region of $1.1 \text{ t}\cdot\text{km}^{-2}$ (R. Watson, *pers. comm.*). However, these biomasses were needed to sustain the large quantities of higher trophic level species.

37-38) Squid (shortfin and Arctic squid)

Two species of squid are present in the area: shortfin squid *Illex illecebrosus* and Arctic squid *Gonatus* sp. Very little is known about Arctic squid other than it stays in the area throughout the year, while shortfin squid is highly migratory and spends only part of its time in the area (Bundy *et al.* 2000). No estimates of squid biomass were available for either the 1900s or the 1500s models, so the biomasses of both shortfin and Arctic squid were estimated by assuming ecotrophic efficiencies of 95% for both species in both models. Bundy *et al.* (2000) estimated P/B ratios for planktivorous and piscivorous small pelagics (Arctic and shortfin squid included) of 0.5 and 0.6 yr^{-1} , respectively, and used a gross efficiency of 0.15 to calculate their Q/B ratios. Thus, a P/B of 0.5 yr^{-1} was used for Arctic squid and 0.6 yr^{-1} for shortfin squid in all four models, with their Q/B ratios calculated by using a GE of 0.15. The diet of shortfin squid was taken from Bundy *et al.* (2000) and adapted by Heymans and Pitcher (*this volume*), while Arctic squid was assumed to consume large and small zooplankton in the ratio of 1:1. Squid was not caught pre-contact or in 1900.

39-41) Large crustaceans (large crabs, small crabs, and lobster)

Large crabs (carapace width > 95 mm) include mostly adult snowcrabs *Chioneocetes opilio* and northern stone crabs *Lithodes maja* (Jonah crabs *Cancer borealis* and red crabs *Geryon quinquedens* do not really occur here). Small crabs include toad crabs *Hyas* sp., hermit crabs, rock crabs *Cancer irroratus*, and the juveniles of the large crabs. The American lobster *Homarus americanus* was split from other large crustaceans, as there is more information on TEK for that species. The biomasses of both large and small crabs and lobsters were estimated for both models by assuming an ecotrophic efficiency of 95%. The P/B (0.4 yr^{-1}) and Q/B (4.4 yr^{-1}) ratios used for large crustaceans in Bundy *et al.* (2000)

were used for all three large crustacean groups in this model. The diet of crustaceans was obtained from Lovrich and Sainte-Marie (1997) and DFO (1996a and 1996b) and adapted for the 1980s and 1990s models (Heymans and Pitcher, *this volume*). The diet of lobster was assumed to be the same as that of large crabs.

Crabs were not caught in 1900, but small crabs did form part of the First Nations diet (Marshall 1996). Lobster of 16 and 25 pounds were caught and lobster was used as bait on a grand scale (Ennis *et al.* 1997). Landing statistics for Newfoundland start in 1874, and there was a peak catch of 7,938 tonnes in 1889 followed by a collapse and a three year closure in the mid 1920s (Ennis *et al.* 1997). Virtually everything caught was processed although lobsters were also used extensively as fertilizer in cottage farming (Ennis *et al.* 1997). The landings of lobster between 1900 and 1905 were approximately 4,000 tonnes (Ennis *et al.* 1997), and if we assume that the catch on the west coast (2J3KLNO) was approximately half the total, then the catch is estimated at about $0.004 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$. Lobster also formed part of the First Nations diet (Marshall 1996), and Heymans (2002) calculates catch of small crabs and lobster by First Nations at approximately $0.011 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ each.

42) Shrimp

Two species of shrimp are common in the 2J3KLNO area: northern shrimp *Pandalus borealis*, and *Pandalus montagui* (Parsons *et al.* 2000). The biomasses of shrimp in the 1900s and 1500s models were estimated by assuming an ecotrophic efficiency of 95%. The P/B (1.5 yr^{-1}) and Q/B (9.7 yr^{-1}) ratios and diet used by Bundy *et al.* (2000) for 1985-1987 were used in both models.

43-46) Benthos

The benthos were divided into echinoderms, polychaetes, bivalves (such as scallops) and other benthic invertebrates. The effects of climate change and "fishing" on these groups should be taken into consideration when estimating the biomass of 1900s and 1500s models, but due to lack of information their biomass was estimated by assuming ecotrophic efficiencies of 95% each. The P/B and Q/B ratios for echinoderms, polychaetes, bivalves and other benthic invertebrates were obtained from Bundy *et al.* (2000) and they were all assumed to feed on detritus.

The resources of the sea, as well as the land, were

essential to the Beothuks (Marshall 1996), and they were known to rely on clams, mussels, and other invertebrates (Pastore 1998). First Nations catches of bivalves and other invertebrates were estimated at $0.033 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ and $0.022 \text{ kg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ each (Heymans 2002).

47-48) Large and small zooplankton

The large zooplankton compartment includes cnidarians, ctenophores, pteropods, hyperiid amphipods, mysids, euphausiids, chaetognaths, tunicates and ichthyoplankton, while the small zooplankton consists of copepods, small tunicates and meroplankton. No biomass estimates were available for zooplankton for the 1900s or 1450s models, and it was estimated by assuming an ecotrophic efficiency of 95%. The P/B and Q/B ratios and diets obtained from Bundy *et al.* (2000) were used in both models.

49) Phytoplankton

No estimates of primary production or phytoplankton biomass were available for 1900 or 1450 and therefore the biomass was estimated by using an ecotrophic efficiency of 95% and a P/B ratio of 93.1 yr^{-1} , obtained from Bundy *et al.* (2000).

50) Detritus

The detritus pool was recalculated from the formula for detritus obtained from Pauly *et al.* (1993):

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E$$

where D = detritus standing stock in $\text{gC}\cdot\text{m}^{-2}$ (grams of carbon per square metre), PP = primary productivity in $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and E = euphotic depth (m). A value of 54.7 m was used for the euphotic zone depth (Bundy *et al.* 2000), and detritus pools of 393 and $296 \text{ t}\cdot\text{km}^{-2}$ were calculated for the 1450 and 1900 models respectively.

BALANCING THE MODELS: 1900-1905

The unbalanced model of 1900-1905 could not estimate a biomass for large crabs, as they are not consumed in the system. It also calculated an ecotrophic efficiency of 11.7 for juvenile cod, 7.4 for adult Greenland halibut, 75.7 for juvenile Greenland halibut and 3.9 for capelin. The estimate of juvenile American plaice was also calculated to be extremely large ($17.7 \text{ t}\cdot\text{km}^{-2}$). To balance the model, it was therefore necessary to

re-examine the diets of all species that feed on capelin, halibut, juvenile cod and juvenile plaice.

Large crabs are not really prey for any species, and were also not caught until 1990, so we assume that the biomass of large crabs was similar to that obtained for the 1985-1987 model (86,345 tonnes from Bundy *et al.* (2000)) and use this biomass as a lower limit to the biomass in 1900 and 1450.

The main predators of juvenile American plaice are harp seals, large demersal benthic-pelagic piscivores and cannibals. We reduce the percentage of juvenile plaice in the diet of harp seals as well as the cannibalism by other juvenile plaice to 0.1%, and recalculate the diets of those groups to reduce the biomass of American plaice to 6.6 t•km⁻².

To balance juvenile Greenland halibut we reduce the juvenile halibut in the diet of their main predators. The surplus is then re-distributed between all other prey species of the specific predator group. The proportion of juvenile Greenland halibut in the diet of their main predators was changed as follows:

- Harp seals – reduced to 0.01%
- Hooded seals – reduced to 0.01%
- Cod (> 40 cm) – reduced to 0.01%
- Cod (≤ 40 cm) – reduced to 0.01%
- Removed juvenile Greenland halibut from the diet of juvenile American Plaice
- Adult American plaice – reduced to 0.01%
- Adult Greenland halibut – reduced to 0.01%
- Cannibalism – reduced to 0.01%
- Large demersal feeders – reduced to 0.01%
- Juvenile demersal feeders – reduced to 0.01%

To balance the adult Greenland halibut, the percentages of adult halibut in the diet of hooded and harp seals (their only predators) were reduced to 0.1% each, and the diets of hooded and harp seals were recalculated to incorporate the surplus diet.

