Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2000–2002)

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ABSTRACT

Savenkoff, C., M. Castonguay, R. Méthot, D. Chabot, and M. O. Hammill. 2005. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2000–2002). Can. Tech. Rep. Fish. Aquat. Sci. 2588: v+91 pp.

Mass-balance models were used to reconstruct trophic flows through the whole northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS) for the 2000–2002 period. The whole-system model of the northern Gulf of St. Lawrence is divided into 31 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of pelagic, demersal, and benthic domains. We present here details of the input data (biomass, production, consumption, export, and diet composition) for each compartment used for modelling. The parameter estimates from inverse modelling are also shown for comparisons. The successful development of ecosystem models will provide powerful new tools to evaluate the impact of human and environmental factors on marine ecosystems.

RÉSUMÉ

Savenkoff, C., M. Castonguay, R. Méthot, D. Chabot, and M. O. Hammill. 2005. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2000–2002). Can. Tech. Rep. Fish. Aquat. Sci. 2588: v+91 pp.

Des modèles d'équilibre de masse ont été utilisés pour représenter les flux trophiques de l'écosystème complet du nord du Golfe du Saint-Laurent (divisions 4RS de l'OPANO) pour la période 2000–2002. L'écosystème du nord du Golfe du Saint-Laurent a été divisé en 31 groupes ou compartiments trophiques depuis le phytoplancton et les détritus jusqu'aux oiseaux et mammifères marins incluant les espèces commerciales des domaines pélagique, démersal et benthique. Nous présentons ici le détail des données (biomasse, production, consommation, export et composition alimentaire) pour chaque groupe utilisé pour les modélisations. Les paramètres estimés par la modélisation inverse sont également montrés pour comparaisons. Le succès de l'élaboration des modèles écosystémiques apportera de nouveaux outils scientifiques puissants pour évaluer l'impact des facteurs humains et environnementaux sur les écosystèmes marins.

INTRODUCTION

In the early 1990s, the abundance of many northwest Atlantic cod (*Gadus morhua*) populations declined to low levels resulting in the cessation of directed fishing for these stocks, thus ending one of the largest and longest running commercial groundfish fisheries in the world (CAFSAC 1994). Ten years later, few stocks show signs of recovery. The reasons for the failure of these stocks to recover are not well understood (DFO 2003a).

Mass-balance models using inverse methodology have been constructed for the northern Gulf of St. Lawrence ecosystem (Savenkoff et al. 2004a; Savenkoff et al. submitted[1]) before and after the collapse of groundfish stocks (hereafter termed mid-1980s and mid-1990s, respectively), in an attempt to understand the ecosystem changes that may explain the failure of these stocks to recover in the 1990s.

Savenkoff et al. (submitted) showed that the ecosystem structure shifted dramatically from one previously dominated by piscivorous groundfish to one now dominated by small-bodied pelagic species and marine mammals. Predation by marine mammals increased from 21 to 53% of the total mortality while predation by fish decreased from 49 to 28%. Due to the drastic decline in the biomass of large cod (from 3.93 to 0.27 t km^{-2}), seals replaced large cod as the main predators in the northern Gulf during the mid-1990s (Savenkoff et al. submitted).

These changes were accompanied by a decrease in total catches and a transition in catches from long-lived piscivorous groundfish toward planktivorous pelagic fish in the northern Gulf (Savenkoff et al. submitted). Total catches in the northern Gulf decreased by a factor of four from the mid-1980s (1.83 ± 0.07 t km^{-2} yr^{-1}) to the mid-1990s (0.47 ± 0.04 t km^{-2} yr^{-1}). Reported cod catches accounted for 51% of the total fishery in the northern Gulf during the mid-1980s while forage fish and invertebrates represented only 26% of total catches. During the mid-1990s, forage fish and invertebrates represented 90% of the total catches while cod accounted for 1% only. Results from ecosystem modelling suggest that overfishing during the mid-1980s also caused major changes in the structure and functioning of the Gulf ecosystems over the last two decades.

This report presents the data and input parameters used to construct inverse models of the northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS; Figure 1) during the 2000–2002 period. Inverse modelling was useful to obtain a first balanced solution using an objective least-squares criterion. Throughout the modelling process, different approaches (comparisons of different flow networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data as well as to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. The final solution obtained was the mean of 31 balanced random perturbations (including a response without perturbation). The estimates from inverse modelling are also shown for comparisons.

[1]: Savenkoff, C., M. Castonguay, D. Chabot, H. Bourdages, L. Morissette, and M.O. Hammill. Effects of fishing and predation in a heavily exploited ecosystem: Comparing mid-1980s, mid-1990s, and early 2000s in the northern Gulf of St. Lawrence (Canada). Submitted to Marine Ecology Progress Series.

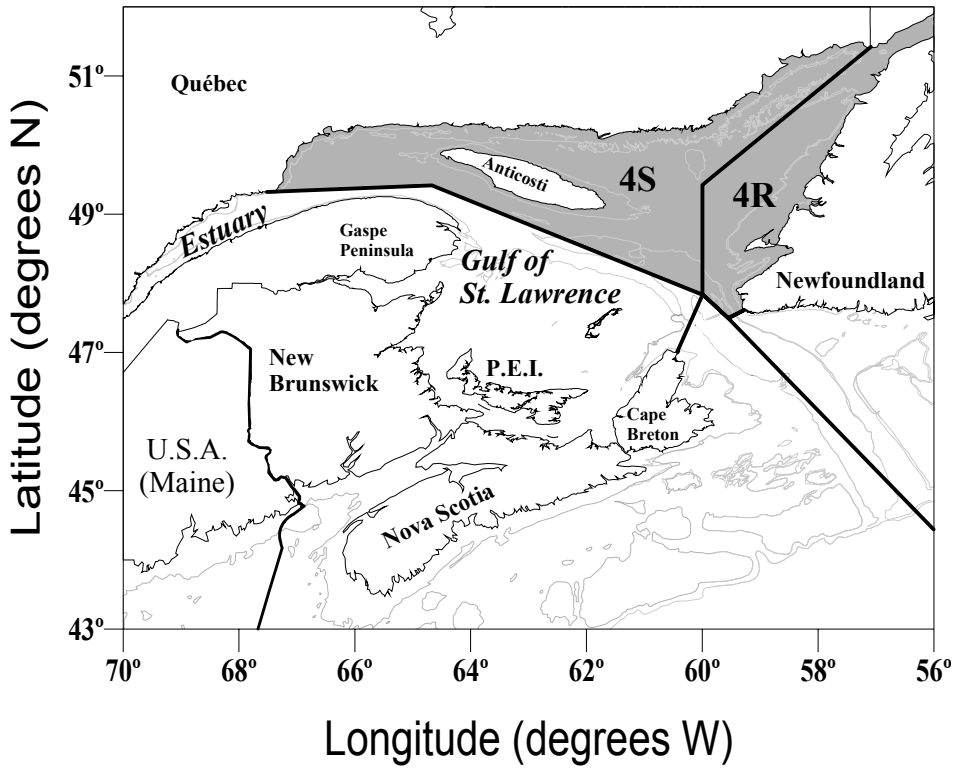

Figure 1. Northern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS), equivalent to a total area of 103,812 km^2.

MATERIAL AND METHODS

Model structure

Inverse methods are mathematical techniques used to generate a "snapshot" of the system at one time. They use mass-balance principles and an objective least-square criterion to estimate flows of organic matter or energy among trophic groups of an ecosystem (Savenkoff et al. 2004a). These models, as opposed to traditional approaches, consider the ecosystem as a whole rather than its components separately and thus provide a description of trophic interactions between all functional groups of the ecosystem. The inverse approach solves flow networks by finding the solution that minimizes both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors (thus minimizing the imbalances between inputs and outputs) consistent with the constraints. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data and straightforward mass balance and metabolic constraints. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques although the details can be inaccurate (Vézina and Pahlow 2003). The inverse methodology is also able to generate alternative scenarios (or solutions) that explain the input data.

Under the steady-state assumption, consumption representing the input must balance the sum of the outputs consisting of production, respiration, and egestion (flux of unassimilated food: feces or detrital flow) for individual compartments. In these models, we assumed that there was no year-to-year change in biomass during the studied time period and that net migration was zero (migration out of or into the study area, food intake by predators that are not part of the system, etc.). Thus, production was simply the biomass lost to fishing mortality (catches), predation, and natural mortality other than predation (disease, other natural causes of death, and unexplained mortality [unsuspected processes occurring in the ecosystem]; hereafter termed "other mortality"). The general mass-balance equation for individual compartments can be written as:

(1) Consumption – egestion – respiration – fishing mortality – predation – other mortality = $0 + \boldsymbol{\varepsilon}$

The equations calculated for this study were not "absolutely" balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero. We refer to these differences as residuals, which are represented by the error term $\boldsymbol{\varepsilon}$. Inverse modelling can thus find a solution that is not necessarily balanced (not in steady state).

For phytoplankton and detritus, the general mass-balance equation was simplified. For the phytoplankton group, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus is assumed to respire.

With the compartmental mass-balance equations, the general structure of an inverse model also includes data equations and constraints. The data equations attempt to fix the value of certain flows or combinations of flows (e.g., incorporate the observations into the model that coincide

with the period/region for which a solution was tested) while the constraints incorporate general knowledge into the model. The input data introduced directly into the model as data equations included values for exports (catches) from the system, production, and diet proportions locally estimated from field studies. Data equations are also used for diet proportions available only as point estimates (no variance estimate) or with low observed values (i.e., <0.5%) and low uncertainty (i.e., SD < 0.6%). The system of equations above was strongly underdetermined, so additional constraints (other conditions that reflect our prior knowledge of this system) were added to obtain a meaningful solution. Each flow was taken to be non-negative, and the flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements. Gross growth efficiency (GE) is the ratio of production to consumption and for most groups should have values between 10 and 30% (Christensen and Pauly 1992). Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast-growing fish larvae or nauplii or bacteria, which can have higher GE (between 25 and 50%) (Christensen and Pauly 1992). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while the non-assimilated food (20%, consisting of urine and feces) was directed to the detritus. For herbivores, the proportion not assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992). We constrained the assimilation efficiency (AE) to fall between 70 and 90% for all groups except for large and small zooplankton (between 50 and 90%).

Certain flows have a minimal and maximal value imposed (export for detritus, production, consumption, diet composition, etc.). The production and consumption values that were not estimated from local field studies were incorporated as constraints. The other diet proportions with higher values (i.e., >0.5%) were also specified as constraints. To facilitate comparisons with Ecopath models, we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is either passed up the food web or exported. These values should be between 0 and 0.95 (Christensen and Pauly 1992, 1998). Here, a value only slightly above zero indicates that the group is not consumed in noticeable amounts by any other group in the system (e.g., top predators). Conversely, a value near or equal to 0.95 indicates that the group is heavily preyed upon and/or highly exploited by a fishery, leaving no individuals to die of other causes (e.g., small prey organisms).

We perturbed the data within their uncertainty range and the unconstrained part of the solution could move within the a priori bounds. By randomly perturbing data inputs, we constructed a set of balanced solutions and we used the mean of these 31 random perturbations (including a response without perturbation).

Study area

The study covers an area of the northern Gulf of St. Lawrence (NAFO divisions 4RS), equivalent to 103,812 km^2 (Fig. 1). The nearshore region (depths < 37 m) was not included in the model. Infra-littoral species such as American lobster (*Homarus americanus*) were not included in this study. This zone was excluded from the model because exchanges between infra-littoral and pelagic zones are still poorly understood. The official sampling area used in our models for the calculation of densities represents the surface of strata sampled during the summer scientific

survey in the northern Gulf of St. Lawrence. The period covered by this analysis was from 2000 to 2002.

Functional groups

Based on data availability and the ecological and commercial significance of the species, the trophic food web is depicted by a number of compartments or functional groups representing the main pelagic, demersal, and benthic species present, which are interconnected by mass flows of matter. The whole-system model of the northern Gulf of St. Lawrence was divided into 31 functional groups or compartments (Table 1). We distinguished four marine mammal groups, one seabird group, fourteen fish groups, ten invertebrate groups, one phytoplankton group, and one detritus group (Table 1). Some groups such as large pelagic feeders and large demersal feeders are composite groups, where the species were aggregated on the basis of similarity in size and ecological role. Cod and Greenland halibut were each separated into two groups based on diet, age/size at first capture, and age/size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but for this model it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of data, we could not distinguish juveniles and adults for other fish species. For the early 2000s, shrimp and crabs were also each separated into two groups. Based on age/size at first capture (22 mm), shrimp were separated into large shrimp, mainly females (≥ 22 mm), which are recruited to the fishery, and small shrimp (< 22 mm), which are not recruited to the fishery. Indeed, one important feature in *Pandalus* spp. shrimp life history is protandric hermaphroditism, i.e., born as male and change into female at the age of 4 or 5 years (DFO 2002a). Consequently, females are larger than males and more subject to fishing. Based on important differences in diet and vulnerability to predation (in particular cannibalism; crab prey ranged in size between 3.9-48.8 mm carapace width [CW]), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large crabs (> 45 mm CW) (Lovrich and Sainte-Marie 1997). Only large crabs are recruited to the fishery and consist almost exclusively of male snow crab, *Chionoecetes opilio*.

Collecting the data

All parameter estimations were made within a collaborative framework, in which experts for the various functional groups were consulted. A considerable effort was expended to obtain input data in the study area and during the period of interest. However, information on several groups (e.g., forage species and benthic invertebrates) was sparse or non-existent for the area and period studied and was thus taken for the same area but for other time periods or from the literature for other areas and/or time periods. Based on these different sources of data (local and literature), we estimated the lower and upper limits of each input data used in inverse modelling. This process partly explains the high coefficients of variation for the production, consumption, and diet data (70, 95, and 139%, respectively) as well as those for biomass and export (51 and 44%, respectively).

Biomass

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant for the 2000–2002 period modelled. The biomass of each box of the model was obtained directly or was estimated from similar ecosystems when it was not available for 4RS. This parameter is expressed in biomass per surface unit (i.e., tons wet weight km^{-2}). Biomass was estimated from sequential population analysis or scientific trawl survey data for most groups.

An annual summer trawl survey for groundfish has been conducted since 1990 in the northern Gulf using a URI 81/114 trawl aboard the CCGS *Alfred Needler*. The sampling strategy used consisted of a stratified random sampling following predetermined strata based on depth (Doubleday 1981). Stratified random means were calculated to estimate the biomass in the area using the *PACES* (*Programme d'Analyse des Campagnes d'Échantillonnage Stratifiées*) software (Bourdages 2001). Note that biomass estimates were minimal trawlable biomass values since the survey starts at 20 fathoms and some resources could be not well sampled.

The abundance data based on length frequencies collected during the 2000–2002 period were corrected for catchability. However, information was not available for different species or functional groups. Also, the use of trawl data to estimate biomass of fish species suffers from inherent problems due to variable catchability of the different species considered. Different species have different degrees of catchability by the fishing gear, making the comparison of biomass estimates among species difficult. Thus, different models were assumed to describe them (Table 2). Trawlable biomass estimates were converted to catchability-adjusted biomass based on catchability coefficients estimated by Harley and Myers (2001) and Savenkoff et al. (2004b). Length-specific corrections were applied to numbers-at-length data before they were converted to biomass estimates. In this way, we hope to lessen the impact of catchability on the biomass estimates and render data comparable between species (Table 2).

Biomass estimates for demersal fish and shrimp were based on catches in the annual summer bottom-trawl surveys. Biomass estimates for several other model compartments (cetaceans, seals, seabirds, capelin, herring, mackerel, crabs, zooplankton, and phytoplankton) were based on data from other surveys or population models. In other cases, biomass was based on densities reported for other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates) or was estimated by initial models to meet predator demands (small demersal feeders).

Standard deviations for biomass and catch were based only on the variations in the point estimates for the three years in each period (i.e., error in the estimates themselves was not included in these standard deviations).

Table 1. Functional groups used in modelling for the 2000–2002 period in the northern Gulf of St. Lawrence.

Group Name	Main species
Mysticeti or baleen whales	*Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*
Odontoceti or toothed whales	*Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals and hooded seals	*Phoca groenlandica*, *Cystophora cristata*
Grey seals and harbour seals	*Halichoerus grypus*, *Phoca vitulina*
Seabirds	*Alca torda*, *Cepphus grylle*, *Fratercula arctica*, *Larus argentatus*, *L. delwarensis*, *L. marinus*, *Morus bassanus*, *Oceanodroma leucorhoa*, *Phalacrocorax auritus*, *P. carbo*, *Sterna hirundo*, *S. paradisaea*, *Rissa tridactyla*, *Uria aalge*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Glyptocephalus cynoglossus*, *Limanda ferruginea*, *Paralichthys oblongus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes fasciatus*, *S. mentella*
Large demersal feeders	*Anarhichas* spp., *Centroscyllium fabricii*, *Cyclopterus lumpus*, *Hippoglossus hippoglossus*, *Lophius americanus*, *Melanogrammus aeglefinnus*, *Urophycis tenuis*, *Lycodes* spp., Macrouridae, Zoarcidae
Small demersal feeders	*Argentina* spp., *Emicrotremus* spp., *Macrozoarces americanus*, *Myoxocephalus* spp., *Tautogolabrus adspersus*, Bleniidae, Cottidae, Phjolidae, Zoarcidae, juvenile large demersal feeders
Capelin	*Mallotus villosus* and *Boreogadus saida*

Table 1. Cont.

Group Name	Main species
Large pelagic feeders	*Merluccius bilinearis*, *Pollachius virens*, *Squalus acanthiass*
Piscivorous small pelagic feeders	*Illex illecebrosus*, *Scomber scombrus*, piscivorous myctophids and other mesopelagics, piscivorous juvenile large pelagic feeders
Planktivorous small pelagic feeders	*Clupea harengus harengus*, *Gonatus* spp., *Scomberesox saurus*, planktivorous myctophids and other mesopelagics, planktivorous juvenile large pelagic feeders, *Ammodytes* spp.
Shrimp, females (≥ 22 mm)	*Pandalus borealis*
Shrimp, males (< 22 mm)	*Pandalus borealis*, *P. montagui*
Large crabs (> 45 mm CW)	*Chionoecetes opilio*, other non-commercial species (*Hyas* spp.)
Small crabs (≤ 45 mm CW)	*Chionoecetes opilio*, other non-commercial species (*Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Ophiura robusta*, *Stronglyocentrotus pallidus*
Molluscs	*Cyrtodaria siliqua*, *Mesodesma deauratum*
Polychaetes	*Exogene hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *Chaetoceros* spp., *Fragilariopsis oceanica*, *F. cylindrus*, *Leptocylindrus minimus*, *Thalassiiosira bioculata*, *T. nordenskioldii*, *T. pacifica*, *T. punctigera*, and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, Prymnesiophytes, and mixotrophic *Stombidium* spp.
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

Production

Production is the total amount of tissue produced in the population or community under study during a given time period (Christensen and Pauly 1992). It includes all living matter produced by a group (even if it is finally consumed, fished, or lost to other mortality) during the model period. In the northern Gulf of St. Lawrence model, it was assumed that there was no year-to-year change in biomass over the 2000–2002 time period and that emigration was zero. Thus production in this model is simply the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. P/B is the ratio of production (P) to biomass (B). Absolute production is a flux expressed in biomass per surface unit per year (i.e., t km^{-2} yr^{-1}).

For most model compartments, estimates of production were obtained using the steady-state assumption that production equals total mortality. Direct estimates of total mortality (Z), based on a modified catch curve analysis of the survey data, were available only for large cod (Sinclair 2001) and American plaice (Morin et al. 2001). An estimate of production was then obtained by multiplying biomass by the annual mortality rate A ($A = 1 - e^{-Z}$ with Z, the instantaneous mortality rate according to Ricker [1980]). For most other model compartments, total mortality was estimated as catch plus biomass multiplied by natural mortality. In these cases, a fixed rate of natural mortality was assumed based on life-history considerations, literature reports, or expert opinion. Minimum and maximum values for production were obtained by using ranges of catch and biomass values. In other cases, a range of production estimates was obtained by using a variety of methods to calculate production (seals, capelin, mackerel, herring, and shrimp) or based on a range of reported values for other areas (benthic invertebrates). Only single point estimates of production could be obtained for seabirds.

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1993). Q/B is the ratio of consumption (Q) to biomass (B). Absolute consumption is a flux expressed in biomass per surface area per year (i.e., t km^{-2} yr^{-1}).

Consumption (Q) was estimated for each model compartment by multiplying biomass (B) by Q/B ratios reported in the literature, by dividing production (P) by gross growth efficiency (GE; the ratio of production to consumption) using the ranges in GE given by Christensen and Pauly (1992), or by using a consumption model (seals and seabirds). For each compartment, a range in Q estimates was obtained based on 1) variation in reported Q/B ratios, 2) the range in possible GE, 3) variation in estimated biomass or production (mean ± standard deviation), and/or 4) variation between the estimates obtained using the different methods described above. This range in Q estimates provided the minimum and maximum estimates used as constraints in inverse modelling. Also, we assumed that the fish species would eat at least as much food as their biomass ($Q/B \geq 1$).

Table 2. Catchability factors (Q) used to estimate biomass of fish species from trawl data. L: length in cm.

Species or species group	Catchability coefficient	Associated species
Cod	$Q = \frac{0.949 * \exp(-5.06 + 0.139 * L)}{1 + \exp(-5.06 + 0.139 * L)}$	
Haddock	$Q = \frac{1.59 * \exp(-2.77 + 0.0646 * L)}{1 + \exp(-2.77 + 0.0646 * L)}$	
Demersal gadoids	$Q = \frac{1.04 * \exp(-3.47 + 0.0914 * L)}{1 + \exp(-3.47 + 0.0914 * L)}$	Grenadiers, fourbeard rockling, eelpouts, longfin hake, white hake, large headed fish (L x 1.25; sculpins, lumpfish, wolffish, sea raven), small headed fish (L x 0.75; seasnails, spiny lumpsucker)
Pelagic gadoids	$Q = \frac{0.64 * \exp(-4.58 + 0.0785 * L)}{1 + \exp(-4.58 + 0.0785 * L)}$	Spiny dogfish, silver hake, pollock, redfish (L x 1.25)
Flatfish	$Q = \frac{0.986 * \exp(-4.43 + 0.109 * L)}{1 + \exp(-4.43 + 0.109 * L)}$	Greenland halibut, American plaice, flounders, skates (L x 1.25)

Diet composition

Diet matrices were constructed using field data from the study area whenever possible. However, these data do not exist for some species. For these species, diet data were taken for the same area but for another time period or from the literature for other areas and/or time periods. Using all the available field samples or literature reports, the minimum and maximum values observed for each diet proportion were used as inputs for inverse modelling. Means and standard deviations were calculated either directly from the lower and upper limits when there was no information on numbers of stomachs (mean and SD of the two extreme values) or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given (mean and SD of all the point estimates). In the diet tables, empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts (<0.1%) or that this represented a potential trophic relation between prey and predator in other ecosystems or another period of time (equal to 0%). There was a large number (89 of 357 flows) of such values during the 2000–2002 period.

FishBase

Occasionally, information was not available for some parameters. When this happened we referred to FishBase (Froese and Pauly 2002), which is a biological database developed at the International Centre for Living Aquatic Resources Management (ICLARM) in collaboration with FAO and other organizations. It includes information on fish species and is updated frequently with regards to information such as maximum size, growth parameters, natural mortality, and standardized diet composition (Froese and Pauly 1995).

RESULTS: DATA GATHERING AND SYNTHESIS

In this section, we describe each functional group of the northern Gulf of St. Lawrence ecosystem and give the respective estimates of biomass, production, consumption, and diet composition that are used as inputs for modelling.

Cetacea: mysticeti and odontoceti

Background

The northern Gulf of St. Lawrence is dominated by boreal cetaceans ranging from large and medium-sized mysticetes and odontocetes to small odontocetes such as porpoises and dolphins (Kingsley and Reeves 1998). Minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), long-finned pilot (*Globicephala melas*), and humpback (*Megaptera novaeangliae*) whales are the most abundant species among the large and medium whales. The harbour porpoise (*Phocoena phocoena*) is the most abundant of the small dolphins in the Gulf while white-sided dolphins (*Lagenorhynchus acutus*) and white-beaked dolphins (*Lagenorhynchus albirostris*) also occur in this area (Kingsley and Reeves 1998). The cetacean survey of the Gulf of St. Lawrence (Kingsley and Reeves 1998) covered 221,950 km^2, so we used this inventory area to calculate the parameters for this group instead of the value habitually used for the other groups (the sampling area for divisions 4RS).

Based on diet and body mass, the cetacea were separated into two groups: the mysticeti (baleen whales) and the odontoceti (toothed whales). For the species included in the model, mysticeti mean weights vary between 5.6 (minke whale) and 38.5 t (fin whale) while odontoceti mean weights range between 0.05 and 0.22 t (references are listed on the next page).

Catch

Canada ceased commercial whaling in 1972 and there has been no hunt since that time in 4RS. However, information from a questionnaire survey conducted in 2000 and 2001 in the Gulf (4RST) indicated an annual average incidental catch from fishing gear of 1,030 odontoceti harbour porpoises (Lesage et al. 2003). This is equivalent to a catch of 51.5 tons within a 244,792

km^2 sampling area ($2.10 \times 10^{-4} \pm 9.04 \times 10^{-5}$ t km^{-2} yr^{-1}). The final solution of inverse modelling (hereafter termed "inverse solution") estimated a catch of 2.12×10^{-4} t km^{-2} yr^{-1} for odontoceti.

Biomass

Aerial survey estimates of cetacean abundance in the Gulf of St. Lawrence, not corrected for visibility bias, are available for the summer of 1995 (Kingsley and Reeves 1998). The area of the strata corresponding to the northern Gulf covers 144,468 km^2. The density in this zone is applied to the present study zone. These estimates were adjusted by a factor of 1.09 to account for animals that were potentially visible to the observers but were not seen (Marsh and Sinclair 1989) and by a factor of 2.27 to account for animals missed owing to water turbidity (Marsh and Sinclair 1989). These adjustments resulted in abundance estimates of 297 humpback whales, 990 fin whales, 2,128 minke whales, 3,019 long-finned pilot whales, 21,427 harbour porpoises, 17,419 white-sided dolphins, and 6,532 white-beaked dolphins. Other whales, like blue whales for instance, were present in the survey of the Gulf of St. Lawrence but were seen too infrequently to allow any estimation of their biomass.

Mean body mass taken from the literature was 31 t for humpback whales (averaged from Hay [1985], Martin [1990], and Kenney et al. [1997]); 38.5 t for fin whales, 5.6 t for minke whales, 1.4 t for long-finned pilot whales, and 0.05 t for harbour porpoises (averaged from Lien [1985], Martin [1990], and Kenney et al. [1997]); 0.13 t for white-sided dolphins (Sergeant et al. 1980); and 0.217 t for white-beaked dolphins (Ridgway and Harrison 1999). To calculate biomass, we used a population growth rate of 6.5% for humpback whales (Barlow and Clapham 1997), 6.7% for fin whales (Bundy et al. 2000), 6.7% for minke whales (Bundy et al. 2000), 4.0% for long-finned pilot whales (Waring et al. 1999), 9.0% for harbour porpoises (Caswell et al. 1998), 2.0% for white-sided dolphins (Heise 1997), and 2.0% for white-beaked dolphins (Heise 1997). For harbour porpoises, an annual incidental catch of 608 individuals was also used. Assuming a residence time of 180 days for all whales within the potential area of Kingsley and Reeves (1998) (144,468 km^2), the average annual biomass was 43,084 tons or 0.298 ± 0.132 t km^{-2} for mysticeti and 5,440 tons or 0.038 ± 0.016 t for odontoceti.

Production

Because there is no information on total mortality for cetaceans, production was assumed to be equivalent to the biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality for a combination of cetaceans was estimated to be 0.068 for mysticeti (Tanaka 1990; Ohsumi 1979) and 0.146 for odontoceti (Ohsumi 1979). No catch has been reported for mysticeti while the mean annual catch for odontoceti used was 2.10×10^{-4} t km^{-2} yr^{-1} (Lesage et al. 2003). This resulted in a total annual production of 0.020 ± 0.009 t km^{-2} yr^{-1} (range: 0.011–0.029 t km^{-2} yr^{-1}) for mysticeti and 0.006 ± 0.002 t km^{-2} yr^{-1} (range: 0.003–0.008 t km^{-2} yr^{-1}) for odontoceti. The inverse solution estimated a production of 0.012 t km^{-2} yr^{-1} (P/B of 0.04 yr^{-1}) for mysticeti and 0.003 t km^{-2} yr^{-1} (P/B of 0.09 yr^{-1}) for odontoceti.

Consumption

The daily consumption by cetaceans was calculated using:

(2) $R = 0.1W^{0.8}$

where R is the daily ration for an individual in kg and W is the mean body mass in kg (Trites et al. 1997). Assuming a residence time of 180 days, the annual consumption by species was 0.212 t km^{-2} yr^{-1} for humpback whales, 0.849 t km^{-2} yr^{-1} for fin whales, and 0.390 t km^{-2} yr^{-1} for minke whales. This gives a mean annual consumption of 1.451 ± 0.588 t km^{-2} yr^{-1} (range: 0.863–2.040 t km^{-2} yr^{-1}) for mysticeti. Gross growth efficiency (GE = P/Q) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production (0.020 t km^{-2} yr^{-1}) and the GE limits, we obtained two other consumption values of 2.025 and 20.249 t km^{-2} yr^{-1}. The value based on the lower GE limit (0.1%) was not realistic; i.e., 10-fold the value based on GE limit of 1%. So the resulting consumption range for mysticeti was 0.863 to 2.040 t km^{-2} yr^{-1}. The mean consumption value was 1.451 ± 0.832 t km^{-2} yr^{-1}. The inverse solution estimated a consumption for mysticeti of 1.501 t km^{-2} yr^{-1}, representing a Q/B of 5.033 yr^{-1}.

For odontoceti, assuming a residence time of 180 days, the annual consumption by species was 0.157 t km^{-2} yr^{-1} for long-finned pilot whales, 0.087 t km^{-2} yr^{-1} for harbour porpoises, 0.120 t km^{-2} yr^{-1} for white-sided dolphins, and 0.068 t km^{-2} yr^{-1} for white-beaked dolphins. This gives a mean annual consumption of 0.432 ± 0.148 t km^{-2} yr^{-1} (range: 0.284–0.580 t km^{-2} yr^{-1}) for odontoceti. Gross growth efficiency (GE = P/Q) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production (0.006 t km^{-2} yr^{-1}) and the GE limits, we obtained two other consumption values of 0.569 and 5.688 t km^{-2} yr^{-1}. The value based on the lower GE limit was not realistic, so the resulting consumption range for odontoceti was 0.284 and 0.580 t km^{-2} yr^{-1}. The mean consumption value was 0.432 ± 0.209 t km^{-2} yr^{-1}. The inverse solution estimated a consumption for odontoceti of 0.338 t km^{-2} yr^{-1}, representing a Q/B of 8.964 yr^{-1}.

Diet composition

Unfortunately, there are few quantitative descriptions of diet for cetaceans. Where the literature refers to prey using terms such as “preponderant” or “predominant,” it was assumed that they make up at least 75% of consumption by mass. If other prey were reported, remaining consumption was divided equally among them. Based on the literature, the following diets were used in the analysis:

- Humpback whales: capelin, sand lance, squid, and euphausiids (Mitchell 1973);
- Fin whales: capelin, sand lance, herring, and euphausiids (Mitchell 1975);
- Minke whales: capelin, small cod, herring, squid, and euphausiids (Horwood 1990);
- Long-finned pilot whales: squid, juvenile cod, and capelin (Lien 1985);
- Harbour porpoises: capelin, herring, redfish, mackerel, cod, squid, and sand lance (Fontaine et al. 1994);

- White-sided dolphins: herring, squid, smelt, silver hake, and crustaceans (Katona et al. 1978);
- White-beaked dolphins: cod, whiting, mackerel, and cephalopods (Santos et al. 1994).

In order to calculate the overall proportion of each prey item by mass, total consumption by prey type was first calculated and overall proportions for mysticeti and odontoceti weighted according to the consumption of each cetacean species (Table 3).

Table 3. Diet compositions (%) for mysticeti (baleen whales) and odontoceti (toothed whales) used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Mysticeti					Odontoceti				
Prey	Mean	±SD[a]	Min	Max	Est	Mean	±SD[a]	Min	Max	Est
Large cod	**0.0**	0.0	0.0	0.0	0.0	1.1	1.5	**0.0**	**2.7**	2.7
Small cod	1.3	2.0	**0.0**	**3.3**	0.0	3.3	4.8	**0.0**	**5.0**	4.3
Large Green. halibut										
Small Green. halibut										
American plaice	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Flounders										
Skates										
Redfish	**0.0**	0.0	0.0	0.0	0.0	1.2	1.5	**0.0**	**2.7**	2.7
Large demersals	**0.0**	0.0	0.0	0.0	0.0	2.2	2.9	**0.0**	**5.0**	3.1
Small demersals	**0.0**	0.0	0.0	0.0	0.0	12.8	15.1	**0.0**	**27.9**	24.7
Capelin	75.0	90.7	**0.0**	**100.0**	86.2	8.1	9.8	**0.0**	**18.0**	18.0
Large pelagics	**0.0**	0.0	0.0	0.0	0.0	1.5	2.2	**0.0**	**3.7**	0.6
Pisci. small pelagics	2.6	4.3	**0.0**	**6.9**	0.5	59.0	98.9	**0.0**	**100.0**	34.9
Plank. small pelagics	13.7	18.5	**0.0**	**32.2**	2.7	9.9	13.4	**0.0**	**23.3**	8.1
Female shrimp	**0.0**	0.0	0.0	0.0	0.0	**0.5**	0.5	0.0	1.0	0.5
Male shrimp	**0.0**	0.0	0.0	0.0	0.0	**0.5**	0.5	0.0	1.0	0.5
Large crabs										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.										
Large zooplankton	7.4	9.3	**0.0**	**16.7**	10.5	**0.0**	0.0	0.0	0.0	0.0
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		0.0	159.1	100.0	100.0		0.0	190.4	100.0
TRN	14					14				

[a]: For these two groups, all the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC^{obs}_{x\to y}$ *CV($DC^{obs}_{x\to u}$)$_{mean}$ (SD = CV*Mean), with $DC^{obs}_{x\to y}$ representing the proportion of prey *x* consumed by the mysticeti or odontoceti group and CV($DC^{obs}_{x\to u}$)$_{mean}$ representing the average of all coefficients of variation of the proportion of prey

x consumed by the other groups *u* of the modelled ecosystem. Min = mean – SD, Max = mean + SD.

Seals

Background

Four species of pinnipeds are common in the Gulf of St. Lawrence. The harp seal (*Phoca groenlandica*) is the most abundant pinniped in Atlantic Canada and usually summers in the Canadian Arctic or northwest Greenland before returning south to overwinter in Canadian Atlantic waters. Reproduction occurs in March on pack ice in the Gulf of St. Lawrence (Gulf herd) and off southern Labrador (Front herd). In the Gulf, animals whelp in two areas: off the lower North Shore and near the Îles-de-la-Madeleine (Sergeant 1991). During the 1994–1996 period, the northwest Atlantic population was estimated to be 5,037,255 (Healey and Stenson 2000), with an average of 2.5% of the pups, 2.5% of juveniles, and 4.1% of the adults found in the northern Gulf of St Lawrence (Hammill and Stenson 2000). During the 2000–2002 period, the northwest Atlantic population was estimated to be 5,404,349. The same proportions of pups, juveniles, and adults as in the 1994–1996 period were assumed in the northern Gulf.

Hooded seals (*Cystophora cristata*), which are larger than harp seals, are the least abundant pinniped within the study area, with an average population of 17,935 individuals for 2000–2002 in the Gulf of St. Lawrence (M. Hammill, unpublished data). Only 36.2% of the animals are located in divisions 4RS (Hammill and Stenson 2000). In the northwest Atlantic, most pups are born in March on pack ice off northeast Newfoundland, with smaller whelping concentrations located in Davis Strait and the Gulf of St. Lawrence. After leaving the whelping patch in late March, adults from the Gulf of St. Lawrence move to the northern Gulf where they remain until mid-May, after which they return to Greenland. Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997).

The grey seal (*Halichoerus grypus*) is slightly smaller than the hooded seal. Major breeding colonies in eastern Canada are located on Sable Island and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After breeding, both juveniles and adults disperse widely over eastern Canada. Large numbers are known to feed in the northern Gulf of St. Lawrence, which makes it the second most abundant pinniped of the zone (Hammill and Stenson 2000). The population in 2000–2002 averaged 37,676 individuals from the Gulf herd (versus 67,690 in 1994–1996) and 241,727 individuals from the Sable Island herd (M. Hammill, unpublished data), with 33.7% of the Gulf herd and 7.9% of the Sable Island herd found in divisions 4RS (Hammill and Stenson 2000).

Harbour seals (*Phoca vitulina*) are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Harbour seal abundance in Atlantic Canada has never been evaluated by direct survey. Based on questionnaires sent to fisheries officers, Boulva and McLaren (1979) estimated about 13,000 animals in eastern Canada. Hammill and Stenson (2000) modelled population changes for this species and estimated that the average population was 42,079 for 2000–2002 (M. Hammill, unpublished data), with 26.4% of the animals situated in the northern Gulf (Hammill and Stenson 2000).

For the purpose of this study, two groups of seals have been distinguished based on similar habitat selection. One is formed with harp and hooded seals and the other with grey and harbour seals.

Catch

Commercial catches (total numbers) for harp, grey, and hooded seals are reported in the Atlantic resource management landing reports (DFO 2003b). For harp seals, catches in number (3,610 in 2000; 124,359 in 2001; 64,227 in 2002) from the west coast of Newfoundland and Québec's North Shore were divided into pups (young of the year) and animals one year and older (Sjare et al. 1996). Numbers-at-age were multiplied by mean mass-at-age (Hammill and Stenson 2000) to obtain total catches in tons. For harp seals, the mean annual catch for 2002–2002 was estimated at $2.25 \times 10^{-2} \pm 2.12 \times 10^{-2}$ t km^{-2} yr^{-1}. The number of hooded seals removed from the northern Gulf of St. Lawrence (data from the west coast of Newfoundland and Québec's North Shore) was obtained directly from catch statistics (17 in 2001 only). The mean annual catch was estimated to be $5.46 \times 10^{-6} \pm 9.45 \times 10^{-6}$ t km^{-2} yr^{-1}. The total mean annual catch for the harp and hooded seals was estimated to be $2.25 \times 10^{-2} \pm 2.12 \times 10^{-2}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch of 5.04×10^{-3} t km^{-2} yr^{-1} for this group.

The grey seal is not hunted commercially in Canadian waters (1 in 2001 in 4RS). However, this species is subject to a scientific removal and bounty hunting. Harvesting activity has declined over the last 50 years and the bounty was eliminated in 1992 (Hammill et al. 1998). These removals resulted in an estimated mean annual catch of $3.06 \times 10^{-7} \pm 5.30 \times 10^{-7}$ t km^{-2} yr^{-1}. Even though harbour seals have been protected since 1976 (Boulva and McLaren 1979), some losses may have occurred through by-catch by commercial fisheries. However, there is no data available to assess this loss and catch was assumed to be negligible. The total mean annual catch for the grey and harbour seals was estimated to be $3.06 \times 10^{-7} \pm 5.30 \times 10^{-7}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch of 3.53×10^{-7} t km^{-2} yr^{-1} for this group.