To balance juvenile cod, the percentages of juvenile cod in the diets of some of its predators were reduced, and the diets of these predators were recalculated to include the surplus consumption:

- Cetaceans – reduced to 0.1%
- Harp seals – reduced to 0.1%
- Hooded seals – reduced to 0.05%
- Adult cod – reduced to 0.1%
- Removed juvenile cod from the diet of juvenile American plaice

- Adult Greenland halibut – reduced to 0.1%
- Redfish – reduced to 0.1%
- Large demersal feeders – reduced to 1%
- Juvenile demersal feeders – reduced to 0.1%
- Transient pelagics – reduced to 0.01%
- Shortfin squid – reduced to 0.1%

To balance capelin, the percentages of capelin in the diets of some of its predators were reduced, and the diets of these predators were recalculated to include the surplus consumption:

- Cetaceans – reduced to 10%
- Harp seals – reduced to 5%
- Adult cod – reduced to 9%
- Juvenile cod – reduced to 10%
- Adult American plaice – reduced to 5%
- Juvenile American plaice – reduced to 0.1%
- Arctic cod – reduced to 1%
- Shortfin squid – reduced to 1%

The ecotrophic efficiency of detritus was calculated at 1.4, and to balance the detritus the ecotrophic efficiency of phytoplankton was assumed to be 50% (instead of 95%). This value is closer to the 34% estimated for the 1985-87 model by Bundy *et al.* (2000), and calculates a phytoplankton biomass of 64.4 t•km⁻², and recalculates the detritus pool to 546.6 t•km⁻².

Hence we effectively assume that primary production in the past was about 2 times higher than in the 1980s and 1990s, which is what seems to be needed to feed all the top predators that we suspect were present. Clearly, this is a controversial finding and could be adjusted in future versions of the model.

Modifications to the balanced model

The balanced model was subsequently modified to include changes made to the bird population. These changes include the inclusion of shearwaters and fulmars in the piscivorous birds rather than planktivorous birds, and the summation of the resident and breeding populations vs. averaging these two populations. The new biomass estimates increased the ecotrophic efficiency of capelin to 1.009. The percentage of capelin in the diet of piscivorous birds was then reduced to 70% (from 78%), with the rest of its diet being recalculated to balance the model.

The biomass of lobster was estimated at 0.08 t•km⁻² for the 1900 model (Tony Pitcher, Fisheries Centre, *pers. comm.*) and the predators of the following three species were expanded, as they were under-represented in the model:

1. The predators of salmon were expanded to include cetaceans (0.0001), grey seals (0.002), piscivorous birds (0.001), skates (0.001) and transient pelagics (0.001).
2. The predators of large crabs were expanded to include grey, harp and hooded seals as well as large cod (all 0.001).
3. The predators of lobster were expanded to include walrus, large cod, skates (all 0.0001), large demersal piscivores (0.001) and other large demersal species (0.0001).

These new changes increased the ecotrophic efficiency of capelin to 1.1, and the percentage of capelin in the diet of Arctic cod was subsequently decreased to 1%, which increased the ecotrophic efficiency of juvenile cod to 1.1. The percentage of juvenile cod in the diet of skates was then reduced to 1% and cannibalism by juvenile cod was reduced to 1% (from 3%) to balance the model. The parameters of the balanced model of 1900-1905 are given in Appendix C.

BALANCING THE MODELS: 1450

The unbalanced model of 1450 could not estimate a biomass for large crabs, as they are not consumed in the system. It also calculated an ecotrophic efficiency of 34.9 for juvenile cod, 18.6 for adult Greenland halibut, 160.9 for juvenile Greenland halibut and 7.5 for capelin. The estimate of juvenile American plaice was also extremely large (41.9 t•km⁻²) and likely unrealistic. The compartments that were unbalanced were similar to those that were unbalanced in the 1900 model, so we used the balanced diet obtained from the 1900 model and included the biomass of large crabs (0.17 t•km⁻²) similar to the 1900 model. The 1900 diet improved the balancing, as the ecotrophic efficiency of cod was reduced to 1.4, that of adult halibut to 1.1 and that of capelin to 1.5. To balance these compartments, it was therefore necessary to re-examine the diets of all species that feed on capelin, adult halibut and juvenile cod.

To balance capelin the percentage of capelin in the diet of piscivorous birds was severely reduced, to 1% (i.e. we are assuming that capelin was not important in the diet of piscivorous birds), and the rest of the diet of piscivorous birds was increased to incorporate the surplus consumption.

To balance juvenile cod, the juvenile cod in the diet of piscivorous birds was reduced to 0.01% and in the diet of grey seals it was reduced to 1%,

while the rest of the diet of piscivorous birds and grey seals was increased to incorporate the surplus consumption.

To balance adult Greenland halibut, the proportion it supplies to the diet of harp seals was further reduced to 0.05 % and the rest of the diet of harp seals was increased to incorporate the surplus consumption.

The ecotrophic efficiency of detritus was calculated at 1.3, and to balance the detritus the ecotrophic efficiency of phytoplankton was assumed to be 50% (instead of 95%). This value is closer to the 34% estimated for the 1985-87 model by Bundy *et al.* (2000), and calculates a phytoplankton biomass of 86.7 t•km⁻² and a detritus pool of 726 t•km⁻².

Modifications to the balanced model

Birds

This balanced model was subsequently modified to include changes made to the bird population. These changes include the inclusion of shearwaters and fulmars in the piscivorous birds rather than planktivorous birds, and the summation of the resident and breeding populations vs. averaging these two populations. The new biomass estimates increased the ecotrophic efficiency of juvenile cod to 1.179, that of juvenile Greenland halibut to 1.058 and that of capelin to 1.441.

To balance capelin, the percentage of capelin in the diets of piscivorous birds and small benthopelagic demersals was reduced to 0.01% each. In the diet of other small demersals the capelin was reduced to 0.5%, and in the diet of Greenland cod it was reduced to 5%. Juvenile cod was balanced by reducing the percentage that it contributes to the diet of juvenile benthopelagic demersals, other small demersals and shortfin squid, to 0.01% respectively. Juvenile Greenland halibut is balanced by reducing the percentage it contributes to the diet of juvenile benthopelagic demersals to 0.001%.

Cetaceans

The biomass of cetaceans in 1450 was estimated by the model. However, the value estimated (0.042 t•km⁻²) was much lower than the 0.5 t•km⁻² assumed for 1900. The parameters of cetaceans were investigated, and it was assumed that the P/B and Q/B of cetaceans would have been lower in 1450, due to the change in species composition from larger, more planktivorous

baleen whales to smaller, faster-growing toothed whales. Thus, the P/B of cetaceans was reduced to 0.05 yr^{-1} and the Q/B to 9 yr^{-1} (these values are higher than those of toothed whales in Hecate Strait, but lower than the values given for the present-day Newfoundland models). The ecotrophic efficiency was also reduced from 0.95 to 0.15, as by definition very little of the unexplained mortality of cetaceans would be accounted for. This recalculates the biomass of cetaceans to $0.53 \text{ t}\cdot\text{km}^{-2}$, but increases the ecotrophic efficiency of juvenile cod and capelin to $> 100\%$.

To rebalance the model the percentages of small cod and capelin in the diet of cetaceans were reduced to 0.001% and 1% respectively, while the percentage of large zooplankton was increased to 20%. This reduced the ecotrophic efficiency of juvenile cod and capelin, but not enough. To balance capelin, the percentages of capelin in the diets of Arctic cod and mesopelagics were reduced to 0.1% each. To balance juvenile cod, the percentage of juvenile cod in the diet of redfish was reduced to 0.01%.