Biomass

Biomass was estimated by multiplying abundance by mean mass-at-age (Hammill and Stenson 2000). The number of seals in each age class was obtained from an updated version of the population model of Hammill and Stenson (2000). Since there was no data from 2002 for hooded and grey seals, the values from 2001 were used for both years as values in the calculation for these two species. Biomass was adjusted for residence time in 4RS (Hammill and Stenson 2000), resulting in mean annual biomass estimates for the 2000–2002 period of 0.148 ± 0.002 t km^{-2} for harp and hooded seals and 0.041 ± 0.002 t km^{-2} for grey and harbour seals. Note that the standard deviation for each seal group was only the variation in the point estimates for the three years of the 2000–2002 period. Since the biomass for each seal group was estimated from the model of Hammill and Stenson (2000), we did not use these variances (SD^2) in the scaling (or weighting) of inverse modelling. We used the average of all known coefficients of variation for biomass (51%) as scaling factors for respiration, egestion, and natural mortality other than predation of each seal group.

Production

The P/B ratio for each group was estimated by dividing the pup biomass by the uncorrected population biomass (minimum value) for the northern Gulf of St. Lawrence as reported in an updated version of the population model of Hammill and Stenson (2000) for the 2000–2002 period. The P/B ratios were 0.073 yr^{-1} for harp seals, 0.061 yr^{-1} for hooded seals, 0.063 yr^{-1} for grey seals, and 0.071 yr^{-1} for harbour seals. Multiplying these P/B ratios by mean biomass for each species resulted in production values of 0.011 ± 0.000 t km^{-2} yr^{-1} for harp and hooded seals and 0.003 ± 0.000 t km^{-2} yr^{-1} for grey and harbour seals.

Production was also estimated by adding annual mass gain for each age class in the population to the mass of pups. Mass at age was obtained from Chabot and Stenson (2002) and Leblanc (2003) for harp seals and hooded seals, respectively. An updated version of the population model of Hammill and Stenson (2000) provided the information for grey and harbour seals. In the 2000–2002 period, this resulted in production values of 0.016 t km^{-2} yr^{-1} for harp and hooded seals and 0.008 t km^{-2} yr^{-1} for grey and harbour seals.

Finally, the resulting upper and lower limit ranges were 0.011 to 0.016 t km^{-2} yr^{-1} (mean: 0.014 ± 0.004 t km^{-2} yr^{-1}) for harp and hooded seals and 0.003 to 0.008 t km^{-2} yr^{-1} (mean: 0.006 ± 0.004 t km^{-2} yr^{-1}) for grey and harbour seals. The inverse solution estimated production values of 0.013 t km^{-2} yr^{-1} (P/B = 0.09 yr^{-1}) for harp and hooded seals and 0.003 t km^{-2} yr^{-1} (P/B = 0.07 yr^{-1}) for grey and harbour seals.

Consumption

The total annual consumption of prey by each seal species in the study area was estimated from an updated version of the consumption model of Hammill and Stenson (2000). The mean annual consumption values were 0.689 ± 0.011 t km^{-2} yr^{-1} (0.677–0.699 t km^{-2} yr^{-1}) for harp and hooded seals and 0.169 ± 0.008 t km^{-2} yr^{-1} (0.164–0.175 t km^{-2} yr^{-1}) for grey and harbour seals.

Based on the mean annual production estimated (see above) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic; i.e., 10-fold the value based on GE limit of 1%), we obtained other consumption values: 1.353 t km^{-2} yr^{-1} for harp and hooded seals and 0.567 t km^{-2} yr^{-1} for grey and harbour seals. Finally, based on these different values, we estimated the lower and upper consumption limits used as constraints in inverse modelling. The resulting mean consumption values of each upper and lower limit range were 1.015 ± 0.478 t km^{-2} yr^{-1} for harp and hooded seals and 0.365 ± 0.285 t km^{-2} yr^{-1} for grey and harbour seals. The inverse solution estimated consumption values of 1.299 t km^{-2} yr^{-1} (Q/B = 8.783 yr^{-1}) for harp and hooded seals and 0.298 t km^{-2} yr^{-1} (Q/B = 7.238 yr^{-1}) for grey and harbour seals.

Diet composition

For harp seals, diet information was available for nearshore waters of the northwest Atlantic during 1990–1993 (Lawson et al. 1995), for inshore 2J3KL during 1991–1992 (Lawson et al. 1993), and for the St. Lawrence Estuary (Murie and Lavigne 1991; Beck et al. 1993;

Lawson et al. 1995; Hammill and Stenson 2000). According to these diet studies, the main prey species were, in order of importance, capelin, Atlantic herring, Atlantic cod, redfish, and Arctic cod.

There was no local diet information available for hooded seals in the northern Gulf. Hammill et al. (1997) used a diet based on work done by Ross (1993), where the main prey items were young Greenland halibut, flounders, and small pelagic feeders. Other information about this species was based on offshore samples from NAFO divisions 2J3KL collected from 1991–1993 (Lawson et al. 1993). In that study, stomachs examined contained mainly Atlantic cod, witch flounder, and squid. Hammill and Stenson (2000) used a diet made up of samples from Ross (1993) and Lawson and Stenson (DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data) in which major prey for the Gulf and 2J3KL inshore regions were Greenland halibut, redfish, Arctic cod, and herring.

Several studies have examined the diet composition of grey seals in the northern Gulf of St. Lawrence. These have determined that Atlantic cod, herring, lumpfish, wolffish, capelin, mackerel, and ocean pout were the main prey items of this species (Benoit and Bowen 1990; Murie and Lavigne 1992; Proust 1996; Hammill and Stenson 2000).

The harbour seal diet composition was examined in two inshore habitats of Atlantic Canada (lower Bay of Fundy and the northeastern coast of Nova Scotia) between 1988 and 1992 (Bowen and Harrison 1996). For the 250 food-containing stomachs examined, the major prey were Atlantic herring, squid, pollock (*Pollachius virens*), and Atlantic cod.

For each seal species, we obtained upper and lower limits resulting from these different diet studies. These upper and lower limits were then weighted according to each seal species' consumption in order to calculate the overall proportion of each prey item by mass for harp/hooded seals and grey/harbour seals. The resulting diet compositions are shown in Table 4.

Table 4. Diet compositions (%) for seals used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Harp/hooded seals					Grey/harbour seals				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	2.3	3.0	**0.1**	**6.1**	1.6	9.6	13.6	**2.0**	**21.3**	10.0
Small cod	4.1	6.8	**0.1**	**11.9**	1.1	9.4	13.3	**2.0**	**20.8**	9.9
Large Green. halibut	2.0	4.1	**0.0**	**6.3**	1.3	**0.0**	0.0	0.0	0.0	0.0
Small Green. halibut	4.9	6.2	**0.2**	**12.5**	12.0	**0.2**	0.4	0.0	0.6	0.2
American plaice	3.6	8.2	**0.0**	**11.6**	2.8	4.4	7.6	**0.0**	**10.7**	10.7
Flounders	7.8	14.0	**0.0**	**23.2**	0.0	7.2	12.0	**0.2**	**17.2**	5.5
Skates	**0.0**	0.0	0.0	0.0	0.0	14.4	24.8	**0.0**	**35.1**	6.2
Redfish	5.6	9.4	**0.6**	**15.8**	3.5	**0.1**	0.1	0.1	0.1	0.1
Large demersals	3.1	6.7	**0.0**	**9.8**	0.5	9.5	4.1	**8.6**	**14.4**	9.7
Small demersals	2.6	3.7	**0.7**	**7.1**	0.7	10.9	16.8	**1.3**	**25.1**	16.2
Capelin	41.2	62.7	**4.2**	**100.0**	51.0	8.0	11.8	**1.3**	**17.9**	17.9
Large pelagics	**0.1**	0.3	0.0	0.4	0.1	1.7	0.8	**1.2**	**2.4**	1.2
Pisci. small pelagics	2.3	4.4	**0.0**	**7.1**	0.5	8.3	7.4	**4.0**	**14.5**	5.8
Plank. small pelagics	8.8	13.8	**0.0**	**27.7**	1.8	15.5	13.5	**4.5**	**31.4**	5.6
Female shrimp	0.9	2.1	**0.0**	**3.0**	1.9	**0.4**	0.0	0.4	0.4	0.4
Male shrimp	0.9	2.1	**0.0**	**3.0**	1.7	**0.4**	0.0	0.4	0.4	0.4
Large crabs	0.7	1.7	**0.0**	**2.4**	2.0	**0.1**	0.1	0.0	0.2	0.1
Small crabs	0.7	1.7	**0.0**	**2.4**	0.0	**0.1**	0.1	0.0	0.2	0.1
Echinoderms										
Molluscs						**0.0**	0.0	0.0	0.0	0.0
Polychaetes										
Other bent. inver.	1.6	3.7	**0.0**	**5.2**	3.9	**0.0**	0.0	0.0	0.0	0.0
Large zooplankton	6.6	15.3	**0.0**	**21.6**	13.6	**0.0**	0.0	0.0	0.0	0.0
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		5.8	277.0	100.0	100.0		26.0	212.6	100.0
TRN	20					21				

Seabirds

Background

In the northern Gulf of St. Lawrence, 64.5% of seabirds are estimated to be found inshore while 35.5% are distributed offshore (Cairns et al. 1991). Inshore seabirds breed in a large number of smaller colonies dispersed along the coastline while offshore species breed in a small number of large colonies (Lack 1967). The main inshore species breeding in the region are the double-crested cormorant (*Phalacrocorax auritus*), ring-billed gull (*Larus delawarensis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), and black guillemot (*Cepphus grylle*). The main offshore species that breed in the region are the northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and Leach's storm-petrel (*Oceanodroma leucorhoa*).

Catch/anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the region: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). In the northern Gulf, a few species of seabirds such as ducks and guillemots are hunted for food along Québec's North Shore. Considerable numbers of seabirds (mostly alcids, i.e., murres and puffins, but also others, e.g., gannets) are also caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounts to 1×10^{-3} t km^{-2} per year. On the basis of information for seabirds from Newfoundland (NAFO divisions 2J3KL) (Bundy et al. 2000), we estimated a catch rate (1×10^{-3} t km^{-2} yr^{-1} divided by the seabird biomass, 0.012 t km^{-2}) for the Newfoundland ecosystem and we applied it to the divisions 4RS. It totalled 3.35×10^{-4} t km^{-2} yr^{-1} of seabirds being removed annually from the study area through anthropogenic mortality. The inverse solution estimated a catch of 2.25×10^{-4} t km^{-2} yr^{-1}.

Biomass

Unlike the open Atlantic coast of Canada, the Gulf of St. Lawrence is not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts of breeding colonies can be used (Cairns et al. 1990). Data on body mass and population estimates for various seabirds were derived from Chapdelaine (Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data). In order to estimate biomass density, we assumed that seabirds were distributed uniformly throughout NAFO divisions 4RST. Consequently, biomass was determined by taking the number of birds multiplied by their respective biomass and divided by the whole 4RST bird inventory area (214,000 km^2) instead of the value usually used for the other groups (the sampling area for divisions 4RS). Population surveys typically enumerated the number of breeding pairs. As such, it was necessary to estimate the number of nestlings and non-breeding birds. For species that breed within NAFO

divisions 4RST, population estimates (Table 5) were calculated as follows (G. Chapdelaine, unpublished data):

(3) Population estimate = breeders
+ nestlings
+ non-breeders

(4) Population estimate (offshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (0.8 x breeding pairs)

or

(5) Population estimate (inshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (1.0 x breeding pairs)

The total biomass estimate for the 4RS study area is 859 t or 0.004 t km^{-2}.

Table 5. Approximate period of occupation, population size, average body mass, and biomass for the main species of seabirds that breed within the study area (NAFO divisions 4RS) or that breed primarily or completely outside but occur in the study area or are nestlings. Note that the shaded section indicates inshore seabirds while the unshaded section corresponds to offshore seabirds.

Species	Period of occupation	Population (numbers) of breeders	Population (numbers) of non-breeders and nestlings	Individual mass (kg)	Adjusted average biomass (t)
Great cormorant	Apr-Oct	4,968	3,478	2.25	11.085
Double-crested cormorant	Apr-Oct	78,000	54,600	1.67	205.148
Ring-billed gull	Apr-Oct	66,784	53,427	0.50	35.060
Herring gull	Mar-Dec	95,774	76,619	1.12	160.861
Black-headed gull	Apr-Oct	20	16	0.28	0.006
Great black-backed gull	Mar-Dec	19,472	15,578	1.68	49.068
Common tern	May-Sep	52,536	42,029	0.12	4.729
Caspian tern	May-Sep	22	18	0.61	0.010
Arctic tern	May-Sep	2,010	1,608	0.11	0.166
Black guillemot	Jan-Dec	9,524	6,667	0.40	6.477
Leach's storm-petrel	May-Oct	1,036	725	0.05	0.044
Northern gannet	Apr-Oct	84,248	58,974	3.20	267.333
Black-legged kittiwake	Apr-Oct	168,752	118,126	0.44	73.628
Common murre	May-Sep	89,320	62,524	0.99	87.685
Thick-billed murre	Apr-Oct	24	17	0.93	0.022
Razorbill	Apr-Oct	16,500	11,550	0.72	11.781
Atlantic puffin	Apr-Oct	48,348	33,844	0.46	22.054
TOTAL	Jan-Dec	651,141	539,790	-	859.176

Production

An energetic model developed for seabirds of the whole Gulf of St. Lawrence (4RST) (G. Chapdelaine, unpublished data) indicates that there are a total of 221,201 nestlings produced each year for all species combined (calculated by assuming that nestlings = number of breeding pairs x 0.6). Multiplying the number of nestlings by the average mass for each species results in a total annual production of 0.001 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.32 yr^{-1}.

Consumption

Estimated food consumption for seabirds in the northern Gulf is 108,419 t yr^{-1} (Chapdelaine, unpublished data). Assuming that consumption is evenly distributed throughout the region results in an estimated annual consumption of 0.507 t km^{-2} yr^{-1}. Based on the previous annual production and the upper GE limit (1%; the value based on the lower GE limit of 0.1% was not realistic), we obtained another consumption estimate of 0.111 t km^{-2} yr^{-1}. This resulted in a mean consumption of 0.309 ± 0.280 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.254 t km^{-2} yr^{-1}, representing a Q/B of 63.156 yr^{-1}.

Diet composition

Seabirds within the study area feed at a variety of trophic levels with most prey being small pelagic fish, benthic invertebrates, and pelagic crustaceans (Cairns et al. 1990). Great cormorants feed mostly on benthic fish, primarily flatfish and cunners (*Tautogolabrus adspersus*), while double-crested cormorants prey heavily on flatfish, sculpins (*Myoxocephalus* sp.), rock gunnels (*Pholis gunnellus*), and sand lance (*Ammodytes* spp.). The only data available from the Gulf of St. Lawrence for black guillemot showed that chicks are fed primarily with benthic fish, particularly sculpins, blennies, and tomcod (*Microgadus tomcod*) (Cairns 1981). Northern gannet, the largest breeding seabird species in the study area, preys on pelagic species such as mackerel but also on sand lance (Burton 1980). Herring gulls, which are the most abundant species in the study area, feed primarily on small pelagic fish and non-marine food (Threlfall 1968; Haycock and Threlfall 1975; Pierroti 1983), but quantitative dietary data from the Gulf are generally lacking for this species as well as for all other gulls, terns, storm-petrels, kittiwakes, and offshore alcids (Cairns et al. 1990). The diet of Arctic tern, recorded on Québec's North Shore (NAFO division 4S; Chapdelaine et al. 1985), as well as the diet of the common tern, the most abundant species in the eastern part of the area (NAFO division 4R), consist mainly of capelin, sand lance, and pelagic invertebrates. Black-legged kittiwakes are the most abundant species in the western part of the study area (NAFO division 4S) and feed primarily on copepods and euphausiids (Threlfall 1968; Maunder and Threlfall 1972). The final seabird diet was modified following Cairns et al. (1990) and Chapdelaine (unpublished data), who used all available information for the Gulf of St. Lawrence as well as extrapolated information from the closest ecosystems to create a complete diet for all seabird species found in the Gulf of St. Lawrence (north and south, NAFO divisions 4RST). There is no diet data available for Leach's storm-petrel, kittiwakes, murres, razorbills, or Atlantic puffins from the northern Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). Based on these different studies, we estimated the diet composition of seabirds used in modelling for the northern Gulf of St. Lawrence (Table 6).

Table 6. Diet composition (%) for seabirds used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Seabirds				
Prey	Mean	±SD	Min	Max	Est
Large cod					
Small cod	**0.2**	0.4	0.0	0.5	0.2
Large Green. halibut					
Small Green. halibut	**0.4**	0.6	0.0	0.8	0.4
American plaice	**0.4**	0.6	0.0	0.8	0.4
Flounders	**0.4**	0.6	0.0	0.8	0.4
Skates	**0.4**	0.6	0.0	0.8	0.4
Redfish					
Large demersals					
Small demersals	8.3	10.8	**1.6**	**16.9**	2.8
Capelin	43.7	34.3	**21.9**	**76.0**	74.6
Large pelagics	**0.0**	0.1	0.0	0.1	0.0
Pisci. small pelagics	9.7	15.1	**0.2**	**21.5**	0.3
Plank. small pelagics	30.1	37.3	**5.8**	**61.6**	7.1
Female shrimp	**0.3**	0.5	0.0	0.7	0.3
Male shrimp	**0.3**	0.5	0.0	0.7	0.3
Large crabs					
Small crabs					
Echinoderms					
Molluscs	**0.0**	0.1	0.0	0.1	0.0
Polychaetes					
Other bent. inver.	0.6	1.0	**0.0**	**1.4**	1.4
Large zooplankton	5.0	7.8	**0.0**	**11.1**	11.1
Small zooplankton	**0.2**	0.4	0.0	0.5	0.2
Phytoplankton					
Detritus					
Total	100.0		29.6	194.5	100.0
TRN	16				

Atlantic cod

Background

The northern Gulf cod stock overwinters in the deep waters off southwestern Newfoundland and then returns to the Gulf, moving northwards off Newfoundland's west coast (NAFO division 4R). Spawning takes place mainly during April and May in Esquiman Channel. During summer, the population migrates to the warmer coastal waters of Québec's lower North Shore and the west coast of Newfoundland.

Commercial landings increased considerably during the late 1950s and 1960s, but the stock declined to low levels by the mid to late 1970s. Following this decline, there was a period of recovery during the early 1980s before the stock collapsed in the early 1990s (Fréchet and Schwab 1998).

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more accurately, into large and small fish. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but here we assume that the change occurs at 35 cm for cod (Lilly 1991). Northern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to recruit to the commercial fishery.

Catch

Landings for large cod (age 4+) in NAFO divisions 3Pn4RS are available for the 2000–2002 period (Fréchet et al. 2003). Since cod from these three zones are considered to be part of the same stock, landings from 3Pn were included in the model. Also, catch from NAFO statistics (NAFO 2003) have been taken for area 3Pn4RS. Mean catch of large cod was $6.50 \times 10^{-2} \pm 4.20 \times 10^{-3}$ t km^{-2} yr^{-1}. In the absence of information on misreported catches for this species (Savenkoff et al. 2004a), we decided to use the upper catch limit (6.94×10^{-2} t km^{-2} yr^{-1}) to constrain the model. Since it was assumed that small cod are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group. The inverse solution estimated catch values of 7.00×10^{-2} t km^{-2} yr^{-1} for large cod.