Lobster, salmon and large crabs

The biomasses of these three compartments were very low in the balanced model and thus the predators of these three species were expanded, to increase the required biomass for balancing:

- The predators of salmon were expanded to include cetaceans (1%), grey seals (0.2%), piscivorous birds (0.02%), skates (1%) and transient pelagics (1%).
- The predators of large crabs were expanded to include grey, harp and hooded seals, large cod (all 0.1%) as well as transient pelagics (1%).
- The predators of lobster were expanded to include walrus (0.1%), large cod (5%), skates (0.1%), large demersal piscivores (0.1%) and other large demersal species (0.1%).

Changed due to large biomass

When the model was balanced, the biomass estimates of witch flounder, redfish, juvenile demersal benthopelagic predators, juvenile demersal feeders and small crabs were extremely high (above $40 \text{ t}\cdot\text{km}^{-2}$ each). To reduce these biomass estimates (all from ECOPATH), some changes were made to their contributions to predators:

- The percentages of redfish in the diet of hooded seals and adult Greenland halibut

were reduced from 20% to 1%, and from 30% to 10% respectively.

- The 14.4% of witch flounder in the diet of harp seals was divided between yellowtail flounder (5%), witch flounder (5%) and winter flounder (4.4%).
- The percentages of juvenile demersal benthopelagic predators and juvenile demersal feeders in the diet of piscivorous birds were both reduced to 0.5% from 1.8%.
- The small crabs in the diet of adult cod were reduced from 12% to 6% and the remaining 6% were assumed to be juvenile lobster. Similarly, the small crabs in the diet of juvenile demersal benthopelagic predators were reduced from 6% to 3% with the remaining 3% being taken from juvenile lobster, and the 10% in the diet of juvenile demersal feeders were assumed to be 5% each small crabs and juvenile lobster.

These changes improved the estimated biomass of redfish ($14 \text{ t}\cdot\text{km}^{-2}$), witch flounder ($8 \text{ t}\cdot\text{km}^{-2}$), juvenile demersal benthopelagic predators ($20 \text{ t}\cdot\text{km}^{-2}$), juvenile demersal feeders ($23 \text{ t}\cdot\text{km}^{-2}$) and small crabs ($25 \text{ t}\cdot\text{km}^{-2}$) to within reasonable limits. The parameters of the balanced model of 1450 are given in Appendix D.

CONCLUSIONS

These models represent our current best attempt at reconstructing these long-past ecosystems. The models may be thought of as an abstract version of what the Newfoundland and southern Labrador ecosystem could have looked like, and if visualized, might resemble an artwork by Picasso where all necessary components of the human form are present, but are misplaced.

Some major features of the models are debatable. For example, our assumption of 95% ecotrophic efficiency for groups that were not heavily fished might be questioned by some. Our argument is that in a mature, very bio-diverse and relatively unfished ecosystem, most trophic flows will likely be accounted for within the system. Others have argued that ecotrophic efficiency would be low in unfished systems. Secondly, our calculation of phytoplankton production as higher than the present day can clearly be questioned, even if the fertilization effect of large numbers of marine mammals and more large animals dying of old age and contributing to the detritus pool could have enhanced primary production.

Some details of the models can undoubtedly be improved. For example, we need to check the

apparently high biomass of mesopelagics, which were unfished in these past times, relative to densities in the present day. Aside from such details, without better information on the biomasses and diets of the groups in the ecosystem — which, for the ancient past, is unlikely to be forthcoming — a substantially more accurate model is not possible. However, there may be some shortcuts to obtaining improved estimates for major biomass pools from comparative analyses of many different marine ecosystems.

These static mass-balance ECOPATH models will be used as baselines for dynamic exploration using ECOSIM. Policy explorations in *Back to the Future* aim to determine what fisheries could be sustained by the Newfoundland marine ecosystem if it were restored to its state in 1900 or 1450.

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REFERENCES

Allen, G. M. 1942. Family Odobenidae: Walruses. Pages 469-477 in *Extinct and vanishing mammals of the Western Hemisphere with Marine Species of all the oceans*. American Committee for International Wild Life Protection Special Publication No. 11. Cooper Sq. Publishers, Inc., New York, N.Y.

Ancellin, J., 1954. Observations sur la morue de Terre-Neuve et du Labrador. Rapp. P.-v. Réun. CIEM 136:72-76.

Andersen, R. 1998. *Voyage to the Grand Banks: The saga of Captain Arch Thornhill*. Creative Publishers, St. John's NF.

Anon. 1970. Northwest Atlantic Fisheries Statistical Bulletin Volume 18 for the year 1968. Northwest Atlantic Fisheries Commission, Dartmouth, N.S.

Anon. 1996a. Blackback (Winter) Flounder in Divisions 3K, 3L and 3Ps. Stock Status Report 96/92, DFO.

Anon. 1996b. Division 3LNO Haddock. Stock Status Report 96/46, DFO.

Anon. 1996c. Divisions 2J3KL Witch Flounder. Stock Status Report 96/49, DFO.

Anon. 1996d. Subarea 2+3K Redfish. Stock Status Report 96/47, DFO.

Anon. 2000a. The English Fishery and Trade in the 18th Century. in *The Heritage Site of Newfoundland and Labrador*, Memorial University of Newfoundland. (<http://www.heritage.nf.ca/exploration/18fishery.html>).

Anon. 2000b. Northwest Atlantic Harp Seals. Stock Status Report E1-01, DFO Science, Ottawa.

Anon. 2001a. Walrus (*Odobenus rosmarus*). in Seal Conservation Society webpage (<http://www.pinnipeds.fsnet.co.uk/species/walrus.htm>).

Anon. 2001b. Report Of The Joint ICES/NAFO Working Group On Harp And Hooded Seals. ICES CM 2001/ACFM:08.

Beattie, A. I. 2001. A New Model for Evaluating the Optimal Size, Placement and Configuration of Marine Protected Areas. Unpublished Master's thesis. University of British Columbia.

Beverton, R.J.H. and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. Pages 142-180 in Wolstenholme, G.E.W. and O'Connor, M. (eds.) *CIBA Foundation colloquia on ageing: the lifespan of animals*. Volume 5. J & A Churchill Ltd, London.

Bowering, W. R. 2000. Stock status update of witch flounder in Divisions 2J, 3K and 3L. Scientific Council Report 00/13, NAFO, St. John's NF.

Bowering, W. R. 2001. Trends in distribution, biomass and abundance of Greenland halibut (*Reinhardtius hippoglossoides*) in NAFO Subarea 2, and Divisions 3KLMNO from Canadian Research vessel surveys during 1978-99. Scientific Council Research Document 00/12, NAFO, St. John's NF.

Bowering, W. R. and Nedreaas, K. H. 2001. Age validation and growth of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)): A comparison of populations in the Northwest and Northeast Atlantic. *Sarsia* 86:53-68.

Brenton, C. 1979. Walrus. Pages 55-57 in *Mammals in the seas*. Volume II Pinniped Species Summaries and Report on Sirenians. FAO, Rome.

Bundy, A. 2002. Adaptations of a Newfoundland-Labrador Ecopath model for 1985-1987 in statistical area 2J3KLNO to the area 2J3KL. Pages 13-21 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) *Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf*. Fisheries Centre Research Reports 10(1), 116 pp.

Burke, C., Davoren, G.K., Montevecchi, W.A. and Stenhouse, I.J. 2002. Winging back to the future: An historic reconstruction of seabird diversity, distribution and abundance in the northwest Atlantic, 1500-2000. Pages 27-37 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) *Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf*. Fisheries Centre Research Reports 10(1), 116 pp.

- Bundy, A., Lilly, G.R. and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Canadian Technical Report of Fisheries and Aquatic Sciences 2310, 157 pp.
- Cairns D.K., Montevecchi, W.A. and Threlfall, W. 1989. Researcher's Guide to Newfoundland Seabird Colonies (2nd edition). Occasional Papers in Biology, Memorial University of Newfoundland No. 14.
- Carr, S. M., Kivlichan, D. S., Pepin, P. and Crutcher, D. C. 1999. Molecular systematics of gadid fishes: implications for the biogeographic origins of Pacific species. Canadian Journal of Zoology 77:19-26.
- Carscadden, J. E., Frank, K. T. and Leggett, W. C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Science 58:73-85.
- Casey, J. M. and Myers, R. A. 2001. Community Changes in an Exploited Marine Ecosystem: Newfoundland Southern Grand Bank and St. Pierre Bank, 1951-1995. *in*.
- Christensen, V. and Pauly, D. 1992. A guide to the Ecopath II software system (version 2.1) ICLARM Software 6. 72 pp.
- Clay, D. and Clay, H. 1991. Determination of age and growth of white hake (*Urophycis tenuis* Mitchell) from the southern Gulf of St. Lawrence, Canada (including techniques for commercial sampling). Can. Tech. Rep. Fish. Aquat. Sci. 1828, 29 pp.
- Cushing, D. H. 1988. The Provident Sea. Cambridge University Press, Cambridge.
- DFO. 1996a. Coastal Zone Species Profile Series No. 2 Rock Crab. in DFO Fisheries and Oceans Canada.
- DFO. 1996b. Coastal Zone Species Profile Series No. 3: Toad Crab. in DFO Fisheries and Oceans Canada.
- Dawe, E. G., Hendrickson, L.C. and Showell, M.A. 2000. An update to commercial catch and survey indices for shortfinned squid (*Illex illecebrosus*) in the Northwest Atlantic for 1999. NAFO SCR Doc. 00/37.
- Dommasnes, A., Christensen, V., Ellertsen, B., Kvamme, C., Melle, W., Nøttestad, L., Pedersen, T., Tjelmeland, S. and Zeller, D. 2001. Ecosystem model for the Norwegian and Barents Seas. Pages 213-241 in S. Guénette, S., Christensen, V. and Pauly, D. (eds) Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4).
- Dorel, D. 1985. Poissons de l'Atlantique nord-est relations taille-poids. Institut Français de Recherche pour l'Exploitation de la Mer.
- Dunfield, R. W. 1985. The Atlantic Salmon in the History of North America. Department of Fisheries and Oceans, Ottawa.
- Elvertowsky, J. 1964. Observations sur les poissons du genre *Sebastes* (Campagne océanographique de la 'Thalassa' en Juillet-Août 1962 dans l'Atlantique Nord-Ouest). Rev. Trav. Inst. Pêch. marit. 28(4):427-435.
- Ennis, G. P., Collins, P. W., Badcock, D. and Dawe, E. G. 1997. Review of Newfoundland Lobster Fishery. Research Document 97/126, Canadian Stock Assessment Secretariat, St. John's, Newfoundland.
- FAO. 1978. Mammals in the seas. Volume I: Report on the FAO Advisory Committee on Marine Resources Research. FAO Advisory Committee on Marine Resources Research working Party on Marine Mammals, Rome.
- Froese, R. and Pauly, D. (eds) 2000. FishBase 2000: concepts, Design and Data Sources. ICLARM, Los Baños, Laguna, Philippines, Vol. 76, 344 pp.
- Ganong, W. F. 1904. The walrus in New Brunswick. Bulletin of the Natural History Society of New Brunswick II 5:240-241.
- Garavis, S. 1985. Lumpfish. Underwater World, Department of Fisheries and Oceans, St. John's Newfoundland, 4 pp.
- Grant, R.F. 1934. The Canadian Atlantic Fishery. Ryerson Press, Toronto, 147 pp.
- Gosling, W.G. 1910. Labrador: its discovery, exploration and development. Alston Rivers Ltd., London.
- Grieve, S. 1885. The Great Auk or Garefowl. Jack, London.
- Hammill, M. O. and Stenson, G. B. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fisheries Science 26:1-23.
- Heymans, J.J. 2002. First Nations impact on the Eastern Newfoundland and Southern Labrador ecosystem during pre-contact times. In Pitcher and Haggan (eds) The Restoration of Past Ecosystems as Policy Goals for Fisheries. Fisheries Centre Research Reports (*in press*).
- Hiller, J. K. 2001. The Newfoundland Seal Fishery. in Heritage Site of Newfoundland and Labrador, Memorial University of Newfoundland.
- Howley, J. P. 1915. Drawings by Shanawdithit. The Beothucks or Red Indians: The Aboriginal Inhabitants of Newfoundland. In David Cantwell (www.cs.mun.ca/~david12).
- Hutchings, J. A. and Myers, R. A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: An exploration of historical changes in exploitation, harvesting technology, and management. Pages 39-92 in Arnason, R. and Felt, L. (eds) The North Atlantic Fisheries: Successes, failures and challenges. The Institute of Island Studies, Charlottetown, Prince Edward Island.
- Kadlec, J.A. and Drury, W.H. 1968. Structure of the New England Herring Gull population. Ecology 49: 644-676.
- Kurlansky, M. 1997. Cod: A Biography of the Fish That Changed the World, 1 edition. Alfred A. Knopf, Toronto.
- Lear, W. H. 1998. History of Fisheries in the Northwest Atlantic: The 500-Year Perspective. Journal of Northwest Atlantic Fisheries Science 23:41-73.
- Lilly, G. R. 2002. Swept area biomass estimates and diets of fish on the Newfoundland Shelf (NAFO Div. 2J3KLNO): inputs for bulk (Ecopath) modelling of the mid-1980s and late 1990s. Canadian Technical Report of Fisheries and Aquatic Sciences (in prep.)
- Lilly, G. R., Hop, H., Stansbury, D. E. and Bishop, C. A. 1994. Distribution and abundance of polar cod