Biomass

The biomass of large cod was based on virtual population analysis estimates of cod biomass at the beginning of the year. The estimated average biomass of large cod was 67,244 t or 0.615 t km^{-2} (SD = 0.067 t km^{-2}) (Fréchet et al. 2003). Mean annual biomass for small cod was 12,994 t or 0.119 t km^{-2} (SD = 0.037 t km^{-2}).

Production

P/B of large cod was estimated by a catch-curve analysis of groundfish survey data from NAFO divisions 4RS for the 2000–2002 period. The estimate of total mortality (Z = 1.06 yr^{-1}) was determined from the slope of the regression line fitted to the downward side of the catch curve (Sinclair 2001). This instantaneous rate was then converted into real mortality rate (A = 0.64 yr^{-1}; $A = 1 - e^{-Z}$ where Z is the instantaneous mortality rate according to Ricker 1980). Since we assume a steady state (no year-to-year change in biomass), total mortality A (0.64 yr^{-1}) is equal to the P/B ratio of cod in 2000–2002 (Allen 1971). The annual production estimate was 0.399 ± 0.044 t km^{-2} yr^{-1} (range: 0.352–0.438 t km^{-2} yr^{-1}). Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality for large cod was estimated at 0.33 yr^{-1} in 2000 (Swain and Castonguay 2000) and 0.20 yr^{-1} in 2001–2002 (A. Fréchet, Institut Maurice-Lamontagne, pers. comm.). We obtained an annual production of 0.216 ± 0.061 t km^{-2} yr^{-1}. Combining the two methods resulted in a mean annual production of 0.327 ± 0.156 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.216 t km^{-2} yr^{-1}, resulting in a P/B of 0.35 yr^{-1}.

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M), plus catch ([B x M] + C). Natural mortality for small cod was assumed to be 0.6 yr^{-1}, while catch estimates of small cod were assumed to be zero. Using the minimum and maximum biomass values for small cod, we estimated a production range of 0.047 to 0.090 t km^{-2} yr^{-1}, corresponding to an annual production of 0.071 ± 0.022 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.087 t km^{-2} yr^{-1}, representing a P/B value of 0.73 yr^{-1}.

Consumption

A range of Q/B values was used to estimate the mean Q/B ratio for large cod. These values were based on different studies of food consumption by cod populations in the northwest Atlantic (Q/B = 3.43; Pauly 1989; Froese and Pauly 2002) as well as in the Gulf of St. Lawrence (Q/B = 1.96; Waiwood et al. 1980). The Q/B ratios for large cod varied between 1.96 and 3.43 yr^{-1}, corresponding to a consumption range between 1.064 and 2.310 t km^{-2} yr^{-1}. Based on the previous mean production (0.327 t km^{-2} yr^{-1}) for large cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.064 and 3.270 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 1.064 and 3.270 t km^{-2} yr^{-1}, corresponding to a mean consumption of 2.167 ± 1.560 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.065 t km^{-2} yr^{-1}, representing a Q/B of 1.732 yr^{-1}.

Two studies were used to estimate the Q/B ratio for small cod extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded Q/B ratios of 3.250 yr^{-1} (Waiwood et al. 1980) and 2.564 yr^{-1} (Grundwald and Koster 1994). This corresponded to a consumption range between 0.200 and 0.488 t km^{-2} yr^{-1}. Based on the previous mean production (0.071 t km^{-2} yr^{-1}) for small cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.238 and 0.713 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.200 and 0.713 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.456 ± 0.362 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.398 t km^{-2} yr^{-1}, representing a Q/B of 3.355 yr^{-1}.

Diet composition

Stomach content data were available for large and small cod groups from NAFO divisions 4RS from 2000 to 2002 (D. Chabot, unpublished data). Number of stomachs sampled for 2000, 2001, and 2002 were 570, 513, and 287 for large cod and 299, 274, and 99 for small cod, respectively. The fullness indices, including empty stomachs, were 0.95, 1.38, and 1.41 for 2000, 2001, and 2002 in large cod and 0.86, 1.10, and 1.73 in small cod. We used the upper and lower limits of the overall proportion of each prey item by mass as constraints in inverse modelling for the two diet compositions. Overall, the most important prey items of large cod, in percent mass of stomach content, were large zooplankton, planktivorous small pelagics (mainly Atlantic herring), male shrimp (small shrimp), and small American plaice (65.0% of the diet; Table 7). The most important prey items of small cod were large zooplankton, male shrimp, capelin, and planktivorous small pelagics (88.2% of the diet; Table 7).

Table 7. Diet compositions (%) for large and small cod used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large cod (> 35 cm)					Small cod (≤ 35 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	3.8	3.5	**0.0**	**4.9**	1.1	**0.0**	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.2	0.0
American plaice	13.0	11.3	**5.4**	**21.4**	11.8	**0.0**	0.1	0.0	0.2	0.0
Flounders	5.7	9.1	**0.0**	**12.9**	0.0	**0.0**	0.1	0.0	0.2	0.0
Skates	**0.0**	0.0	0.0	0.0	0.0					
Redfish	2.0	1.7	**0.2**	**2.6**	1.7	**0.0**	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	4.0	1.8	**2.9**	**5.4**	2.9	2.2	2.4	**1.9**	**5.3**	1.9
Capelin	4.6	2.9	**4.0**	**8.2**	7.8	9.0	9.1	**2.4**	**15.3**	8.1
Large pelagics										
Pisci. small pelagics	**0.1**	0.2	0.0	0.3	0.1	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	15.7	15.5	**5.0**	**26.9**	5.0	8.7	13.1	**0.0**	**18.5**	0.0
Female shrimp	3.8	3.3	**1.6**	**6.3**	5.5	6.3	4.6	**2.8**	**9.4**	7.0
Male shrimp	13.0	4.8	**8.0**	**14.7**	12.2	15.8	9.4	**8.7**	**22.1**	13.2
Large crabs	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Small crabs	9.7	4.5	**5.0**	**11.5**	5.0	1.0	1.2	**0.1**	**1.7**	0.1
Echinoderms	**0.5**	0.5	0.1	0.7	0.5	**0.0**	0.0	0.0	0.0	0.0
Molluscs	0.4	0.7	**0.1**	**1.1**	1.1	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	**0.4**	0.3	0.2	0.5	0.4	1.0	1.6	**0.0**	**2.3**	2.2
Other bent. inver.	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.1	0.0	0.1	0.0
Large zooplankton	23.4	23.3	**12.6**	**45.5**	45.1	54.7	30.1	**38.1**	**80.7**	65.9
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	1.2	1.8	**0.0**	**2.6**	1.6
Phytoplankton										
Detritus										
Total	100.0		45.0	163.0	100.0	100.0		54.0	158.6	100.0
TRN	20					19				

Greenland halibut

Background

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish present in the North Atlantic and North Pacific. In the northwest Atlantic, it is found from Arctic regions to Georges Bank (Bowering 1983). The Gulf of St. Lawrence population is considered to be a small stock, isolated from the main northwest Atlantic stock, completing its entire life cycle within the Gulf (DFO 2002b).

Directed fishing for this species with bottom trawls and gillnets developed after the mid-1970s. Landings increased in the 1980s to reach an all-time high in 1987 (11,000 t), but have declined at the beginning of the 1990s and are now around 3,000 t (DFO 2002b).

Greenland halibut were divided into large and small fish. Although there is an apparent change in diet composition when fish reach lengths of about 20 cm (Bundy et al. 2000), we separated Greenland halibut into fish larger or smaller than 40 cm, the size at which they are first recruited to the fishery (Brodie 1991). Greenland halibut greater than 40 cm in length are equivalent to fish aged six years and older (Brodie 1991).

Catch

According to the NAFO fisheries statistics (NAFO 2003), the mean annual landing of large Greenland halibut during the 2000–2002 period was 835 tons or 8.05 x 10^{-3} t km^{-2} yr^{-1} (SD = 2.55 x 10^{-3} t km^{-2} yr^{-1}). The inverse solution estimated a catch of 8.01 x 10^{-3} t km^{-2} yr^{-1}.

Since it was assumed that small Greenland halibut are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group.

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 2000–2002 period. Length-frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software to obtain an estimate of halibut abundance for this zone. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean mass-at-length (derived from length–mass relationships) and summing the results. This resulted in mean biomass estimates for the 2000–2002 period of 23,714 t or 0.228 t km^{-2} (SD = 0.017 t km^{-2}) and 165,726 t or 1.596 t km^{-2} (SD = 0.413 t km^{-2}) for large (> 40 cm) and small (≤ 40 cm) Greenland halibut, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) for this species, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch. Natural mortality for large Greenland halibut (M = 0.09 yr^{-1}) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 96.5 cm along with a water temperature of 3°C. When the minimum and maximum biomass values were used, we obtained a production range of 0.026 to 0.031 t km^{-2} yr^{-1}, corresponding to a mean production of 0.029 ± 0.002 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.029 t km^{-2} yr^{-1}, representing a P/B of 0.13 yr^{-1}.

For small Greenland halibut, it was assumed that natural mortality was higher (younger fish generally have a higher M than older fish), so a textbook range of 0.4 to 0.6 yr^{-1} was assigned to this group. It was also assumed that there was no catch. When the minimum and maximum biomass values were used, we obtained a production range of 0.476 to 1.209 t km^{-2} yr^{-1}, corresponding to a mean production of 0.798 ± 0.257 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.478 t km^{-2} yr^{-1}, representing a P/B of 0.30 yr^{-1}.

Consumption

A Q/B ratio (1.660 yr^{-1}) was estimated using daily food requirements for 6- to 20-year-old Greenland halibut from the northwest Atlantic (Chumakov and Podrazhanskaya 1986). Another Q/B ratio (1.400 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish at 3°C and having a maximum mass of 9.217 g (B. Morin, Institut Maurice-Lamontagne, pers. comm.). When the minimum and maximum biomass values and the two previous Q/B ratios were used, we obtained a total consumption of 0.349 t km^{-2} yr^{-1} (range: 0.299–0.409 t km^{-2} yr^{-1}) for large Greenland halibut. Based on the previous mean production (0.029 t km^{-2} yr^{-1}) for large Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.095 and 0.286 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.228 t km^{-2} yr^{-1} instead of 0.095 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.228 and 0.409 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.319 ± 0.128 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.233 t km^{-2} yr^{-1}, representing a Q/B of 1.019 yr^{-1}.

Q/B values for small Greenland halibut were obtained from three different sources. Using the mean daily consumption of 5-year-old Greenland halibut (< 40 cm) (Chumakov and Podrazhanskaya 1986), the Q/B ratio was 4.427 yr^{-1}. The estimate obtained from FishBase (Froese and Pauly 2002), for fish at 3°C with a maximum mass of 586 g (the maximum mass of 40 cm fish from NAFO divisions 4RS; B. Morin, Institut Maurice-Lamontagne, pers. comm.), was slightly lower, with a Q/B value of 2.500 yr^{-1}. A third estimate (Q/B: 2.665 yr^{-1}) was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a). When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of 5.104 t km^{-2} yr^{-1} (range: 2.975–8.923 t km^{-2} yr^{-1}) for small Greenland halibut. Based on the previous minimum and maximum production values (0.476–1.209 t km^{-2} yr^{-1}) for small Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.587 and 12.092 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 1.587 and 12.092 t km^{-2} yr^{-1}, corresponding to a mean

consumption of 6.840 ± 7.428 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.608 t km^{-2} yr^{-1}, representing a Q/B of 1.007 yr^{-1}.

Diet composition

Stomach content data for Greenland halibut from NAFO divisions 4RS were available from 1993 to 2002 (except for 2000; D. Chabot, unpublished data). Sample sizes for 2001 and 2002 were 257 and 176 for large Greenland halibut and 948 and 507 for small Greenland halibut, respectively. The stomach fullness indices, including empty stomachs, were 0.40 and 0.70 for 2001 and 2002 in large Greenland halibut and 0.52 and 0.79 in small Greenland halibut. We used the upper and lower limits of the overall proportion of each prey item by mass as constraints in inverse modelling for the two diet compositions. Overall, the most important prey items of large Greenland halibut, in percent mass of stomach content, were small demersals, male shrimp (i.e., small shrimp), female shrimp (i.e., large shrimp), and planktivorous small pelagics (mainly Atlantic herring) (87.5% of the diet; Table 8). The most important prey items of small Greenland halibut were capelin, large zooplankton, male shrimp, and female shrimp (91.2% of the diet; Table 8).

Table 8. Diet compositions (%) for large and small Greenland halibut used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large Greenland halibut (> 40 cm)					Small Greenland halibut (≤ 40 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.0**	0.0	0.0	0.0	0.0	0.7	1.0	**0.0**	**1.4**	0.1
Large Green. halibut										
Small Green. halibut	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
American plaice	**0.0**	0.0	0.0	0.0	0.0					
Flounders	1.6	3.6	**0.0**	**5.0**	0.7	**0.0**	0.0	0.0	0.0	0.0
Skates	**0.0**	0.0	0.0	0.0	0.0					
Redfish	2.5	2.7	**0.0**	**3.8**	3.7	**0.0**	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	29.2	2.3	**29.1**	**32.3**	29.4	7.7	3.3	**5.2**	**9.9**	5.2
Capelin	3.3	1.3	**2.8**	**4.7**	4.2	33.0	9.1	**26.3**	**39.1**	33.5
Large pelagics	**0.0**	0.0	0.0	0.0	0.0					
Pisci. small pelagics	1.8	2.0	**0.0**	**2.8**	0.7	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	15.8	17.4	**0.0**	**24.6**	1.3	**0.2**	0.3	0.0	0.5	0.2
Female shrimp	18.8	8.3	**13.9**	**25.6**	24.9	13.1	1.1	**12.4**	**13.9**	13.2
Male shrimp	23.6	9.2	**18.2**	**31.2**	30.3	22.2	2.2	**20.4**	**23.5**	20.4
Large crabs	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Small crabs	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Echinoderms	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Molluscs	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large zooplankton	3.2	2.5	**1.2**	**4.7**	4.6	22.9	8.4	**17.5**	**29.4**	27.0
Small zooplankton	**0.1**	0.0	0.0	0.1	0.1	**0.2**	0.2	0.1	0.3	0.2
Phytoplankton										
Detritus										
Total	100.0		65.3	134.7	100.0	100.0		82.0	118.0	100.0
TRN	21					18				

American plaice, flounders, and skates

Background

All flatfish other than Greenland halibut were divided into three groups: American plaice (*Hippoglossoides platessoides*), flounders, and skates.

American plaice is widely distributed throughout the northwest Atlantic (from west Greenland to the Gulf of Maine) and is usually found at intermediate depths (80–250 m) (Morin et al. 1998). It has been exploited in NAFO divisions 4RS since 1947, with commercial catches peaking in 1977. Annual catches then began to fall until the mid-1980s, when they levelled off at around 2,000 t, but yearly landings have since declined to around 1,000 t.

The flounder group consists of witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), fourspot flounder (*Paralichthys oblongus*), and winter flounder (*Pseudopleuronectes americanus*). Flounders were grouped together on the basis of their similar feeding behaviour. These four species are sedentary bottom-dwelling flatfish that live in relatively deep water, except for winter flounder, which lives mostly in infra-littoral waters. Their distribution ranges from the coast of Labrador to North Carolina. Since the 1950s, important commercial catches have occurred in the deep waters bordering the Laurentian Channel. A long-standing fishery has also been in place in shallower waters for winter flounder. The key species of the flounder group is witch flounder, mainly because of its high biomass and commercial significance, but also because there were no captures of the other species by the research surveys, which indicates that their biomass was quite low. These other species are occasionally found in the stomachs of certain predators (e.g., seals).

The skate group included two species: the thorny skate (*Amblyraja radiata*), considered here as the key species for the group, and the smooth skate (*Malacoraja senta*). The thorny skate is widely distributed throughout the North Atlantic. The greatest concentrations are generally found in the higher part of continental shelves, at depths greater than 110 m (McEachran et al. 1976). The smooth skate is found throughout the northwest Atlantic, from the Gulf of St. Lawrence to Georges Bank (Scott and Scott 1988). Surveys conducted since the 1940s have shown that the greatest concentrations are found in the Gulf of St. Lawrence, on the Grand Banks, and on the Scotian Shelf. This species lives at depths of 50 to 700 m but is mostly caught between 90 and 325 m (McKone and LeGrow 1983). Fishing activity is less important for the smooth skate than for the thorny skate.

Catch

According to the landing statistics (NAFO 2003), mean annual landings during the 2000–2002 period in NAFO divisions 4RS were 208 t or $2.01 \times 10^{-3} \pm 9.34 \times 10^{-4}$ t km^{-2} yr^{-1} for American plaice, 475 t or $4.57 \times 10^{-3} \pm 3.38 \times 10^{-5}$ t km^{-2} yr^{-1} for witch flounder, and 79 t or $7.64 \times 10^{-4} \pm 2.74 \times 10^{-4}$ t km^{-2} yr^{-1} for skates. The inverse solution estimated catch values of 2.30×10^{-3}, 4.56×10^{-3}, and 7.48×10^{-4} t km^{-2} yr^{-1} for American plaice, flounders, and skates, respectively.

Biomass

Annual biomass estimates for the three groups were obtained using *PACES* to analyze research survey data from NAFO divisions 4RS during the 2000–2002 period. Mean biomass in NAFO divisions 4RS was estimated at 34,886 t or 0.336 t km^{-2} (SD = 0.266 t km^{-2}) for American plaice, 6,578 t or 0.063 t km^{-2} (SD = 0.047 t km^{-2}) for flounders, and 7,650 t or 0.074 t km^{-2} (SD = 0.046 t km^{-2}) for skates.

Production

There was no information available on production or total mortality (Z) of American plaice, flounders, or skates within the study area. However, Morin et al. (2001) estimated a Z of 0.46 (and then A = P/B = 0.37 yr^{-1} according to Ricker [1980]) for American plaice from 1998 to 2000 in the southern Gulf. When the minimum and maximum biomass values were used, we obtained production ranges of 0.030 to 0.226 t km^{-2} yr^{-1}. Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to be 0.220 yr^{-1} for American plaice (Pitt 1982). We obtained production ranges of 0.019 to 0.138 t km^{-2} yr^{-1} when the minimum and maximum biomass values were used. Combining the two methods resulted in a mean annual production of 0.100 ± 0.077 t km^{-2} yr^{-1} (range: 0.019–0.226 t km^{-2} yr^{-1}). The inverse solution estimated a production for American plaice of 0.223 t km^{-2} yr^{-1}, resulting in a P/B of 0.66 yr^{-1}.

For flounders and skates, production was estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to be 0.214 yr^{-1} for skates (Simon and Frank 1996). Due to a lack of information, natural mortality of flounders was assumed to be 0.200 yr^{-1}. When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.009 to 0.028 t km^{-2} yr^{-1} for flounders and 0.010 to 0.028 t km^{-2} yr^{-1} for skates. Production values estimated by the inverse solution were 0.027 t km^{-2} yr^{-1} (P/B = 0.43 yr^{-1}) for flounders and 0.023 t km^{-2} yr^{-1} (P/B = 0.31 yr^{-1}) for skates.

Consumption

Consumption estimates for these three groups were derived from different sources. For all three groups, FishBase provided an initial Q/B estimate based on fish at 3°C (Froese and Pauly 2002). The Q/B values obtained in this way were 2.2 yr^{-1} for American plaice, 2.4 yr^{-1} for flounders (this value was the only one available for the group), and 1.5 yr^{-1} for skates.