- (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. ICES CM O6:1-21.
- Loring, S.G. 1992. Princes and princesses of ragged fame: Innu archaeology and ethnohistory in Labrador, Ph.D. thesis, Department of Anthropology, University of Massachusetts, 607 pp.
- Lovrich, G. A. and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *Journal of Experimental Marine Biology and Ecology* 211:225-245.
- Lowry, L. F. and Fay, F. H. 1984. Seal eating by walrus in the Bering and Chukchi Seas. *Polar Biology* 3:11-18.
- Mari, A. and Dominguez, R. 1979. Distribucion, edad y crecimiento de la merluza plateada (*Merluccius bilinearis*) en la plataforma de Nueva Escocia. *Rev. Cub. Inv. Pesq.* 4:78-106.
- Marshall, I. 1996. A History and Ethnography of the Beothuk, First edition. McGill-Queen's University Press, Montreal.
- Masters, D.C. 1969. Reciprocity, 1846-1911. Historical Booklet No. 12, The Canadian Historical Association, Ottawa.
- Mercer, M. C. 1967. Records of the Atlantic Walrus, *Odobenus rosmarus rosmarus*, from Newfoundland. *Journal of the Fisheries Research Board of Canada* 24:2631-2635.
- Montevicchi, W. A. and Tuck, L. M. 1987. Newfoundland Birds: Exploitation, study, conservation. Nuttall Ornithological Club, Cambridge, Massachusetts.
- Montevicchi, W. A. and Kirk, D. A. 1996. Great Auk (*Pinguinus impennis*). Pages 1-20 in Poole, A. and Gill, F. (eds) *The Birds of North America. The American Ornithologists' Union and The Academy of Natural Sciences*, Philadelphia, PA.
- Morgan, M. J., Brodie, W. B. and Kulka, D. W. 2000. The collapse of 2+3K American plaice: was it overfishing? Research Document 2000/131, DFO, Canadian Science Advisory Secretariat.
- Mowat, F. 1965. *West Viking*. Boston, Little Brown. 245 pp.
- Mowat, F. 1984. *Sea of Slaughter*. Seal Books, McClelland and Stewart Limited, Toronto. 438 pp.
- Myers, R. A. 2001. Testing ecological models: The influence of catch rates on settlement of fishermen in Newfoundland from 1710 to 1833. *International Journal of Maritime History*.
- Nammack, M.J., Musick, J.A. and Colvocoresses, J.A. 1985. Life history of spiny dogfish off the northeastern United States. *Trans. Am. Fish. Soc.* 114:367-376.
- Nettleship, D. N. and Birkhead, T. R. 1985. *The Atlantic Alcidae*. Academic Press, New York.
- Palomares, M. L. D. and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine Freshwater Research* 49: 447-453.
- Parsons, D. G., Veitch, P. J., Orr, D. and Evans, G. T. 2000. Assessment of northern shrimp (*Pandalus borealis*) off Baffin Island, Labrador and northeastern Newfoundland. Research Document 2000/069, Canadian Stock Assessment Secretariat, Ottawa.
- Pastore, R.T. 1997. The Beothuk. in *Heritage Site of Newfoundland and Labrador*, Memorial University of Newfoundland.
- Pastore, R. T. 1998. The Beothuk Culture. in *Heritage Site of Newfoundland and Labrador*, Memorial University of Newfoundland.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39: 175-192
- Pauly, D., Soriano-Bartz, M.L. and Palomares, M.L.D. 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. Pages 1-13 in Pauly, D. and Christensen, V. (eds) *Trophic Models Of Aquatic Ecosystems*. ICLARM conference proceedings 26: 390 pp.
- Pitcher, T. J. 2002. Rebuilding ecosystems as a new goal for fisheries Management: Reconstructing the past to salvage the future. *Ecological Applications* 11: (In Press).
- Pitt, T. K. 1970. Distribution, Abundance, and Spawning of Yellowtail Flounder, *Limanda ferruginea*, in the Newfoundland Area of the Northwest Atlantic. *Journal of the Fisheries Research Board of Canada* 27:2261-2271.
- Pitt, T.K. 1975. Changes in the abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides plattessoides*. *J. Fish. Res. Board Can.* 32(8):1383-1398.
- Prowse, D.W. 1972. *A history of Newfoundland*. Mika Studio Belleville, originally published by MacMillan and Co. London, 1895.
- Reeks, H. 1871. Notes on the Zoology of Newfoundland. *The Zoologist Series* 2 6:2540-2557.
- Reeves, R. R., Breiwick, J. M. and Mitchell, E. 1999. History of Whaling and Estimated Kill of Right Whales, *Balaena glacialis*, in the Northeastern United States, 1620-1924. *Marine Fisheries Review* 61:1-36.
- Regier, H. A. and McCracken, F. D. 1975. Science for Canada's shelf-seas fisheries. *Journal of the Fisheries Research Board of Canada* 32:1887-1932.
- Rostlund, E. 1952. *Freshwater fish and fishing in native North America*. (U of California Publications in Geography, Vol. 9) U California Press, Berkeley.
- Ryan, S. 1994. *The Ice Hunters: A history of Newfoundland Sealing to 1914*. Breakwater, St. John's NF.
- Sanger, C. W. 1998. Seal Fishery: Hunting Methods. *in* *Heritage Site of Newfoundland and Labrador*, Memorial University of Newfoundland.
- Sanger, C. W., Dickinson, A. B. and Handcock, W. G. 1998. Commercial Whaling in Newfoundland and Labrador in the 20th Century. in *The Heritage Site of Newfoundland and Labrador*, Memorial University of Newfoundland.
- Sissenwine, M. P. 1987. Fish and squid production. Pages 347-350 in Backus, R.H. and Bourne, D.W. (eds) *Georges Bank*. MIT Press, Cambridge, Mass.
- Stenson, G. and Hammill, M. 2002a. Harp seals. Page 40 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) *Information Supporting Past And Present Ecosystem Models Of Northern British*

- Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stenson, G. and Hammill, M. 2002b. Hooded seals. Pages 40-41 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stenson, G., Sjure, B. and Hammill, M. 2002. Whales and Porpoises. Page 39 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Stevenson, S.C. and Baird, J.W. 1988. The fishery for lumpfish (*Cyclopterus lumpus*) in Newfoundland waters. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1595, 26 pp.
- Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A. and Blaber, S. J. M. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science 57:531-547.
- Trites, A., Livingston, P., Mackinson, S., Vasconcellos, M., Springer, A. and Pauly, D. 1999. Ecosystem Change and the Decline of Marine Mammals in the Eastern Bering Sea. Fisheries Centre Research Reports 7(1): 106 pp.
- Tuck, J.A. 1975. Ancient people of Port au Choix. ISER Memorial University of Newfoundland, St. John's.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002a. Workshop notes on seabirds. Page 42 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Heymans, J.J., Pitcher, T. 2002b. Historic reference points for models of past ecosystems in Newfoundland. Pages 7-13 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002c. Workshop notes on small piscivorous pelagic fish. Pages 54-55 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002d. Workshop notes on Greenland Halibut. Pages 45-46 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002e. Workshop notes on Skates. Pages 47-48 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Vasconcellos, M., Power, M., Heymans, J.J. and Pitcher, T. 2002f. Workshop notes on Arctic cod. Page 53 in Pitcher, T., Heymans, J.J. and Vasconcellos, M. (eds) Information Supporting Past And Present Ecosystem Models Of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10(1), 116 pp.
- Walsh, D., Sjure, B. and Stenson, G. B. 2000. Preliminary estimates of Harp Seal by-catch in the Newfoundland Lumpfish Fishery. Research Document 2000/078, Department of Fisheries and Oceans, Ottawa, 16 pp.
- Waring, G.T. 1984. Age, growth, and mortality of the little skate off the northeast coast of the United States. Trans. Am. Fish. Soc. 113: 314-321.
- Winters, G. H., and Dalley, E. L. 1988. Meristic Composition of Sand Lance (*Ammodytes* spp.) in Newfoundland Waters with a Review of Species Designations in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science 45: 516-529.
- Wright, B. S. 1951. A walrus in the Bay of Fundy; the first record. The Canadian Field-Naturalist 65:61-63.
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APPENDICES

APPENDIX A: MODEL GROUPS AND SPECIES — M AND P/B ESTIMATES

The P/B and Q/B ratios of all fish species were calculated by using empirical formulas obtained from Palomares and Pauly (1998). The formula used for M was:

$$\log M = 0.0066 - (0.279 \cdot \log_{10}(L_{00})) + (0.65431 \cdot \log_{10}(k)) + (0.4631 \cdot \log_{10}(T))$$

while the Q/B ratio was estimated from the formula:

$$\log Q/B = 7.964 - 0.204 \log W_{00} - 1.965T' + 0.083A + 0.532h + 0.398d$$

W_{00} was estimated from the length-weight formula $W(g) = a \cdot L^b$ and the values used for the growth parameters k and L_{00} (cm), the temperature T (°C), a and b were obtained from FishBase 2000 (Froese and Pauly 2000) and references therein.

“h” was 1 for herbivores and 0 for all other groups, while “d” was 1 for detritivores and 0 for all other groups. In most instances the M and Q/B estimates of juveniles were assumed to be 1.5 x that of adults and the sex ratio was assumed to be 50:50.

Table A1. M estimated for all fish compartments.

Species	K	L ₀₀ (cm)	T (°C)	Adult M	Juvenile M	FishBase Ref
Cod	0.07	176	7	0.1037	0.155	934
American plaice (3L)	0.067	72.5	2	0.0723		
American plaice (3N)	0.099	72.90	2	0.0931		
American plaice				0.0827	0.123	
Greenland halibut	0.024	271.82	2	0.0255		(Bowering and Nedreaas 2001)
Greenland halibut	0.032	253.71	2	0.0314		
Greenland halibut	0.03	206.67	2	0.0319		
Greenland halibut	0.027	264.72	2	0.0278		
Greenland halibut	0.026	256.09	2	0.0274		
Greenland halibut	0.025	268.81	2	0.0263		
Greenland halibut	0.022	293.44	2	0.0236		
Greenland halibut	0.024	268.64	2	0.0256		
Greenland halibut	0.021	284.63	2	0.0231		
Greenland halibut	0.023	280.52	2	0.0246		
Greenland halibut	0.024	249.05	2	0.0262		
Greenland halibut	0.022	278.21	2	0.0240		
Greenland halibut				0.0264	0.0397	
Yellowtail flounder	0.335	50	4	0.3167		1801
Witch flounder	0.2	43.7	4	0.2346		3992
Winter flounder	0.4	44	2	0.2674		1726
Little skate	0.35	52.7	2	0.2330		
Spiny dogfish	0.106	101	7	0.1589		
Redfish female	0.058	52.5	2	0.0719		
Redfish male	0.151	32.7	2	0.1535		
Average redfish		42.6		0.1127		
Mackerel	0.36	42.9	10	0.5296		1212
Silver hake	0.28	62.2	2	0.1922		5841
White hake female	0.106	136	2	0.0818		8900
White hake male	0.218	84	2	0.1501		8900
Atlantic halibut female	0.02	250	2	0.0232		1103
Atlantic halibut male	0.04	170	2	0.0406		1103
Cusk	0.08	89	2	0.0766		27397
Pollock	0.1	111	4.4	0.1201		5760
Average Benthopelagic piscivores				0.0978	0.1457	
Haddock	0.28	73	7	0.3284		953
Red hake	0.19	60.2	10	0.3172		5760
Atlantic wolffish	0.098	150	3	0.091	0.137	731
Northern wolffish male	0.044	167	3	0.052	0.079	731
Northern wolffish female	0.043	158	3	0.052	0.079	731
Spotted wolffish	0.061	181	3	0.064	0.095	731
Female round-nose grenadier	0.099	110	8	0.1578		312
Male round-nose grenadier	0.082	105	8	0.1413		312
Ocean pout	0.076	91	10	0.1552		1362
American eel	0.13	155.3	10	0.1899		
Average demersals				0.1550	0.2324	

Goat sculpin female	0.358	32.3	8	0.5151	865
Goat sculpin male	0.758	19.6	8	0.9673	865
Longhorn sculpin	0.72	30	8	0.8305	869
Arctic staghorn sculpin male	0.383	14	5.4	0.5666	33314
Arctic staghorn sculpin female	0.338	11	5.4	0.5585	33314
Fourbeard rockling	0.2	36	8	0.3414	27396
Snake blenny	0.205	47.6	2	0.1689	1282
Average small demersals				0.5640	
Lumpfish	0.12	55	2	0.1143	872
Greenland cod	0.19	79.5	1	0.1010	
Salmon	0.13	38.9	10	0.2795	7479
Capelin male	0.48	20	5	0.5738	1080
Capelin female	0.48	19	5	0.5820	1080
Average capelin				0.5779	
Arctic cod	0.67	22	3.3	0.5733	796
Herring	0.33	33.5	9	0.5105	5871
Bluefin tuna	0.12	313	10	0.1482	5795
Swordfish	0.23	365	10	0.2174	7174
Transient pelagics				0.1828	
American butterfish	0.8	18.3	10	1.1326	12001
American shad	0.13	78.5	10	0.2298	
Alewife female	0.47	19.9	10	0.7812	4513
Alewife male	0.484	19.4	10	0.8020	4586
Greater argentine	0.12	50.7	10	0.2463	737
Small pelagics				0.6384	
Glacier lanternfish	0.36	8.5	4	0.5442	1058
Small-fin lanternfish	3.65	3.3	4	3.2260	4882
Spotted lanternfish	0.32	9	4	0.4959	1062
Jewel lanternfish		31.5	4		
Mesopelagics				1.4220	

Table A2. Calculations of Q/B for all fish compartments.

Species	L _∞	a	b	Temp. (Kelvin)	W _∞ (g)	h	d	Aspect ratio	Q/B	Juvenile Q/B	FishBase reference
Cod	176.00	0.0068	3.1010	3.5695	62494	0	0	0.8	1.0913	1.6370	
American plaice (3L)	72.50	0.0011	3.3450	3.6344	1854	0	0	1.3	1.8350		
American plaice (3N)	72.90	0.0044	3.2040	3.6344	4089	0	0	1.3	1.5616		
American Plaice									1.6983	2.5474	
Greenland halibut male	284.63	0.0039	3.2060	3.6344	143712	0	0	1.3	1.2084		
Greenland halibut female	280.52	0.0025	3.3280	3.6344	16312	0	0	1.3	1.1776		
Greenland halibut	264.69								1.1930	1.7895	
Yellowtail flounder	50.00			3.5952				0.7	3.2710		
Witch flounder	43.70	0.0017	3.3900	3.6082	619	0	0	0.7	2.3045		268
Winter flounder	44.00	0.0213	3.0000	3.6344	1814	0	0	0.7	1.6436		6323
Little skate	52.70	0.0078	2.9720	3.6344	1020	0	0	0.5	1.7789		2753
Spiny dogfish	101.00			3.5695	4156	0	0	1.6	2.2105		
Redfish	42.60	0.0115	3.1370	3.6610	1486	0	0	1.3	1.7019		268
Mackerel	42.90	0.0046	3.1800	3.5317	716	0	0	4	5.9404		
Silver hake	62.20	0.0107	3.0090	3.6344	2672	0	0	0.9	1.5778		12286
White hake female	136.00	0.0043	3.1470	3.6344	22373	0	0	0.9	1.0228		8900
White hake male	84.00	0.0040	3.1720	3.6344	5080	0	0	0.9	1.3840		8900
Atlantic halibut female	250.00	0.0276	2.9530	3.6344	332680	0	0	0.9	0.5897		1105
Atlantic halibut male	170.00	0.0130	3.2490	3.6344	229442	0	0	0.9	0.6362		1105
Cusk	89.00	0.0132	3.0000	3.6344	9338	0	0	0.9	1.2224		
Pollock	111.00	0.0077	3.0480	3.6030	13219	0	0	0.9	1.3127		6014
Bentho-pelagic piscivores									1.1065	1.6598	
Haddock	73.00	0.0132	2.9010	3.5695	3358	0	0	0.9	2.0197		6014
Red hake	60.20	0.0125	3.0000	3.5317	2717	0	0	0.9	2.5024		
Atlantic wolffish	150.00	0.0780	2.6150	3.6212	38245	0	0	1	0.9919		719
Northern wolffish	158.00	0.0068	3.6410	3.6212	683305	0	0	1	0.5509		719
Spotted wolffish	181.00	0.0017	3.3990	3.6212	81167	0	0	1	0.8507		719
Roundnose grenadier	110.00	0.7320	2.5870	3.5568	139828	0	0	0.5	0.9261		27581
American eel	155.30	0.0018	3.0350	3.5317	7999	0	0	0.5	1.8599		3989
Large Demersals									1.3859	2.0789	
Goat sculpin female	32.30	0.0126	3.1240	3.5568	653	0	0	1.3	3.2245		
Goat sculpin male	19.60	0.0126	3.1240	3.5568	137	0	0	1.3	4.4333		
Arctic staghorn sculpin male	14.00	0.0057	3.2900	3.5900	34	0	0	1.3	5.0771		33314
Arctic sculpin female	11.00	0.0057	3.2900	3.5900	15	0	0	1.3	5.9691		33314
Fourbeard rockling	36.00	0.0035	3.1060	3.5568	239	0	0	0.9	3.6682		
Small demersals									4.4744		
Lumpfish	55.00	0.0587	2.9390	3.6344	7648	0	0	1.3	1.3743		
Greenland cod	79.50	0.0117	3.0000	3.6476	5879	0	0	0.9	1.2652		7275
Salmon	38.90	0.0116	3.0000	3.5317	683	0	0	2	4.0928		682
Capelin male	20.00	0.0015	3.4100	3.5952	41	0	0	1.3	4.7686		
Capelin female	19.00	0.0022	3.2500	3.5952	32	0	0	1.3	5.0315		
Capelin									4.9001		
Sandlance female	23.20	0.0014	3.0850	3.5952	23	0	0	1.3	5.3728		4667
Sandlance male	23.20	0.0010	3.4910	3.5952	58	0	0	1.3	4.4352		4667
Sandlance									4.9040		
Arctic cod	22.00	0.0054	3.0560	3.6173	68	0	0	0.9	3.6009		33278
Herring	33.50	0.0088	3.0330	3.5442	373	0	0	1.7	4.1310		
Bluefin tuna	313.00	0.0196	3.0090	3.5317	632920	0	0	5.5	1.9826		26805
Swordfish	365.00	0.0027	3.3000	3.5317	773634	0	0	5.8	2.0154		11991
Transient pelagics									1.9990		
American butterfish	18.30	0.0056	3.2600	3.5317	73	0	0	1.9	6.3344		12035
American shad	78.50	0.0065	2.9590	3.5317	2629	0	0	1.9	3.0498		3762
Alewife female	19.90	0.0076	3.0100	3.5317	62	0	0	2.1	6.8158		4513
Alewife male	19.40	0.0126	2.9100	3.5317	70	0	0	2.1	6.6305		4513
Greater argentine	50.70	0.0039	3.2030	3.5317	1128	0	0	1.9	3.6246		
Small pelagics									5.2910		
Spotted lanternfish	9.00	0.0080	3.0000	3.6082	6	0	0	1	6.3145		
Jewel lanternfish	31.50	0.0051	2.9800	3.6082	149	0	0	1	3.2642		26178
Mesopelagics									4.7894		