For American plaice, a second estimate of consumption was derived from daily ration data using the model of Elliott and Persson (1978) with fish from the Grand Banks of Newfoundland (Zamarro 1992). Daily consumption values were 0.04% to 0.64% of body mass per day, with a final mean of 0.34%. Accordingly, the mean annual Q/B ratio was 1.241 yr^{-1}. A third study, with fish from Passamaquody Bay (New Brunswick), was used to determine consumption for American plaice (MacDonald and Waiwood 1987). The authors estimated food consumption to be 1.28% of body mass per day, resulting in a Q/B ratio of 4.672 yr^{-1} (assuming that feeding is constant throughout the year). When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of 0.909 t km^{-2} yr^{-1} (range:

0.102–2.865 t km^{-2} yr^{-1}) for American plaice. Based on the previous mean production (0.100 t km^{-2} yr^{-1}) for American plaice and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.333 and 0.999 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.336 t km^{-2} yr^{-1} instead of 0.102 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.336 and 2.865 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.600 ± 1.788 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.165 t km^{-2} yr^{-1} for American plaice, representing a Q/B of 6.443 yr^{-1}.

For the flounder group, the only available value was obtained from FishBase as described above. When the minimum and maximum biomass values were used, this resulted in a total consumption range of 0.056 to 0.277 t km^{-2} yr^{-1}. Based on the previous mean production (0.017 t km^{-2} yr^{-1}) for flounders and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.057 and 0.172 t km^{-2} yr^{-1}, respectively. However, assuming that these species would eat at least as much food as their biomass (Q/B ≥ 1), we used 0.063 t km^{-2} yr^{-1} instead of 0.056 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.063 and 0.277 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.170 ± 0.151 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.132 t km^{-2} yr^{-1} for flounders, representing a Q/B of 2.086 yr^{-1}.

For skates, two other estimates of the Q/B ratio were taken into account. The first of these was determined for thorny skates from the Barents Sea (Dolgov 1997). Estimated annual consumption from this study was divided by mean biomass, resulting in an annual Q/B ratio of 2.369 yr^{-1} for our study area. The other estimate, based on thorny skate stomachs collected in the North Sea (Vinter 1989), produced a Q/B ratio of 2.865 yr^{-1} for our study area. When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a consumption range of 0.066 to 0.365 t km^{-2} yr^{-1} for skates. Based on the previous mean production (0.017 t km^{-2} yr^{-1}) for skates and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.055 and 0.165 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.074 t km^{-2} yr^{-1} instead of 0.055 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.074 and 0.365 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.219 ± 0.206 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.075 t km^{-2} yr^{-1} for skates, representing a Q/B of 1.018 yr^{-1}.

Diet composition

Diet data from NAFO divisions 4RS during the 2000–2002 period were unavailable for all three groups, so studies from other areas and time periods were used instead. For American plaice, we used the diet compositions found by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used to constrain values in inverse modelling (Table 9). The most important prey items of American plaice were large zooplankton, molluscs, other benthic invertebrates, and capelin (71.1% of the diet; Table 9).

For flounders, very little diet information was available. The summer diet of witch flounder on Flemish Cap was used and is principally made up of polychaetes (80.2% by volume), other benthic invertebrates (8.4% by volume), echinoderms (5.7% by volume), and bivalves (4.6% by

volume) (Rodriguez-Marin et al. 1994). Due to the uncertainties with diet data, we also used the diet compositions found by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s). The most important prey items in the resulting diet of flounders were polychaetes, other benthic invertebrates, molluscs, and echinoderms (87.8% of the diet; Table 9).

The diet of the thorny skate was assumed to be representative of the entire skate group. Templeman (1982) examined the annual diet of thorny skates from the northwest Atlantic and found that the main prey species were by volume, small demersal feeders (25.5%), redfish (23.6%), sand lance (15.8%), crustaceans (14.3%), and small Atlantic cod (5.7%). We also used the diet compositions found by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s). The most important prey items in the resulting diet of skates were small planktivorous pelagics, small crabs, small demersals, and redfish (78.9% of the diet; Table 9).

Table 9. Diet compositions (%) for American plaice, flounders, and skates used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	American plaice					Flounders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.2**	0.3	0.0	0.5	0.2					
Large Green. halibut										
Small Green. halibut	**0.2**	0.5	0.0	0.8	0.2					
American plaice	0.7	1.5	**0.0**	**2.1**	0.1					
Flounders	0.3	0.6	**0.0**	**0.9**	0.0					
Skates										
Redfish	**0.0**	0.0	0.0	0.0	0.0					
Large demersals										
Small demersals	0.8	1.8	**0.0**	**2.5**	0.0	1.8	3.2	**0.0**	**4.6**	0.0
Capelin	11.1	25.0	**0.0**	**35.3**	0.8	1.8	3.3	**0.0**	**4.7**	1.3
Large pelagics										
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0					
Plank. small pelagics	4.8	10.7	**0.0**	**15.2**	0.0	3.0	4.0	**0.0**	**7.7**	0.0
Female shrimp	2.1	4.8	**0.0**	**6.8**	1.9	0.5	0.9	**0.0**	**1.3**	0.6
Male shrimp	2.1	4.8	**0.0**	**6.8**	1.2	0.5	0.9	**0.0**	**1.3**	0.3
Large crabs						**0.0**	0.0	0.0	0.0	0.0
Small crabs	1.6	3.7	**0.0**	**5.2**	0.0	0.9	1.6	**0.0**	**2.2**	0.0
Echinoderms	9.7	21.9	**0.0**	**30.9**	30.3	15.2	26.9	**0.4**	**38.4**	7.7
Molluscs	16.1	36.3	**0.0**	**51.4**	45.0	15.9	28.7	**0.0**	**40.6**	21.6
Polychaetes	6.1	13.7	**0.0**	**19.4**	8.6	34.6	50.8	**8.2**	**80.1**	40.0
Other bent. inver.	12.1	27.2	**0.0**	**38.5**	9.2	22.1	28.9	**7.9**	**48.7**	26.2
Large zooplankton	31.8	68.4	**2.3**	**99.1**	2.4	2.0	3.6	**0.0**	**5.1**	1.1
Small zooplankton	0.3	0.8	**0.0**	**1.1**	0.3	**0.0**	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus						1.6	2.9	**0.0**	**4.1**	1.2
Total	100.0		2.3	316.5	100.0	100.0		16.5	239.0	100.0
TRN	18					14				

Table 9. Cont.

	Skates				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	2.4	4.4	**0.0**	**6.2**	5.4
Large Green. halibut					
Small Green. halibut	**0.1**	0.1	0.0	0.2	0.1
American plaice	**0.1**	0.1	0.0	0.2	0.1
Flounders	0.4	0.7	**0.0**	**0.9**	0.7
Skates	**0.0**	0.0	0.0	0.0	0.0
Redfish	9.0	16.7	**0.0**	**23.6**	23.6
Large demersals					
Small demersals	14.5	23.3	**2.6**	**35.5**	10.0
Capelin	3.9	7.2	**0.0**	**10.2**	10.2
Large pelagics					
Pisci. small pelagics	2.8	5.1	**0.0**	**7.2**	4.9
Plank. small pelagics	37.8	70.4	**0.0**	**99.6**	13.6
Female shrimp	1.8	2.7	**0.4**	**4.3**	4.1
Male shrimp	1.8	2.7	**0.4**	**4.3**	3.9
Large crabs					
Small crabs	17.6	26.5	**4.4**	**41.9**	7.2
Echinoderms	**0.2**	0.3	0.0	0.4	0.2
Molluscs	0.6	0.9	**0.2**	**1.5**	1.4
Polychaetes	6.6	7.3	**3.5**	**13.8**	13.1
Other bent. inver.	0.5	0.9	**0.0**	**1.3**	1.3
Large zooplankton	**0.2**	0.3	0.0	0.4	0.2
Small zooplankton	**0.1**	0.1	0.0	0.1	0.1
Phytoplankton					
Detritus					
Total	100.0		11.5	251.6	100.0
TRN	19				

Redfish and demersal feeders

Background

The demersal feeders represent deep-water demersal species from NAFO divisions 4RS. Because of its economic and ecological importance in the system, redfish was treated separately while the remaining demersal species were divided into large and small demersal feeders.

Redfish distribution in the northwest Atlantic ranges from west Greenland to the Gulf of Maine (Atkinson and Melteff 1987). Two redfish species are known to be the main component of

the northwest Atlantic stock: *Sebastes mentella*, which generally occupies waters deeper than 250 m, and *S. fasciatus*, usually found in shallower waters down to 300 m. Redfish usually inhabit waters from 100 to 700 m in depth and are ovoviviparous. Mating usually occurs in September or October, and females release live young from April to July. Redfish grow quite slowly, generally taking 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. These species have been commercially fished since the early 1950s, but a moratorium was imposed on redfish fishing in 1995 in the Gulf of St. Lawrence.

The large demersal feeder group is mainly made up of white hake (*Urophycis tenuis*), black dogfish (*Centroscyllium fabricii*), marlin spike grenadier (*Nezumia bairdi*), Atlantic halibut (*Hippoglossus hippoglossus*), wolffish (*Anarhichas* spp.), common lumpfish (*Cyclopterus lumpus*), haddock (*Melanogrammus aeglefinus*), longfin hake (*Urophycis chesteri*), large eelpout (Zoarcidae), monkfish (*Lophius americanus*), and grenadiers (Macrouridae). Information was very limited for most of these species in NAFO divisions 4RS.

The small demersal feeders group includes sculpins (Cottidae), small eelpouts (Zoarcidae), fourbeard rockling (*Enchelyopus cimbrius*), cunners (*Tautogolabrus adspersus*), gunnels (Pholidae), lumpsuckers (*Eumicrotremus* sp.), and blennies (Stichaeidae). Juvenile large demersals were also considered as small demersal feeders. Unfortunately, little is known about these species and only scant information from the study area was available.

Catch

Total landings for redfish and the large demersal feeder group in NAFO divisions 4RS during the 2000–2002 period were calculated by summing the NAFO landing statistics for each of the species listed above (NAFO 2003). Since there is no fishery for species in the small demersal feeder group and by-catch information was unavailable, catch was set at zero for this group. For redfish, the average annual landings were 767 t or 7.39×10^{-3} t km^{-2} yr^{-1} (SD = 6.61×10^{-4} t km^{-2} yr^{-1}). For the large demersal feeders, Atlantic halibut, wolffish, and white hake were the main species caught in 4RS during the 2000–2002 period (97% of total landings). The average annual catch of the large demersal feeders was estimated at 335 t or 3.23×10^{-3} t km^{-2} yr^{-1} (SD = 7.71×10^{-5} t km^{-2} yr^{-1}). The inverse solution estimated catch values of 7.34×10^{-3} and 3.23×10^{-3} t km^{-2} yr^{-1} for redfish and large demersal feeders, respectively.

Biomass

The scientific survey provided data from NAFO divisions 4RS during the 2000–2002 period to estimate annual biomass. For redfish, length-frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean mass-at-length (derived from length–mass relationships) and summing the results. For the large demersal feeder group, total biomass in the study area for each species was directly computed with *PACES* and results were summed. Average annual biomass estimates were 110,976 t or 1.069 t km^{-2} (SD = 0.130 t km^{-2}) for redfish and 15,358 t or 0.148 t km^{-2} (SD = 0.092 t km^{-2}) for large demersal feeders.

Biomass for the small demersal feeder group was determined in the same way as for their large counterparts. Average annual biomass was estimated at 11,450 t or 0.110 t km^{-2} (SD = 0.051 t km^{-2}) corresponding to a range of 0.059 to 0.161 t km^{-2} for the entire study area during the 2000–2002 period. However, based on initial inverse modelling runs (see the following production section) and due to the large uncertainty related to the biomass of this group, the previous values seemed too low to meet predator demands. Hence these values were increased for small demersals (0.504 ± 0.630 t km^{-2}; range: 0.059–0.950 t km^{-2}).

Production

Information on production and total mortality (Z) of redfish and large demersal species was lacking. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality (M) was assumed to be 0.125 yr^{-1} for redfish (Bundy et al. 2000) and 0.200 yr^{-1} for large demersal feeders (Hurlbut and Poirier 2001). When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.123 to 0.155 t km^{-2} yr^{-1} for redfish and 0.018 to 0.053 t km^{-2} yr^{-1} for large demersal feeders. Production values estimated by the inverse solution were 0.147 t km^{-2} yr^{-1} (P/B = 0.14 yr^{-1}) for redfish and 0.052 t km^{-2} yr^{-1} (P/B = 0.35 yr^{-1}) for large demersal feeders.

Due to the large uncertainty related to the data of the small demersal feeders, we used the mean P/B value (0.42 yr^{-1}) obtained for the mid-1980 (0.46 yr^{-1}) and mid-1990 (0.38 yr^{-1}) models. When the initial minimum and maximum biomass values were used, we obtained a production range of 0.025 to 0.068 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.046 ± 0.022 t km^{-2} yr^{-1}. However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.400 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.950 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were thus 0.025 to 0.400 t km^{-2} yr^{-1}, corresponding to a mean of 0.212 ± 0.265 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 0.396 t km^{-2} yr^{-1} (P/B = 0.79 yr^{-1}) for small demersal feeders.

Consumption

FishBase was used to estimate the Q/B ratio of both redfish and large demersal feeders, assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in Q/B ratios of 2.1 and 3.1 yr^{-1}, respectively, for redfish and the large demersal feeders.

Other information on redfish consumption is available. Dolgov and Revetnyak (1990) estimated annual food consumption to biomass ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr^{-1} for fingerlings down to around 1.3 yr^{-1} for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of the biomass, the mean Q/B of fish from 10 to 19 years of age was computed. This produced a mean Q/B ratio of 1.490 yr^{-1}. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992b). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr^{-1}.

On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr^{-1} (Pauly 1989). When the minimum and maximum biomass values and the four previous Q/B ratios were used, we obtained a consumption range of 1.378 to 9.392 t km^{-2} yr^{-1} for redfish. Based on the previous mean production (0.141 t km^{-2} yr^{-1}) for redfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.470 and 1.410 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 1.069 t km^{-2} yr^{-1} instead of 0.470 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 1.069 and 9.392 t km^{-2} yr^{-1}, corresponding to a mean consumption of 5.230 ± 5.885 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.145 t km^{-2} yr^{-1} for redfish, representing a Q/B of 1.071 yr^{-1}.

For the large demersal feeders, the only available value was obtained from FishBase as described above. When the minimum and maximum biomass values were used, this resulted in a consumption range of 0.225 to 0.775 t km^{-2} yr^{-1} for the large demersal feeders. Based on the previous mean production (0.033 t km^{-2} yr^{-1}) for large demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.109 and 0.328 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.148 t km^{-2} yr^{-1} instead of 0.109 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.148 and 0.775 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.461 ± 0.443 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.251 t km^{-2} yr^{-1} for large demersal feeders, representing a Q/B of 1.697 yr^{-1}.

The only information available for the small demersal feeders were Q/B estimates computed from FishBase (Froese and Pauly 2002). We averaged the Q/B ratios obtained in this way for two species of the group, fourbeard rockling (2.70 yr^{-1}) and Atlantic soft pout (4.30 yr^{-1}). When the resulting minimum and maximum biomass values were used, this resulted in a consumption range of 0.158 to 4.086 t km^{-2} yr^{-1} for the small demersal feeders. Based on the previous mean production (0.212 t km^{-2} yr^{-1}) for small demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.708 and 2.124 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.504 t km^{-2} yr^{-1} as lower limit. The resulting lower and upper consumption limits were 0.504 and 4.086 t km^{-2} yr^{-1}, corresponding to a mean consumption of 2.295 ± 2.532 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.653 t km^{-2} yr^{-1} for small demersal feeders, representing a Q/B of 5.259 yr^{-1}.

Diet composition

Diet data from NAFO divisions 4RS during the 2000–2002 period were unavailable for all three groups, so studies from other areas and time periods were used instead. For redfish, we used the diet compositions found by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004b) for the northern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used to constrain values in inverse modelling (Table 10). The most important prey items of the resulting diet of redfish were large zooplankton, shrimp, and small planktivorous pelagics (79.5% of the diet; Table 10).

For large demersal feeders, diet was assumed to be that of white hake, the key species of the group. There was no diet information available for the Gulf of St. Lawrence, but some was found for the northeast United States and Scotian Shelf (Langton and Bowman 1980). In 169

white hake stomachs from these areas, small piscivorous pelagic feeders, small demersal feeders, and small planktivorous pelagic feeders were the most important prey items. We also used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf, by Bowman et al. (2000) for the Scotian Shelf, and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 10). The most important prey items of the resulting diet of large demersals were small planktivorous pelagics, small crabs, polychaetes, and small piscivorous pelagics (62.9% of the diet; Table 10).

There was no information found on the diet of small demersal feeders. So, we used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s). The most important prey items of the resulting diet of small demersals were small crabs, other benthic invertebrates, small demersals, and American plaice (58.7% of the diet; Table 10).

Table 10. Diet compositions (%) for redfish, large demersal feeders, and small demersal feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Redfish					Large demersal feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.1**	0.1	0.0	0.2	0.1	1.5	4.7	**0.0**	**6.6**	0.1
Large Green. halibut										
Small Green. halibut						0.3	0.8	**0.0**	**1.1**	0.9
American plaice						0.4	1.2	**0.0**	**1.7**	0.4
Flounders						0.3	0.8	**0.0**	**1.1**	0.0
Skates						2.2	6.7	**0.0**	**9.4**	0.0
Redfish	1.1	1.7	**0.0**	**2.4**	1.4	1.1	3.4	**0.0**	**4.8**	2.8
Large demersals										
Small demersals	0.9	1.3	**0.1**	**1.9**	0.1	6.2	18.5	**0.1**	**26.3**	0.1
Capelin	10.3	14.4	**0.7**	**21.1**	21.1	3.8	11.3	**0.0**	**16.0**	6.5
Large pelagics										
Pisci. small pelagics	**0.3**	0.4	0.0	0.5	0.3	9.9	29.8	**0.0**	**42.1**	0.0
Plank. small pelagics	12.2	18.3	**0.0**	**25.9**	0.0	22.7	68.5	**0.0**	**96.9**	4.0
Female shrimp	15.5	20.8	**1.8**	**31.2**	14.8	3.4	10.1	**0.0**	**14.3**	3.1
Male shrimp	15.5	20.8	**1.8**	**31.2**	2.4	3.4	10.1	**0.0**	**14.3**	4.8
Large crabs										
Small crabs						16.7	50.3	**0.1**	**71.3**	0.1
Echinoderms						4.7	14.1	**0.0**	**19.9**	11.6
Molluscs	**0.0**	0.0	0.0	0.0	0.0	1.6	4.7	**0.0**	**6.7**	4.3
Polychaetes	**0.0**	0.0	0.0	0.0	0.0	13.5	40.8	**0.0**	**57.7**	45.3
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	3.3	9.9	**0.0**	**14.1**	8.5
Large zooplankton	36.3	21.7	**23.1**	**53.8**	43.7	4.8	14.4	**0.0**	**20.4**	7.0
Small zooplankton	7.8	11.1	**0.4**	**16.1**	16.1	0.3	1.0	**0.0**	**1.4**	0.4
Phytoplankton										
Detritus										
Total	100.0		27.8	184.3	100.0	100.0		0.2	425.9	100.0
TRN	13					19				

Table 10. Cont.

	Small demersal feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	4.6	10.3	**0.0**	**14.6**	0.0
Large Green. halibut					
Small Green. halibut					
American plaice	9.2	20.6	**0.0**	**29.1**	0.2
Flounders	6.6	14.8	**0.0**	**20.9**	0.0
Skates					
Redfish					
Large demersals					
Small demersals	10.2	21.5	**1.0**	**31.4**	1.0
Capelin	0.8	1.5	**0.0**	**2.5**	0.8
Large pelagics					
Pisci. small pelagics	**0.1**	0.1	0.0	0.2	0.1
Plank. small pelagics	3.1	6.3	**0.0**	**9.9**	0.0
Female shrimp	3.4	6.4	**0.9**	**9.9**	1.9
Male shrimp	3.4	6.4	**0.9**	**9.9**	1.0
Large crabs					
Small crabs	26.0	57.4	**0.5**	**81.6**	0.5
Echinoderms	3.2	7.1	**0.0**	**10.0**	10.0
Molluscs	3.2	7.1	**0.0**	**10.0**	10.0
Polychaetes	6.3	14.1	**0.0**	**20.0**	18.8
Other bent. inver.	13.3	29.7	**0.0**	**42.0**	41.5
Large zooplankton	5.0	11.1	**0.0**	**15.7**	10.1
Small zooplankton	1.6	3.5	**0.0**	**5.0**	4.2
Phytoplankton					
Detritus					
Total	100.0		3.3	312.7	100.0
TRN	16				

Capelin

Background

There was very little information available on forage fish from NAFO divisions 4RS. In most cases, data from other areas were used for the model. Two species were identified and aggregated into the capelin group: capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*). Capelin is a small, short-lived pelagic fish that spends most of its life offshore, moving

inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the northern Gulf of St. Lawrence.

The Arctic cod has a circumpolar distribution and is found in the northwest Atlantic from arctic waters in the north down to the southern Gulf of St. Lawrence (Scott and Scott 1988). This species is pelagic and feeds mainly on invertebrates found in the upper part of the water column. Arctic cod is a key component of the marine food web of arctic waters (Hop et al. 1997) and an important link in the transfer of energy from zooplankton to other fish, marine mammals, and seabirds (Lilly et al. 1994). However, because its biomass is generally low, we included it in the capelin group.

Catch

For capelin, the average annual landings for the 2000–2002 period in the study area were estimated from NAFO landing statistics to be 3,055 t or 2.94 x 10^{-2} ± 2.12 x 10^{-2} t km^{-2} yr^{-1} (NAFO 2003). There was no catch data entered in the model for Arctic cod. The inverse solution estimated catch values of 2.76 x 10^{-2} t km^{-2} yr^{-1} for capelin.

Biomass

Annual biomass estimates of capelin were obtained from the scientific surveys for the 2000–2002 period using the *PACES* software. This resulted in a mean annual biomass estimate of 5,299,117 t or 50.083 ± 36.354 t km^{-2} (range: 19.299–90.211t km^{-2}) for the 4RS ecosystem. Since the biomass of this group was a gross approximation, we also used an estimate (0.070 t km^{-2}) from acoustic surveys in the Lower St. Lawrence Estuary (Y. Simard, Institut Maurice-Lamontagne, pers. comm.). For Arctic cod, the mean annual biomass estimate was 1,154 t or 0.011 ± 0.010 t km^{-2}. The resulting biomass for the capelin group was then 45.141 ± 63.724 t km^{-2}.

Production

There was no information available concerning the P/B ratios in the study area for capelin. Production was assumed to be equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was set to 0.6 yr^{-1} to reflect the biology of this short-lived species (F. Grégoire, Institut Maurice-Lamontagne, pers. comm.). When the mean, minimum, and maximum biomass values were used, we obtained a mean annual production of 27.114 ± 38.273 t km^{-2} yr^{-1} (range: 0.049–54.176 t km^{-2} yr^{-1}). The production value estimated by the inverse solution for capelin was 4.233 t km^{-2} yr^{-1} (P/B = 0.09 yr^{-1}).

Consumption

Consumption rates for capelin and Arctic cod were taken from various sources. The Q/B ratio was determined using FishBase (Froese and Pauly 2002). Q/B ratios for capelin and Arctic cod were estimated for a water temperature of 1°C, considering that these species are generally found near the cold intermediate layer in the Gulf of St. Lawrence. We obtained Q/B ratio values of 3.8 and 2.7 yr^{-1} for capelin and Arctic cod, respectively.

Other studies on the consumption of capelin were available. We used a second estimate based on the feeding ecology of capelin in the estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% body mass in summer and 2.50% body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.688 yr^{-1}. A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.333 yr^{-1}. Finally, Panasenko (1981) estimated a Q/B ratio of 27.558 yr^{-1} in another study in the Barents Sea. When the mean, minimum, and maximum biomass values as well as the four previous Q/B ratios were used, we obtained a consumption range of 0.267 to 2,485.997 t km^{-2} yr^{-1}. In addition to the FishBase value, a second Q/B ratio (3.941 yr^{-1}) was available for Arctic cod from Canadian arctic waters (Hop et al. 1997). In this study, mean daily rations (% body mass per day) of juvenile and adult Arctic cod were estimated. When the minimum and maximum biomass values and the two previous Q/B ratios were used, we obtained a consumption range of 0.001 to 0.083 t km^{-2} yr^{-1}. This resulted in a consumption range of 0.268 to 2,486.080 t km^{-2} yr^{-1} for the capelin group.

Based on the previous mean production (27.114 t km^{-2} yr^{-1}) for the capelin group and the minimum and maximum GE limits (10–30%), we obtained consumption values of 90.381 and 271.143 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.268 and 2,486.080 t km^{-2} yr^{-1}, corresponding to a mean annual consumption of 1,243.174 ± 1,757.735 t km^{-2} yr^{-1}. The consumption value estimated by the inverse solution was 22.010 t km^{-2} yr^{-1} (Q/B = 0.488 yr^{-1}) for capelin, which makes it the largest fish predator in the northern Gulf.

Diet composition

For capelin, the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Jangaard (1974) for the North Atlantic were used. Main prey items were copepods (*Temora longicornis*, *Calanus finmarchicus*, and *Pseudocalanus minutus*) and euphausiid eggs. We used also the study of Vesin et al. (1981) in the estuary and western Gulf of St. Lawrence. In that study, euphausiids and copepods were the main prey (59 and 41%, respectively). The final diet compositions are shown in Table 11.

Table 11. Diet compositions (%) for capelin used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Capelin				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin	0.5	0.7	**0.0**	**1.0**	0.8
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics	0.5	0.7	**0.0**	**1.0**	0.0
Female shrimp					
Male shrimp					
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0
Large zooplankton	51.2	11.0	**43.4**	**59.0**	50.3
Small zooplankton	47.8	9.6	**41.0**	**54.6**	48.9
Phytoplankton					
Detritus					
Total	100.0		84.4	115.6	100.0
TRN	5				

Pelagic feeders

Background

The pelagic feeders are also an important part of the ecosystem, and some species are commercially fished. Three boxes are designed to represent these species: large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders.

The large pelagic feeder group includes spiny dogfish (*Squalus acanthias*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). The most abundant large pelagic feeder in NAFO divisions 4RS is spiny dogfish (68% of biomass). Juveniles of these species were classified as either piscivorous or planktivorous small pelagic feeders according to juvenile feeding behaviour.

The piscivorous small pelagic feeders group includes Atlantic mackerel (*Scomber scombrus*), short-finned squid (*Illex illecebrosus*), and juveniles of large pelagics. Atlantic mackerel was the most important in terms of biomass (99% of biomass) and was therefore considered the key species for the group. Mackerel populations in the northwest Atlantic form a stock complex that overwinters off the New England coast. A part of this stock complex then migrates northwards in May and June to spawn in the southern Gulf of St. Lawrence (Moores et al. 1975). After spawning, they disperse throughout the Gulf for the rest of the summer.

The planktivorous small pelagic feeders group includes Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*), planktivorous myctophids, sand lance (northern sand lance *Ammodytes dubius* and American sand lance *Ammodytes americanus*), and other mesopelagics. Atlantic herring was the most important in terms of biomass (99% of biomass) and was therefore considered the key species for the group. The spring-spawning population congregates off the west coast of Newfoundland and in and around St. George's Bay; the autumn-spawning stock regroups further up the coast, north of Point Riche, to reproduce (McQuinn et al. 1999). Outside of the spawning season, these two stocks are mainly found in St. George's Bay in the spring, north of Point Riche and in the Strait of Belle Isle in the summer, and off Bonne Bay in the fall (McQuinn et al. 1999).

Catch

For the large pelagic feeders, landings for pollock (the only species for which data were available) were 0.3 t or 3.21×10^{-6} t km^{-2} yr^{-1} (SD = 5.56×10^{-6} t km^{-2} yr^{-1}) (NAFO 2003). The inverse solution estimated a catch value of 3.41×10^{-6} t km^{-2} yr^{-1}.

Concerning piscivorous small pelagic feeders, the mean landings in NAFO divisions 4RS for 2000–2002 were 7,078 t or 6.82×10^{-2} t km^{-2} yr^{-1} (SD = 4.63×10^{-2} t km^{-2} yr^{-1}) (NAFO 2003). The inverse solution estimated a catch value of 6.73×10^{-2} t km^{-2} yr^{-1}.

Finally, for the planktivorous small pelagic feeders, the average landings in the study area during the 2000–2002 period were 12,978 t or 1.25×10^{-1} t km^{-2} yr^{-1} (SD = 6.56×10^{-3} t km^{-2} yr^{-1}) (NAFO 2003). The inverse solution estimated a catch value of 1.25×10^{-1} t km^{-2} yr^{-1}.

Biomass

For the large pelagic feeders, biomass was calculated from scientific research survey data covering NAFO divisions 4RS during the 2000–2002 period. Biomass estimates were only available for silver hake, pollock, and spiny dogfish. The biomasses of all three species were then summed to obtain an estimate for the group. The mean biomass for the large pelagic feeders was estimated to be 1,113 t or 0.011 t km^{-2} (SD = 0.011 t km^{-2}).

Biomass estimates for Atlantic mackerel were derived from an egg production index calculated for 1983 to 2002 for the southern Gulf of St. Lawrence (DFO 2003c). We did not apply a residence time factor to reduce biomass by two (6 months outside the Gulf) because this kind of fish feeds mainly during the summer period when they are in the Gulf. Only the 2000–2002 estimates were used to calculate the mean annual biomass. After spawning, mackerel disperse throughout the entire area (NAFO divisions 4RS and 4T). There is a little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. We assumed that one third of the biomass moved into 4RS while the other two thirds were distributed in 4T. Knowing that the northern Gulf represents 59.7% of the trawlable surface area of the entire Gulf of St. Lawrence, mackerel biomass was estimated to be 90,680 t or 0.521 t km^{-2} (SD = 0.290 t km^{-2}). All the other small piscivorous pelagic biomasses were evaluated from scientific research survey data but were very low. For the whole group, biomass was estimated to be 0.524 ± 0.290 t km^{-2}.

For the planktivorous small pelagic feeders, the average biomass of herring (the key species for the group) during the 2000–2002 period in the eastern part of the study area (NAFO division 4R) was taken from the sequential population analysis (SPA) (DFO 2003d). Since herring populations in 4S are considered to be small and data for this region were unavailable, it was assumed that the 4R population represented all the herring in the study area. The total biomass was 118,825 t or 1.145 ± 0.054 t km^{-2}. All the other small planktivorous pelagic biomasses were evaluated from research survey data at 894 t or 0.009 ± 0.003 t km^{-2}. Total biomass for the planktivorous small pelagic group was 1.153 ± 0.055 t km^{-2}.

Production

There was no information on specific P/B ratios for the large pelagic feeders in the study area. Bundy et al. (2000) estimated a P/B of 0.4 yr^{-1} for large pelagic feeders on the Newfoundland–Labrador Shelf. When the minimum and maximum biomass values were applied to this ratio, we obtained a production range of 0.001 to 0.009 t km^{-2} yr^{-1}, corresponding to a mean production of 0.004 ± 0.004 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.008 t km^{-2} yr^{-1}, representing a P/B of 0.73 yr^{-1}.

For the piscivorous small pelagic feeders, a value of 0.2 yr^{-1} was used for natural mortality in the absence of better information (F. Grégoire, DFO, Institut Maurice-Lamontagne, pers. comm.). For squid, a value of 1.0 yr^{-1} was used for natural mortality. When the minimum and maximum biomass values were used, we obtained a production range of 0.082 to 0.255 t km^{-2} yr^{-1}, corresponding to a mean production of 0.168 ± 0.122 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.254 t km^{-2} yr^{-1}, representing a P/B of 0.48 yr^{-1}.

For the planktivorous small pelagic feeders, natural mortality was assumed to be 0.2 yr^{-1} (Grégoire and Lefebvre 2002). When the minimum and maximum biomass values were used, we

obtained a production range of 0.346 to 0.369 t km^{-2} yr^{-1}, corresponding to a mean production of 0.357 ± 0.009 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.365 t km^{-2} yr^{-1}, representing a P/B of 0.32 yr^{-1}.

Consumption

For the large pelagic feeders, FishBase made available two Q/B estimates (3.850 and 4.260 yr^{-1}) for silver hake from American waters, one Q/B estimate (4.760 yr^{-1}) for pollock from Canadian waters, and one Q/B estimate (4.770 yr^{-1}) for spiny dogfish also from Canadian waters (Froese and Pauly 2002). Three other consumption estimates were also available for silver hake. Edwards and Bowman (1979) studied the food consumed by fish on the continental shelf: a total of 17,000 stomachs obtained from 1963 to 1974 on the continental shelf between New Jersey and Halifax were analyzed. These authors estimated a Q/B ratio of 11.315 yr^{-1} for silver hake. A Q/B ratio of 7.869 yr^{-1} was estimated from stomach content analysis and the estimation of daily ration for silver hake (Durbin et al. 1983). Finally, in another study, Cohen and Grosslein (1981) examined food consumption of fish from Georges Bank. Q/B ratios of 7.605 and 9.516 yr^{-1}, respectively, were estimated for silver hake and pollock. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 0.003 to 0.171 t km^{-2} yr^{-1}. Based on the mean production (0.004 t km^{-2} yr^{-1}) for the large pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.014 and 0.043 t km^{-2} yr^{-1}. However, assuming that these species would eat at least as much food as their biomass (Q/B ≥ 1), we used 0.011 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 0.011 and 0.171 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.091 ± 0.113 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.042 t km^{-2} yr^{-1} for the large pelagic feeders, representing a Q/B ratio of 3.898 yr^{-1}.

For the piscivorous small pelagic feeders, a Q/B estimate of 4.400 yr^{-1} for Atlantic mackerel was taken from FishBase. Also, Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day (n = 3,674). A Q/B ratio of 2.190 yr^{-1} was thus estimated from this information. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 0.700 to 3.208 t km^{-2} yr^{-1}. Based on the mean production (0.168 t km^{-2} yr^{-1}) for the piscivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.561 and 1.684 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.561 and 3.208 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.885 ± 1.872 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.088 t km^{-2} yr^{-1} for the piscivorous small pelagic feeders, representing a Q/B ratio of 2.075 yr^{-1}.

For planktivorous small pelagics, Q/B estimates were derived from Pauly (1989), Rudstam et al. (1992), and Fetter and Davidjuka (1996). During summer, specific consumption rates of herring in the Baltic Sea were estimated from 10 to 20% of the body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups (Rudstam et al. 1992). During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1}. Values taken from Pauly (1989) were 4.590 yr^{-1} for fish from Georges Bank and 10.100 yr^{-1} for fish from the North Sea. Finally, Fetter and Davidjuka (1996) estimated daily food consumption for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual

Q/B of 2.798 yr^{-1}. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 3.042 to 16.342 t km^{-2} yr^{-1}. Based on the mean production (0.357 t km^{-2} yr^{-1}) for the planktivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.189 and 3.568 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 1.189 and 16.342 t km^{-2} yr^{-1}, corresponding to a mean consumption of 8.766 ± 10.715 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.499 t km^{-2} yr^{-1} for the planktivorous small pelagic feeders, representing a Q/B ratio of 2.167 yr^{-1}.

Diet composition

Diet data from NAFO divisions 4RS during the 2000–2002 period were unavailable for the large pelagic feeders, so studies from other areas and time periods were used instead. We used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf, by Bowman et al. (2000) for the Gulf of Maine, and by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 12). The most important prey items of the resulting diet of large pelagics were small planktivorous pelagics, large zooplankton, and small piscivorous pelagics (80.7% of the diet; Table 12).

Diet composition for the piscivorous small pelagic feeders was derived from four sources of information on Atlantic mackerel, the key species for this group. On the Scotian Shelf, the main prey in 199 mackerel stomachs were hyperid amphipods, euphausiids, and fish larvae (mainly blennoids and gadoids) (Kulka and Stobo 1981). The other diet study examined 359 mackerel stomachs from the Gulf of St. Lawrence and the Scotian Shelf (Grégoire and Castonguay 1989). In this study, the main prey species (in % abundance) were found to be nematodes (which were probably stomach parasites), copepods, and unidentified larvae. In the southern Gulf, Darbyson et al. (2003) found that the main prey in 265 mackerel stomachs were capelin, euphausiids, and copepods. We also used the diet composition estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) based on stomach content data for mackerel from June to September 1999 (n = 515). The resulting diet composition is shown in Table 12.

For the diet of the planktivorous small pelagic group, we used the diet composition estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and the stomach content data available from NAFO division 4T from April to September 1999 (n = 718) (Savenkoff et al. 2004c). We used also the study of Darbyson et al. (2003) in the southern Gulf. The most important prey items of the resulting diet of small planktivorous pelagics were large and small zooplankton (86.9% of the diet; Table 12).

Table 12. Diet compositions (%) for large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large pelagic feeders					Piscivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.1**	0.2	0.0	0.3	0.1	**0.0**	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut										
American plaice	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Flounders	2.9	5.1	**0.0**	**7.2**	0.8	**0.0**	0.0	0.0	0.0	0.0
Skates	2.1	3.7	**0.0**	**5.2**	1.1					
Redfish	0.5	0.9	**0.0**	**1.3**	1.1					
Large demersals										
Small demersals	2.8	4.9	**0.0**	**7.0**	1.4	**0.1**	0.2	0.0	0.2	0.1
Capelin	4.0	7.1	**0.0**	**10.0**	9.3	8.4	21.9	**0.0**	**31.0**	17.2
Large pelagics										
Pisci. small pelagics	13.6	24.0	**0.0**	**34.0**	3.0	0.1	0.4	**0.0**	**0.5**	0.1
Plank. small pelagics	45.2	59.5	**14.4**	**98.5**	18.4	12.4	32.1	**0.0**	**45.4**	0.0
Female shrimp	1.1	1.9	**0.0**	**2.6**	2.0	11.0	28.5	**0.0**	**40.3**	16.0
Male shrimp	1.1	1.9	**0.0**	**2.6**	2.0	11.0	28.5	**0.0**	**40.3**	2.4
Large crabs										
Small crabs	0.9	1.5	**0.0**	**2.1**	0.2					
Echinoderms	**0.0**	0.0	0.0	0.0	0.0					
Molluscs						**0.1**	0.3	0.0	0.4	0.1
Polychaetes	1.8	3.1	**0.0**	**4.5**	4.5					
Other bent. inver.	1.4	2.5	**0.0**	**3.5**	3.0	2.6	6.8	**0.0**	**9.7**	7.1
Large zooplankton	21.9	38.6	**0.0**	**54.6**	51.6	27.1	70.4	**0.0**	**99.6**	20.2
Small zooplankton	0.7	1.3	**0.0**	**1.8**	1.5	27.2	70.7	**0.0**	**100.0**	36.9
Phytoplankton										
Detritus										
Total	100.0		14.4	235.3	100.0	100.0		0.0	367.4	100.0
TRN	17					13				

Table 12. Cont.

	Planktivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	**0.0**	0.0	0.0	0.0	0.0
Large Green. halibut					
Small Green. halibut					
American plaice	**0.0**	0.0	0.0	0.0	0.0
Flounders	**0.0**	0.0	0.0	0.0	0.0
Skates					
Redfish					
Large demersals					
Small demersals	**0.0**	0.0	0.0	0.0	0.0
Capelin	1.9	**2.9**	**0.0**	**4.1**	1.1
Large pelagics					
Pisci. small pelagics	**0.5**	0.0	0.5	0.5	0.5
Plank. small pelagics	**0.1**	0.2	0.0	0.3	0.1
Female shrimp	3.1	**4.8**	**0.0**	**6.9**	2.7
Male shrimp	3.1	**4.8**	**0.0**	**6.9**	0.4
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.	4.5	**7.1**	**0.0**	**10.0**	9.8
Large zooplankton	42.0	**66.2**	**0.0**	**93.7**	35.7
Small zooplankton	44.9	**70.7**	**0.0**	**100.0**	49.7
Phytoplankton					
Detritus					
Total	100.0		0.6	222.4	100.0
TRN	12				

Crustaceans

Background

Lobster is not included here because only waters deeper than 37 m were considered. The main crustaceans of the northern Gulf of St. Lawrence ecosystem are shrimp and snow crab. Both are exploited commercially.