APPENDIX B: EXPORTS OF SALMON FROM NEWFOUNDLAND

Export of salmon from Newfoundland. A tierce contained 214 kg round weight, a barrel 143 kg, there was a 48% weight loss for a packages (from Dunfield 1985).

Year	# tierces	barrels	Packages	cwt.	Weight (t)	Export (kg·km ² ·yr ⁻¹)
1801	1688				362	0.731
1802						
1803	3709				795	1.606
1804	3739				801	1.619
1805	1916				411	0.829
1806	2040				437	0.883
1807	3469				743	1.502
1808	3272				701	1.417
1809	4064				871	1.759
1810	5747				1232	2.488
1811	2694				577	1.166
1812	3831				821	1.659
1813	3737				801	1.618
1814	3425				734	1.483
1815	2752				590	1.191
1816	2659				570	1.151
1817	2858				612	1.237
1818	1663				356	0.72
1819	2125				455	0.92
1820	1808				387	0.783
1821	1916				411	0.829
1822	2650				568	1.147
1823	2257				484	0.977
1824	2546				546	1.102
1825	3127				670	1.354
1826	3204				687	1.387
1827	2889				619	1.251
1828	2330.5				499	1.009
1829	2795				599	1.21
1830	4322				926	1.871
1831	3710				795	1.606
1832	3302.5				708	1.43
1833	2901				622	1.256
1834	2625				563	1.136
1835	2477				531	1.072
1836	2130				456	0.922
1837	2262				485	0.979
1838	4408				945	1.908
1839	2922				626	1.265
1840	3396				728	1.47
1841	3642				780	1.577
1842	4715				1010	2.041
1843	4058				870	1.757
1844	3753				804	1.625
1845	3545				760	1.535
1846		5201			743	1.501
1847		4917			702	1.419
1848		3822			546	1.103
1849		5911			844	1.706
1850	1933	1700			657	1.327
1851	2965	1613	18		867	1.751
1852	2899	765			731	1.476
1853	2840	1626	1387		911	1.841
1854	2601	602	167		652	1.317
1855	2481	647	176		633	1.279
1856	1216	1156	190		435	0.88
1857	2486	815	46		652	1.316
1858	2726		109		590	1.191
1859	3716		29		798	1.612
1860	3963			51	849	1.716
1861	2924				627	1.266
1862	4227			14	906	1.83
1863	3179	1767		46	934	1.886
1864	1765	1257		11.5	558	1.127
1865	2418	1598		103	746	1.508
1866	2917	977	873		809	1.634
1867	2472	1867	516		823	1.662
Average						1.37

APPENDIX C: BALANCED MODEL AND DIET MATRIX 1900-1905

Input parameters of the balanced 1900-1905 model (values in bold are estimated by ECOPATH).

Group name	Trophic level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.31	0.000001	0.060	16.846	0.000	0.004
Cetaceans	4.1	0.502	0.100	11.790	0.880	0.008
Grey seals	4.4	0.000001	0.060	15.000	0.281	0.004
Harp Seals	4.13	0.591	0.102	17.412	0.274	0.006
Hooded Seals	4.42	0.102	0.109	13.100	0.169	0.008
Ducks	3	0.000453	0.250	54.750	0.009	0.005
Piscivorous Birds	4.28	0.027	0.250	54.750	0.215	0.005
Planktivorous Birds	3.53	0.006	0.250	54.750	0.009	0.005
Adult Cod > 40cm	3.95	8.162	0.198	1.091	0.535	0.182
Juv Cod ≤ 40 cm	3.63	1.360	0.155	1.637	0.918	0.095
American plaice >35cm	3.45	2.745	0.083	1.698	0.950	0.049
American plaice ≤35cm	3.37	13.849	0.124	2.547	0.950	0.049
Greenland halibut >65cm	4.38	0.929	0.030	1.193	0.548	0.025
Greenland halibut ≤ 65 cm	4.22	0.283	0.040	1.789	0.746	0.022
Yellowtail Flounders	3.12	2.391	0.317	3.271	0.950	0.097
Witch flounder	3.02	7.790	0.235	2.304	0.950	0.102
Winter flounder	3.08	0.191	0.267	1.644	0.950	0.163
Skates	4.23	0.469	0.233	1.779	0.800	0.131
Dogfish	4	0.078	0.159	2.210	0.950	0.072
Redfish	3.68	20.586	0.113	1.702	0.950	0.066
Transient Mackerel (>29cm)	3.85	0.002	0.530	5.940	0.950	0.089
Large demersal piscivores (> 40 cm)	4.29	1.336	0.098	1.107	0.950	0.088
Large demersal piscivores (≤ 40cm)	3.93	20.007	0.147	1.660	0.950	0.088
Large Demersal Feeders (> 30cm)	3.36	1.958	0.155	1.386	0.950	0.112
Small demersal feeders	3.28	20.425	0.232	2.079	0.950	0.112
Other small demersals	3.11	7.899	0.564	4.474	0.950	0.126
Lumpfish	3.59	0.586	0.114	1.374	0.950	0.083
Greenland cod	4.04	0.572	0.101	1.265	0.950	0.080
Salmon	4.26	0.034	0.279	4.093	0.950	0.068
Capelin	3.26	16.080	0.578	4.900	0.931	0.118
Sandlance	3.2	22.607	0.981	4.904	0.950	0.200
Arctic cod	3.38	9.228	0.573	3.601	0.950	0.159
Herring	3.29	6.023	0.510	4.131	0.950	0.124
Transient Pelagics	4.08	0.115	0.183	1.999	0.950	0.091
Small Pelagics	3.42	2.006	0.638	5.291	0.950	0.121
Small Mesopelagics	3.38	10.353	1.422	4.789	0.950	0.297
Shortfin squid	3.96	3.315	0.600	4.000	0.950	0.150
Arctic Squid	3.28	8.859	0.500	3.333	0.950	0.150
Large Crabs (>95 cm)	2.92	0.174	0.380	4.420	0.310	0.086
Small Crabs (≤ 95 cm)	3.08	27.270	0.380	4.420	0.950	0.086
Lobster	2.93	0.080	0.380	4.420	0.222	0.086
Shrimp	2.46	14.405	1.450	9.670	0.950	0.150
Echinoderms	2	61.087	0.600	6.670	0.950	0.090
Polychaetes	2	25.228	2.000	6.330	0.950	0.316
Bivalves	2	66.225	0.570	22.220	0.950	0.026
Other benthic invertebrates	2	28.586	2.500	12.500	0.950	0.200
Large zooplankton	2.56	93.738	3.433	13.732	0.950	0.250
Small zooplankton	2	107.043	8.400	28.000	0.950	0.300
Phytoplankton	1	74.873	93.100	-	0.500	-
Detritus	1	546.612	-	-	0.514	-

1900-1905 diet continued...