The shrimp group consists of several species of penaeid and caridean shrimp and is represented by the key species northern shrimp, *Pandalus borealis*, which dominates the biomass

and is fished commercially. Generally, shrimp are found throughout the Estuary and the northern Gulf of St. Lawrence at depths of 150–350 m, but migrations do occur during breeding (the females migrate to shallower waters at the channel heads) and feeding (at night, they leave the ocean floor to feed on small planktonic organisms) (DFO 2002a). One important feature in *Pandalus* spp. shrimp life history is protandric hermaphroditism, i.e., individuals are born male and change to female at the age of 4 or 5 years (DFO 2002a). Consequently, females are larger than males and more subject to fishing. Thus, based on age/size at first capture (22 mm), shrimp was separated into females (≥ 22 mm) and males (< 22 mm) (L. Savard, Institut Maurice-Lamontagne, pers. comm.). The striped shrimp, *Pandalus montagui*, is also found in the northern Gulf but is less abundant.

The snow crab (*Chionoecetes opilio*) represents the key species of the crab group, which also includes other species such as toad crabs (*Hyas* spp.). Snow crab is highly exploited in the northern Gulf of St. Lawrence, particularly along Québec's North Shore. Because of important differences in diet, vulnerability to predation (particularly cannibalism; Lovrich and Sainte-Marie 1997), minimal carapace width of adult snow crabs (40 mm carapace width [CW]), and fishing pressure, the crab group was separated into small (CW ≤ 45 mm) and large crabs (CW > 45 mm).

Catch

Information on commercial landings of northern shrimp are available since 1982 for the three management units in the northern Gulf: Sept-Îles, Anticosti, and Esquiman (Savard et al. 2002). Since length frequencies of commercial landings are very similar to the CCGS *Alfred Needler* frequencies (L. Savard, Institut Maurice-Lamontagne, pers. comm.), we used the sex-ratio established from this scientific survey to separate the commercial catch into females and males. The annual total landings from 2000 to 2002 were 14,832 t or 1.43×10^{-1} t km^{-2} yr^{-1} (SD = 1.71×10^{-2} t km^{-2} yr^{-1}) for females and 9,746 t or 9.39×10^{-2} t km^{-2} yr^{-1} (SD = 2.14×10^{-2} t km^{-2} yr^{-1}) for males. The inverse solution estimated catch values of 1.45×10^{-1} and 9.22×10^{-2} t km^{-2} yr^{-1} for females and males, respectively.

For large crabs, a mean of 8,565 t was taken annually between 2000 and 2002, resulting in total landings of 8.25×10^{-2} t km^{-2} yr^{-1} (SD = 7.17×10^{-3} t km^{-2} yr^{-1}) (NAFO 2003). No catch values have been recorded for small crabs. The inverse solution estimated a catch value of 8.29×10^{-2} t km^{-2} yr^{-1} for large crabs.

Biomass

Shrimp biomass was calculated from scientific research survey data covering NAFO zones 4RS during the 2000–2002 period taking into account diurnal variation in catch rate (L. Savard, Institut Maurice-Lamontagne, pers. comm.). Mean biomass was 0.934 ± 0.198 t km^{-2} and 0.609 ± 0.123 t km^{-2} for females and males respectively. Since sex change occurs at a similar length for both *P. borealis* and *P. montagui* (Savard et al. 2002; Orr et al. 2003), the sex-ratio of *P. borealis* has been used to separate *P. montagui* by sex. The biomass of *P. montagui* was 0.012 ± 0.011 t km^{-2} for females and 0.007 ± 0.006 t km^{-2} for males. For the shrimp group, biomass was thus 98,240 t or 0.946 ± 0.207 t km^{-2} for females and 64,031 t or 0.617 ± 0.127 t km^{-2} for males.

Current snow crab assessments do not estimate the total biomass in the Gulf of St. Lawrence. Biomass for the crab groups was estimated using the abundances of snow crabs estimated by a complete bottom trawl survey conducted in Baie Sainte-Marguerite (B. Sainte-Marie, Institut Maurice-Lamontagne, unpublished data) and off the North Shore (R. Dufour, Institut Maurice-Lamontagne, unpublished data) in 1994 (period of high abundance of small crabs) and 1999 (period of low abundance of small crabs) in order to have extreme values. Abundance values were converted into biomass values using carapace width and biomass relationships for female, male, and immature crabs for the two size classes (B. Sainte-Marie, Institut Maurice-Lamontagne, unpublished data). Assuming that size structure and biomass density were similar throughout the Gulf for areas shallower than 200 m depth (103,812 – 57,858 = 45,954 km^2; 57,858 km^2 represents the area deeper than 200 m depth according to the "Petrie box" area in Gilbert et al. [1995]), we obtained a mean biomass estimate of 5.710 ± 6.675 t km^{-2} (range: 0.991–10.430 t km^{-2}) and 0.816 ± 1.102 t km^{-2} (range: 0.037–1.595 t km^{-2}) for large and small crabs, respectively. Since the Baie Sainte-Marguerite was not representative of the whole northern Gulf, we decided to use the previous minimum and mean values as lower and upper biomass limits (0.991–5.710 t km^{-2} and 0.037–0.816 t km^{-2} for large and small crabs, respectively). The resulting biomass values were 3.351 ± 3.916 t km^{-2} and 0.426 ± 0.576 t km^{-2} for large and small crabs, respectively

Production

Due to the lack of information, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. For female and male shrimp, natural mortality was assumed to be 0.64 yr^{-1} (Fréchette and Labonté 1981). When the minimum and maximum biomass values were used, we obtained a production range of 0.581 to 0.848 t km^{-2} yr^{-1} for females and 0.386 to 0.570 t km^{-2} yr^{-1} for males. However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands and fishing pressure. We used the mean P/B ratio (1.38 yr^{-1}) obtained by Bundy et al. (2000) for the Newfoundland–Labrador Shelf ecosystem (1.45 yr^{-1}), by Morissette et al. (2003) for the northern Gulf for the mid-1980s (0.93 yr^{-1}), and by Savenkoff et al. (2004b) for the northern Gulf for the mid-1990s (1.74 yr^{-1}). Multiplying this mean P/B ratio by maximum biomass for each group resulted in production values of 1.542 t km^{-2} yr^{-1} for females and 0.991 t km^{-2} yr^{-1} for males. The production ranges used were 0.581 to 1.542 t km^{-2} yr^{-1} for females and 0.386 to 0.991 t km^{-2} yr^{-1} for males. The inverse solution estimated a production of 1.163 t km^{-2} yr^{-1} (P/B = 1.23 yr^{-1}) for females and 0.886 t km^{-2} yr^{-1} (P/B = 1.44 yr^{-1}) for males.

For large and small crabs, assumed natural mortality values of 0.2 and 0.35 yr^{-1}, respectively, were used to take into account the high natural mortality of juveniles and the lower natural mortality of adults (B. Sainte-Marie, pers. comm.). Using minimum and maximum biomasses, this resulted in a production range of 0.277 to 1.230 t km^{-2} yr^{-1} (mean: 0.753 ± 0.674 t km^{-2} yr^{-1}) for large crabs and 0.013 to 0.286 t km^{-2} yr^{-1} (mean: 0.149 ± 0.193 t km^{-2} yr^{-1}) for small crabs. The inverse solution estimated a production of 1.070 t km^{-2} yr^{-1} (P/B = 0.32 yr^{-1}) for large crabs and 0.286 t km^{-2} yr^{-1} (P/B = 0.67 yr^{-1}) for small crabs.

Consumption

In the absence of information on food consumption by northern shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption). Based on the mean production for each shrimp group (females: 1.062 t km^{-2} yr^{-1}; males: 0.688 t km^{-2} yr^{-1}) and the minimum and maximum GE limits (10–30%), we obtained consumption ranges of 3.540 to 10.619 t km^{-2} yr^{-1} (mean: 7.079 ± 5.006 t km^{-2} yr^{-1}) for females and 2.294 to 6.882 t km^{-2} yr^{-1} (mean: 4.588 ± 3.244 t km^{-2} yr^{-1}) for males. The inverse solution estimated a consumption of 6.620 t km^{-2} yr^{-1} (Q/B = 6.995 yr^{-1}) for females and 3.975 t km^{-2} yr^{-1} (Q/B = 6.444 yr^{-1}) for males.

Snow crab consumption data were obtained from a study conducted in the Baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984). A daily ration of 0.4% of body mass was estimated, resulting in a Q/B ratio of 1.460 yr^{-1}. A second estimate was derived from a study of the physiological energetics of the snow crab (Thompson and Hawryluk 1990). The estimated Q/B ratio was 1.302 yr^{-1}. When the minimum and maximum biomass values for each crab group and the two previous Q/B ratios were used, we obtained a consumption range of 1.290 to 8.337 t km^{-2} yr^{-1} for large crabs and 0.048 to 1.191 t km^{-2} yr^{-1} for small crabs. Based on the minimum and maximum production values for each crab group and the minimum and maximum GE limits (10–30%), we obtained consumption ranges of 0.922 to 12.300 t km^{-2} yr^{-1} for large crabs and 0.043 to 2.855 t km^{-2} yr^{-1} for small crabs. The resulting consumption ranges were 0.922 to 12.300 t km^{-2} yr^{-1} (mean: 6.611 ± 8.046 t km^{-2} yr^{-1}) for large crabs and 0.043 to 2.855 t km^{-2} yr^{-1} (mean: 1.449 ± 1.989 t km^{-2} yr^{-1}) for small crabs. The inverse solution estimated a consumption of 9.922 t km^{-2} yr^{-1} (Q/B = 2.961 yr^{-1}) for large crabs and 2.849 t km^{-2} yr^{-1} (Q/B = 6.686 yr^{-1}) for small crabs.

Diet composition

For shrimp, feeding occurs in both the benthic and pelagic environments as a result of their daily vertical migrations. In their model, Bundy et al. (2000) assumed that 30% of the total diet was benthic and 70% was pelagic. Annelids, small crustaceans, detritus, and bottom plants were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration. We used this diet composition for both female and male shrimp (Table 13).

For large crabs, diet data were available from the Baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984) as well as from the Baie Sainte-Marguerite (Lovrich and Sainte-Marie 1997). Based on Brêthes et al. (1984), abundance estimates were multiplied by the mean mass of each prey to obtain biomass indices for the diet. The main prey items of the 480 snow crabs were polychaetes, gastropods, echinoderms, and decapods. In the stomachs of large snow crabs analyzed by Lovrich and Sainte-Marie (1997), the main prey items were benthic invertebrates (molluscs, polychaetes, and others) and small crabs. We also used the diet composition estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s). In that study, molluscs, echinoderms, polychaetes, and crabs (59.2% of the diet) were the main prey; there was also a high proportion of detrital matter (31%). The final diet composition for large crabs is shown in Table 14. For small crabs, we used the diet composition estimated by

Lovrich and Sainte-Marie (1997) for the Baie Sainte-Marguerite. The main prey were other benthic invertebrates, echinoderms, and molluscs (85.7% of the diet) (Table 14).

Table 13. Diet compositions (%) for female and male shrimp used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Female shrimp					Male shrimp				
Prey	Mean	± SD[a]	Min	Max	Est	Mean	± SD[a]	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Female shrimp	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Male shrimp	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large crabs										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes	1.5	1.9	**0.0**	**3.4**	3.2	1.5	1.9	**0.0**	**3.4**	3.1
Other bent. inver.	1.5	2.2	**0.0**	**3.7**	3.3	1.5	2.2	**0.0**	**3.7**	3.3
Large zooplankton	12.0	15.0	**0.0**	**27.0**	15.8	12.0	15.0	**0.0**	**27.0**	16.2
Small zooplankton	24.0	30.3	**0.0**	**54.3**	43.4	24.0	30.3	**0.0**	**54.3**	42.2
Phytoplankton	8.5	7.0	**1.5**	**15.5**	12.2	8.5	7.0	**1.5**	**15.5**	12.0
Detritus	52.5	43.5	**9.0**	**96.0**	22.1	52.5	43.5	**9.0**	**96.0**	23.3
Total	100.0		10.4	199.9	100.0	100.0		10.4	199.9	100.0
TRN	8					8				

[a]: For these two groups, all the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC^{obs}_{x \to y}$ *CV($DC^{obs}_{x \to u}$)$_{mean}$ (SD = CV*Mean), with

$DC^{obs}_{x \to y}$ representing the proportion of prey *x* consumed by female or male shrimp and CV($DC^{obs}_{x \to u}$)$_{mean}$ representing the average of all coefficients of variation of the proportion of prey *x* consumed by the other groups *u* of the modelled ecosystem. Min = mean – SD, Max = mean + SD.

Table 14. Diet compositions (%) for large and small crabs used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large crabs					Small crabs				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals	4.4	8.2	**0.0**	**11.6**	0.0	2.0	1.8	**0.0**	**2.5**	0.0
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Female shrimp	0.7	1.3	**0.0**	**1.9**	0.0					
Male shrimp	0.7	1.3	**0.0**	**1.9**	0.1					
Large crabs										
Small crabs	14.3	23.9	**2.0**	**35.7**	2.0	3.4	4.7	**0.0**	**6.6**	0.0
Echinoderms	9.1	15.0	**1.4**	**22.7**	20.7	26.5	13.9	**8.8**	**28.5**	28.1
Molluscs	29.7	43.5	**8.4**	**69.9**	67.9	23.7	20.3	**1.8**	**30.5**	28.8
Polychaetes	11.3	13.3	**5.5**	**24.3**	5.5	8.9	7.0	**2.5**	**12.4**	7.9
Other bent. inver.	16.4	27.8	**2.0**	**41.4**	3.8	35.5	42.7	**14.7**	**75.1**	35.2
Large zooplankton	0.8	1.4	**0.0**	**2.0**	0.0	**0.0**	0.0	0.0	0.0	0.0
Small zooplankton	0.8	1.4	**0.0**	**2.0**	0.0					
Phytoplankton										
Detritus	11.8	22.0	**0.0**	**31.1**	0.0					
Total	100.0		19.3	244.5	100.0	100.0		27.7	155.6	100.0
TRN	11					7				

Benthic invertebrates

Background

The benthic invertebrates other than shrimp and crabs were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. This last group consisted mainly of miscellaneous crustaceans, nematodes, and other meiofauna. Benthic data for the northern Gulf of St. Lawrence were lacking. Consequently, in many cases it was assumed that benthic biomass ranged between that of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000) and that of the eastern Scotian Shelf (Bundy 2004).

Only part of the mollusc biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shells beds on the ocean floor (Hutcheson et al. 1981). In order to reduce the biomass and account for soft body tissue only, the ratio of the body mass to whole mass of the mollusc *Mesodesma deauratum* was estimated. The mean ratio between blotted wet mass of tissue to whole mass for animals with a shell length between 30 and 35 mm was 0.166 ± 0.023 (n = 10; K. Gilkinson, DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 2000–2002 period. Only molluscs were commercially harvested. Commercial species are sea scallops (*Placopecten magellanicus*), soft-shelled clams (*Mya arenaria*), whelks (*Busycon* sp.), and periwinkles (*Littorina* sp.). Average annual landings were taken from the NAFO statistics and were 2,224 t or 2.14×10^{-2} t km^{-2} yr^{-1} (SD = 6.54×10^{-3} t km^{-2} yr^{-1}) (NAFO 2003). Using the previous ratio (16.6%) of blotted wet mass of tissue to whole mass for animals, we corrected the previous landings estimated for the whole mass including the shell to landings for soft body tissue only. We obtained $3.56 \times 10^{-3} \pm 1.09 \times 10^{-3}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch value of 3.51×10^{-3} t km^{-2} yr^{-1} for molluscs.

Biomass

The mean biomasses for 4RS were assumed to range between those of the Newfoundland–Labrador Shelf ecosystem (NFLD; Bundy et al. 2000) and those of the eastern Scotian Shelf (ESS; Bundy 2004). The biomass ranges were from 63.700 (ESS) to 112.300 t km^{-2} (NFLD) for echinoderms (mean: 88.000 ± 34.365 t km^{-2}), 42.100 (NFLD) to 57.400 t km^{-2} (ESS) for molluscs (mean: 49.750 ± 10.819 t km^{-2}), 10.500 (NFLD) to 11.900 t km^{-2} (ESS) for polychaetes (mean: 11.200 ± 0.990 t km^{-2}), and 4.900 (ESS) to 7.800 t km^{-2} (NFLD) for other benthic invertebrates (mean: 6.350 ± 2.051 t km^{-2}).

Production

There is no information available on production estimates of benthic invertebrates in the northern Gulf. All the estimates are taken from the literature for other areas.

Echinoderms

Warwick et al. (1978) estimated an annual production of 0.229 t km^{-2} yr^{-1} (P/B = 0.343 yr^{-1}) for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) obtained an estimate of 0.108 t km^{-2} yr^{-1} (P/B = 0.300 yr^{-1}). However, higher echinoderm productions have been reported in the New York Bight (70.108 t km^{-2} yr^{-1} or P/B = 1.200; Steimle 1985) and on Georges Bank (64.221 t km^{-2} yr^{-1} or P/B = 1.000; Steimle 1987). Also, Robertson (1979) estimated an annual P/B of 0.650 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.600 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 19.110 to 134.760 t km^{-2} yr^{-1}, corresponding to an annual production of 60.023 ± 81.777 t km^{-2} yr^{-1}. The inverse solution estimated a production of 19.101 t km^{-2} yr^{-1}, representing a P/B of 0.22 yr^{-1}.

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of 3.824 t km^{-2} yr^{-1} (P/B = 0.848 yr^{-1}) in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated 4.671 t km^{-2} yr^{-1} (P/B = 2.135 yr^{-1}) in Long Island Sound. Higher production estimates were reported by Steimle (1985) (82.121 t km^{-2} yr^{-1} or P/B = 1.000 yr^{-1}) and by Borkowski (1974) (23.530 t km^{-2} yr^{-1} or P/B = 3.830 yr^{-1}), as well as lower estimates such as 0.600 t km^{-2} yr^{-1} in Buchanan and Warwick (1974). Also, Robertson (1979) estimated an annual P/B of 0.760 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.700 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 29.470 to 219.842 t km^{-2} yr^{-1}, corresponding to an annual production of 73.793 ± 134.613 t km^{-2} yr^{-1}. The inverse solution estimated a production of 29.500 t km^{-2} yr^{-1}, representing a P/B of 0.59 yr^{-1}.

Polychaetes

Estimates of the annual polychaete production ranged between 0.206 and 74.564 t km^{-2} yr^{-1} (0.206 t km^{-2} yr^{-1} or P/B = 1.298 yr^{-1} in Buchanan and Warwick [1974], 0.939 t km^{-2} yr^{-1} or P/B = 2.258 yr^{-1} in Warwick et al. [1978], 5.522 t km^{-2} yr^{-1} or P/B = 2.050 yr^{-1} in Sanders [1956], 6.310 t km^{-2} yr^{-1} or P/B = 2.530 yr^{-1} in Collie [1987], 8.250 t km^{-2} yr^{-1} or P/B = 4.300 yr^{-1} in Peer [1970], 16.050 t km^{-2} yr^{-1} or P/B = 4.320 yr^{-1} in Nichols [1975], 21.600 t km^{-2} yr^{-1} or P/B = 1.090 yr^{-1} in Curtis [1977], and 74.564 t km^{-2} yr^{-1} or P/B = 3.000 yr^{-1} in Steimle [1985]). When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 11.445 to 51.408 t km^{-2} yr^{-1}, corresponding to an annual production of

29.184 ± 28.258 t km^{-2} yr^{-1}. The inverse solution estimated a production of 22.376 t km^{-2} yr^{-1}, representing a P/B of 2.00 yr^{-1}.