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	
1																				
2																				
3																				
4																				
5																				
6																				
7																				
8																				
9																				
10					0.000			0.001												
11																				
12																				
13																				
14																				
15																				
16																				
17																				
18																				
19																				
20					0.002															
21																				
22																				
23					0.012			0.001												
24																				
25					0.012			0.001												
26					0.011			0.001												
27																				
28					0.001															
29					0.001															
30	0.005		0.011		0.075		0.010	0.011												
31	0.005				0.086			0.292												
32			0.002					0.007												
33					0.115			0.135												
34																				
35					0.115															
36					0.115		0.050	0.067												
37					0.057															
38					0.057		0.040	0.067												
39																				
40										0.001		0.010								
41																				
42					0.012					0.020	0.050	0.020								
43										0.303	0.050	0.300								
44					0.003					0.303	0.100	0.300	0.015							
45										0.120	0.250	0.120								
46					0.100	0.019				0.120	0.150	0.120	0.015							
47	0.439	0.35	0.658	0.513	0.295	0.75	0.450	0.418	0.500	0.020	0.200	0.020	0.120						0.05	
48	0.551	0.65	0.329	0.387	0.013	0.25	0.450		0.500	0.010	0.150	0.010	0.240						0.48	
49													0.085						0.37	1.0
50										0.103	0.050	0.100	0.525	1.0	1.0	1.0	1.0	0.10		

APPENDIX D: BALANCED MODEL AND DIET MATRIX 1450

Input parameters of the balanced 1450 model (values in bold are estimated by ECOPATH).

Group name	Trophic level	Biomass	P/B	Q/B	EE	P/Q
Walrus	3.310	0.246	0.060	16.846	0.001	0.004
Cetaceans	4.070	0.533	0.050	9.000	0.150	0.006
Grey seals	4.380	0.078	0.060	15.000	0.890	0.004
Harp Seals	4.130	1.313	0.102	17.412	0.032	0.006
Hooded Seals	4.360	0.263	0.109	13.100	0.145	0.008
Ducks	3.000	0.008	0.250	54.750	0.001	0.005
Piscivorous Birds	4.310	0.448	0.250	54.750	0.028	0.005
Planktivorous Birds	3.530	0.097	0.250	54.750	0.001	0.005
Adult Cod > 40cm	3.940	8.162	0.104	1.091	0.441	0.095
Juv Cod ≤ 40 cm	3.630	1.452	0.155	1.637	0.657	0.095
American plaice >35cm	3.450	6.207	0.083	1.698	0.950	0.049
American plaice ≤35cm	3.360	14.501	0.124	2.547	0.950	0.049
Greenland halibut >65cm	4.310	0.929	0.026	1.193	0.649	0.022
Greenland halibut ≤ 65 cm	4.220	0.283	0.040	1.789	0.911	0.022
Yellowtail Flounders	3.120	6.729	0.317	3.271	0.950	0.097
Witch flounder	3.020	8.277	0.235	2.304	0.950	0.102
Winter flounder	3.080	4.771	0.267	1.644	0.950	0.163
Skates	4.230	0.441	0.233	1.779	0.950	0.131
Dogfish	4.000	0.054	0.159	2.210	0.950	0.072
Redfish	3.680	13.864	0.113	1.702	0.950	0.066
Transient Mackerel (>29cm)	3.850	0.107	0.530	5.940	0.950	0.089
Large demersal piscivores (> 40 cm)	4.280	1.134	0.098	1.107	0.950	0.088
Large demersal piscivores (≤ 40cm)	3.890	20.017	0.147	1.660	0.950	0.088
Large Demersal Feeders (> 30cm)	3.360	3.335	0.155	1.386	0.950	0.112
Small demersal feeders	3.260	23.046	0.232	2.079	0.950	0.112
Other small demersals	3.090	15.148	0.564	4.474	0.950	0.126
Lumpfish	3.590	4.796	0.114	1.374	0.950	0.083
Greenland cod	3.910	5.618	0.101	1.265	0.950	0.080
Salmon	4.260	0.448	0.279	4.093	0.950	0.068
Capelin	3.260	18.812	0.578	4.900	0.887	0.118
Sandlance	3.200	41.176	0.981	4.904	0.950	0.200
Arctic cod	3.370	31.853	0.573	3.601	0.950	0.159
Herring	3.290	13.951	0.510	4.131	0.950	0.124
Transient Pelagics	4.030	0.645	0.183	1.999	0.950	0.091
Small Pelagics	3.420	3.787	0.638	5.291	0.950	0.121
Small Mesopelagics	3.380	11.051	1.422	4.789	0.950	0.297
Shortfin squid	3.960	5.571	0.600	4.000	0.950	0.150
Arctic Squid	3.280	13.766	0.500	3.333	0.950	0.150
Large Crabs (>95 cm)	2.920	0.174	0.380	4.420	0.680	0.086
Small Crabs (≤ 95 cm)	3.080	25.839	0.380	4.420	0.950	0.086
Lobster	2.930	10.297	0.380	4.420	0.950	0.086
Shrimp	2.460	18.796	1.450	9.670	0.950	0.150
Echinoderms	2.000	103.215	0.600	6.670	0.950	0.090
Polychaetes	2.000	40.733	2.000	6.330	0.950	0.316
Bivalves	2.000	82.387	0.570	22.220	0.950	0.026
Other benthic invertebrates	2.000	44.746	2.500	12.500	0.950	0.200
Large zooplankton	2.560	148.956	3.433	13.732	0.950	0.250
Small zooplankton	2.000	168.784	8.400	28.000	0.950	0.300
Phytoplankton	1.000	118.114	93.100	-	0.500	-
Detritus	1.000	725.759	-	-	0.461	-

1450 diet continued...

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
1																	
2																	
3																	
4																	
5																	
6																	
7																	
8																	
9																	
10					0			0									
11																	
12																	
13																	
14																	
15																	
16																	
17																	
18																	
19																	
20					0.002												
21																	
22																	
23					0.012			0.001									
24																	
25					0.012			0.001									
26					0.011			0.001									
27																	
28					0.001												
29					0.01												
30	0.005		0.001		0.075		0.001	0.011									
31	0.005				0.086			0.293									
32			0.002					0.007									
33					0.115			0.135									
34																	
35					0.115												
36					0.115		0.05	0.067									
37																	
38					0.057		0.04	0.067									
39					0.01												
40										0.001		0.01					
41																	
42					0.012					0.02	0.05	0.02					
43										0.303	0.05	0.3					
44					0.003					0.303	0.1	0.3	0.015				
45										0.12	0.25	0.12					
46				0.1	0.019					0.12	0.15	0.12	0.015				
47	0.439	0.35	0.665	0.513	0.295	0.75	0.454	0.418	0.5	0.02	0.2	0.02	0.12				
48	0.551	0.65	0.332	0.387	0.013	0.25	0.454		0.5	0.01	0.15	0.01	0.24				
49													0.085				
50										0.103	0.05	0.1	0.525	1	1	1	1