Other benthic invertebrates

Estimates of annual production for other benthic invertebrates ranged between 0.517 and 15.677 t km^{-2} yr^{-1} (0.517 t km^{-2} yr^{-1} or P/B = 3.400 yr^{-1} in Sheader [1977], 5.000 t km^{-2} yr^{-1} or P/B = 4.000 yr^{-1} in Klein et al. [1975], 15.500 t km^{-2} yr^{-1} or P/B = 1.650 yr^{-1} in Cederwall [1977], and 15.677 t km^{-2} yr^{-1} or P/B = 2.800 yr^{-1} in Collie [1985]). Also, Mills and Fournier (1979) estimated an annual P/B of 0.250 yr^{-1} on the Scotian Shelf and Jarre-Teichmann and Guénette (1996) used an estimate of 0.250 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 8.085 to 31.200 t km^{-2} yr^{-1}, corresponding to an annual production of 17.833 ± 16.345 t km^{-2} yr^{-1}. The inverse solution estimated a production of 11.021 t km^{-2} yr^{-1}, representing a P/B of 1.74 yr^{-1}.

Consumption

In the absence of information on food consumption, consumption values were estimated using a gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992). For echinoderms, this produced a consumption range between 63.700 and 1,497.333 t km^{-2} yr^{-1}, corresponding to a mean consumption of 780.517 ± 1,013.732 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 69.057 t km^{-2} yr^{-1}, representing a Q/B ratio of 0.785 yr^{-1}.

For molluscs, this produced a consumption range between 98.233 and 2,442.689 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1,270.461 ± 1,657.780 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 126.412 t km^{-2} yr^{-1}, representing a Q/B ratio of 2.541 yr^{-1}.

For polychaetes, this produced a consumption range between 38.150 and 571.200 t km^{-2} yr^{-1}, corresponding to a mean consumption of 304.675 ± 376.923 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 117.158 t km^{-2} yr^{-1}, representing a Q/B ratio of 10.461 yr^{-1}.

For other benthic invertebrates, this produced a consumption range between 26.950 and 346.667 t km^{-2} yr^{-1}, corresponding to a mean consumption of 186.808 ± 226.074 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 87.608 t km^{-2} yr^{-1}, representing a Q/B ratio of 13.796 yr^{-1}.

Diet composition

For echinoderms, diet information was taken from the three most abundant species in NAFO divisions 2J3KL: the sand dollar (*Echinarchnius parma*), the sea urchin (*Strongylocentrotus pallidus*), and the brittle star (*Ophiura robusta*). The resulting diet is 100% detritus (Bundy et al. 2000).

For molluscs, Bundy et al. (2000) analyzed the diet composition of a suspension feeder (*Macoma deauratum*), a deposit feeder (*Macoma calcarea*), and a suspension or detrital feeder (*Liocyma fluctuosa*). Suspension feeders feed on organic detrital matter that is resuspended in the water immediately above the sediment surface. Deposit feeders can be considered as detrital

feeders. Thus, the molluscs are assumed to be detrital feeders of various forms and the diet of the mollusc group is 100% detritus. However, in shallower waters, molluscs can consume phytoplankton (M. Fréchette, Institut Maurice-Lamontagne, pers. comm.). This potential food was also accounted for in the final diet composition (Table 15).

The polychaetes are considered to have a diet of 100% detritus (Nesis 1965; Fauchald and Jumars 1979). However, recent studies at two deeper Laurentian trough stations (275 and 325 m depth) showed that polychaetes could also consume phytoplankton and that cannibalism could have a significant impact in the diet composition (Desrosiers et al. 2000). The resulting diet is shown in Table 15.

The key organisms for the other benthic invertebrate group are gammarid amphipods. These species feed mainly on organic detritus (Nesis 1965; Hutcheson et al. 1981).

Table 15. Diet compositions (%) for molluscs and polychaetes used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Molluscs					Polychaetes				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Female shrimp										
Male shrimp										
Large crabs										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes						13.4	16.5	**1.8**	**25.1**	12.7
Other bent. inver.										
Large zooplankton										
Small zooplankton										
Phytoplankton	5.0	7.1	**0.0**	**10.0**	8.6	43.3	8.2	**37.5**	**49.1**	46.7
Detritus	95.0	7.1	**90.0**	**100.0**	91.4	43.3	8.2	**37.5**	**49.1**	40.6
Total	100.0		90.0	110.0	100.0	100.0		76.7	123.3	100.0
TRN	2					3				

Large zooplankton

Background

Organisms and species representing this group are greater than 5 mm in length and include euphausiids (mainly *Thysanoessa rashii, T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula*, *Parathemisto abyssorum*, and *P. gaudichaudi*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis artica*), tunicates, and ichthyoplankton. This group contains herbivorous (some euphausiid species), omnivorous (most euphausiids, hyperiid amphipods, mysids, and large tunicates), and carnivorous (chaetognaths and jellyfish) species.

Catch

There was no commercial fishery for species in this group during the 2000–2002 period in the northern Gulf.

Biomass

Biomass was calculated from zooplankton data gathered of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2000–2002 period (M. Harvey, Institut Maurice-Lamontagne, unpublished data). This gives a biomass estimate of 7.135 ± 0.236 t km^{-2} for the study area.

Production

The production estimate of large zooplankton was obtained from several different sources. These sources included P/B ratios for euphausiids of 4.000 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977), 2.750 yr^{-1} (range: 1.300–4.200 yr^{-1}; Lindley 1980) to 3.800 yr^{-1} (range: 1.300–6.300 yr^{-1}; Lindley 1982) for the North Sea, and 1.600 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985). The resulting mean P/B was 3.038 yr^{-1} for euphausiids. Pauly and Christensen (1996) reported P/B ranges of 2.000 to 4.000 yr^{-1} (mean: 3.000 yr^{-1}) for carnivorous jellies and 1.000 to 3.000 yr^{-1} (mean: 2.000 yr^{-1}) for chaetognaths in mass-balance models of northeastern Pacific ecosystems. For amphipods, Ikeda and Shiga (1999) estimated a daily P/B ratio of 0.016 d^{-1} (or 5.840 yr^{-1}) in Toyama Bay, southern Japan Sea. When the minimum and maximum biomass values were applied to the overall mean P/B ratio (3.469 yr^{-1}), we obtained a production range of 24.067 to 25.658 t km^{-2} yr^{-1}. We also used another production value (9.822 t km^{-2} yr^{-1}) based on the annual consumption (see below) and the lower GE limit (10%). The resulting mean production value was 17.740 ± 11.198 t km^{-2} yr^{-1} (range: 9.822–25.658 t km^{-2} yr^{-1}) for large zooplankton. The inverse solution estimated a production of 19.784 t km^{-2} yr^{-1} (P/B of 2.77 yr^{-1}) for large zooplankton.

Consumption

Consumption was firstly estimated from data on euphausiids in the Gulf of St. Lawrence (mean Q/B = 11.254 yr^{-1}; Sameoto 1976). Pauly and Christensen (1996) reported a Q/B value of 10.000 yr^{-1} for carnivorous jellies and a Q/B range of 10.000 to 40.000 yr^{-1} for chaetognaths in mass-balance models of northeastern Pacific ecosystems. For chaetognaths, three other values were estimated from Kotori (1976) in the Bering Sea and the northern Pacific Ocean, Feigenbaum (1979) in the Gulf Stream near Miami, and Falkenhaug (1991) in the Barents Sea. Kotori (1976) estimated that the carbon requirement of a chaetognath community was 4.71 mg C m^{-2} d^{-1} (or 17.192 t WW km^{-2} yr^{-1}) and that the chaetognath biomass was 227 mg C m^{-2} (or 2.27 t WW km^{-2}). A Q/B ratio of 0.021 d^{-1} (or 7.57 yr^{-1}) was thus obtained. Feigenbaum (1979) found specific daily rations between 0.08 and 0.12 dry weight basis for chaetognaths, corresponding to a mean Q/B ratio of 36.50 yr^{-1}. In Falkenhaug (1991), a mean daily specific ingestion (dry weight basis) was estimated at 0.022 d^{-1} corresponding to a Q/B ratio of 8.15 yr^{-1}. The resulting mean Q/B ratio for chaetognaths was 20.44 yr^{-1}. To estimate the Q/B ratio of hyperiid amphipods, two studies were used. Auel and Werner (2003) estimated daily ingestion of 1.9 ± 0.6% of body carbon per day for the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. Pakhomov and Perissinotto (1996) estimated *in situ* daily rations equivalent to 6.3% of body dry weight for *Themisto gaudichaudi* in the South Georgia region. The resulting mean Q/B ratio for hyperiid amphipods was 0.041 d^{-1} or 14.97 yr^{-1}. Finally, for mysids, Toda et al. (1987) estimated that ingestion represented 2% body C d^{-1} (equivalent to a Q/B of 0.02 d^{-1} or 7.30 yr^{-1}) at 3°C in lakes while Bowers and Vanderploeg (1982) found ingestion rates of 2 to 6% body weight d^{-1} (equivalent to a Q/B range of 0.02 to 0.06 d^{-1} or 7.30 to 21.90 yr^{-1}) at 5-11°C in Lake Michigan. The resulting mean Q/B ratio for mysids was 12.17 yr^{-1}. When the minimum and maximum biomass values were applied to the overall mean Q/B ratio (13.766 yr^{-1}), we obtained a consumption range of 95.493 to 101.806 t km^{-2} yr^{-1}.

Based on the mean production (17.740 t km^{-2} yr^{-1}) for large zooplankton and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 59.133 and 177.399 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 59.133 and 177.399 t km^{-2} yr^{-1}, corresponding to a mean consumption of 118.266 ± 83.627 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 73.299 t km^{-2} yr^{-1} for large zooplankton, representing a Q/B ratio of 10.273 yr^{-1}.

Diet composition

No diet information was available for these species in the northern Gulf of St. Lawrence. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and copepods (Mauchline 1980). Chaetognaths and jellyfish eat copepods (Sullivan 1980; Smayda 1993). The relative proportions of these prey in the resulting large zooplankton diet were 5% large zooplankton, 43% small zooplankton, 37% phytoplankton, and 15% detritus (Bundy et al. 2000) (Table 16).

Table 16. Diet composition (%) for large zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large zooplankton (> 5 mm)				
Prey	Mean	± SD[a]	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Female shrimp					
Male shrimp					
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	5.0	6.2	**0.0**	**11.2**	2.7
Small zooplankton	43.0	54.2	**0.0**	**97.2**	24.8
Phytoplankton	37.0	30.7	**6.3**	**67.7**	67.5
Detritus	15.0	12.4	**2.6**	**27.4**	5.0
Total	100.0		8.9	203.6	100.0
TRN	4				

[a]: For this group, all the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC^{obs}_{x\to y}$ *CV($DC^{obs}_{x\to u}$)$_{mean}$ (SD = CV*Mean), with $DC^{obs}_{x\to y}$ being the proportion of prey *x* consumed by large zooplankton and CV($DC^{obs}_{x\to u}$)$_{mean}$ being the average of all coefficients of variation of the proportion of prey *x* consumed by the other groups *u* of the modelled ecosystem. Min = mean – SD, Max = mean + SD.

Small zooplankton

Background

The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus* and *Oithona similis*, are the most numerous small zooplankton. Also included in the small zooplankton category are meroplankton and tunicates < 5 mm, which are generally underestimated by sampling gear (Strong 1981). Calanoid copepods accounted for 20 to 70% of the numerical abundance of all zooplankton species present, with *Calanus finmarchicus/glacialis* (not distinguished in the counts) and *C. hyperboreus* generally dominant among the mid-sized organisms (i.e., those retained by the 500 μm mesh) (Roy et al. 2000). The greatest numbers of the *Calanus* spp. were observed in the deeper Laurentian channel (Roy et al. 2000). The small cyclopoid copepod *Oithona similis* was also very abundant, ranging from 20 to 70% of the numerical abundance of all species (Roy et al. 2000).

Catch

None.

Biomass

Biomass was calculated from zooplankton data gathered of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2000–2002 period (M. Harvey, Institut Maurice-Lamontagne, unpublished data). This gives a biomass estimate of 70.742 ± 3.366 t km^{-2} for the study area.

Production

On the eastern Scotian Shelf, Bundy (2004) estimated a P/B value of 8.400 yr^{-1} for calanoid copepods (*Calanus finmarchicus*) and 23.000 yr^{-1} for cyclopoid copepods (*Oithona similis*). The proportion of calanoid copepods was 79% of the small zooplankton biomass (21% for the cyclopoid copepods) in the northern Gulf (M. Harvey, Institut Maurice-Lamontagne, unpublished data). When the minimum and maximum biomass values weighted by the proportions of calanoid and cyclopoid copepods were applied to these P/B ratios, we obtained a production range of 369.331 to 575.738 t km^{-2} yr^{-1}, corresponding to an annual production of 448.766 ± 145.952 t km^{-2} yr^{-1}. The inverse solution estimated a production of 443.417 t km^{-2} yr^{-1}, representing a P/B of 6.27 yr^{-1}.

Consumption

Vézina et al. (2000) estimated a minimum consumption value (120.04 mg C m^{-2} d^{-1} or 438.135 t wet mass km^{-2} yr^{-1}) for the summer and fall periods and a maximum (425.94 mg C m^{-2} d^{-1} or 1,554.666 t wet mass km^{-2} yr^{-1}) value for the winter and spring periods. Based on the mean production (448.766 t km^{-2} yr^{-1}) for small zooplankton and the minimum and maximum GE limits (25–50%), we obtained two other consumption values of 897.532 and 1,795.063 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 438.135 and 1,795.063 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1,116.599 ± 959.493 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1,070.721 t km^{-2} yr^{-1}, representing a Q/B of 15.136 yr^{-1}.

Diet composition

The small zooplankton feed on both autotrophic and heterotrophic microplankton. However, heterotrophic microplankton (heterotrophic dinoflagellates, ciliates, and small metazoans) were included in the small zooplankton group here. Moreover, there is ample empirical evidence that mesozooplankton are omnivorous (Stoecker and Capuzzo 1990; Ohman and Runge 1994; Vézina et al. 2000). Small zooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to small zooplankton (Table 17).

Table 17. Diet composition (%) for small zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Small zooplankton (< 5 mm)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Female shrimp					
Male shrimp					
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton					
Small zooplankton	50.2	32.3	**27.4**	**73.1**	33.7
Phytoplankton	47.2	35.4	**22.2**	**72.2**	65.1
Detritus	2.6	3.1	**0.4**	**4.8**	1.1
Total	100.0		50.0	150.0	100.0
TRN	3				

Phytoplankton

Background

Diatoms are the most abundant phytoplankton in terms of both cell numbers and biovolumes during spring and winter (Savenkoff et al. 2000). A mixture of autotrophic and mixotrophic organisms including Cryptophytes, diatoms, dinoflagellates, Prasinophytes, and mixotrophic *Stombidium* spp. (in the Spirotrichea) dominated during summer and fall. Prymnesiophytes were important in terms of cell numbers during spring and winter. The diatoms were dominated by *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, and *Thalassiiosira nordenskioldii* during winter and by *Thalassiiosira* spp. (*T. punctigera*, *T. nordenskioldii*, *T. pacifica*, and *T. bioculata*) and *Fragilariopsis* spp. (*F. oceanica* and *F. cylindrus*) during spring. During summer, the importance of diatoms in the phytoplankton composition was lower, with the majority observed being smaller centric diatoms such as *Minidiscus* sp., *Chaetoceros minimus*, and occasionally larger *Coscinodiscus* spp.

Phytoplankton biomass and production are the only two parameters required for modelling. There is no harvest, and, since they are autotrophs, there is no consumption and no diet.

Biomass

Biomass was calculated from chlorophyll *a* data gathered of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2000–2002 period (M. Starr, Institut Maurice-Lamontagne, unpublished data). Phytoplankton biomass is measured as chlorophyll *a* biomass in the 0-100 m surface layer. To facilitate comparisons with other studies in the Gulf of St. Lawrence, phytoplankton carbon biomass was estimated by converting measured chlorophyll *a* concentrations (CHL) to carbon (C) using a C/CHL ratio of 50 (Rivkin et al. 1996; Savenkoff et al. 2000). We then used a conversion factor of 10 g wet mass equal to 1g C (Christensen and Pauly 1992). The mean biomass for the entire area was 15.302 ± 7.851 t km^{-2}.

Primary Production

After correcting for phytoplankton respiration (75 ± 38 mg C m^{-2} d^{-1}), a value of 599 ± 303 mg C m^{-2} d^{-1} was estimated over the euphotic zone (Savenkoff et al. 2000), giving production rates of 218.55 ± 110.75 g C m^{-2} yr^{-1} or 2,185.476 ± 1,107.451 t km^{-2} yr^{-1}. The minimum–maximum range was 1,078.025 to 3,292.927 t km^{-2} yr^{-1}. The inverse solution estimated a production of 1,159.113 t km^{-2} yr^{-1}, representing a P/B of 75.75 yr^{-1}.

Detritus

Background

Detritus represents sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria).

Biomass

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth:

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

where D is the standing stock of detritus (g C m^{-2}), PP is primary productivity (g C m^{-2} yr^{-1}), and E is the euphotic depth (m).

The annual value for primary production was 245.9 ± 109.9 g C m^{-2} yr^{-1}. The euphotic depth is estimated from Savenkoff et al. (2000) as 28.2 ± 5.9 m. The primary production estimate and euphotic depth were substituted into equation 6 above, giving a range of detritus biomass estimates from 6.2 to 22.2 g C m^{-2}, or 61.630 to 222.058 t km^{-2}, using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992). This resulted in a mean detritus biomass of 132.608 ± 113.440 t km^{-2}.

Here, bacteria were considered part of the detritus compartment. Detritus estimates had a wide range, and it was assumed that this range should allow for the bacterial biomass (bacterial biomass: 184 ± 40 mg C m^{-2} or 1.8 ± 0.4 t km^{-2}; Savenkoff et al. 2000).

Respiration

Detritus is usually assumed not to respire. However, as bacteria were considered part of the detritus in this study, there would be respiration involved. Based on Savenkoff et al. (2000), we estimated a planktonic respiration (organisms < 200 μm including bacteria) close to 162 ± 33 mg C m^{-2} d^{-1} and 383 ± 152 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively, in the euphotic zone of the northern Gulf of St. Lawrence. Vézina et al. (2000) applied inverse modelling to the data collected from July 1992 to June 1994 to estimate trophic flows in the planktonic food web and to calculate export fluxes consistent with mass balance. These authors estimated that phytoplankton respiration represented 8 and 20% of the primary production for the winter–spring and summer–fall periods, respectively (R_{PHY} = 80 ± 41 mg C m^{-2} d^{-1} for winter–spring and 70 ± 64 mg C m^{-2} d^{-1} for summer–fall). By subtracting, we could estimate a detrital (or bacterial) respiration of 82 ± 53 mg C m^{-2} d^{-1} and 313 ± 165 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively. This represented 198 ± 86 mg C m^{-2} d^{-1} or 72 ± 32 g C m^{-2} yr^{-1} for the euphotic zone.

Based on the data collected from July 1992 to June 1994 at three stations located in the Laurentian Channel, Savenkoff et al. (1996) estimated a bacterial respiration of 44 ± 9 mg C m^{-2} d^{-1} or 16 ± 28 g C m^{-2} yr^{-1} in the aphotic layer (up to 300 m depth). By adding bacterial respiration values estimated in the euphotic and aphotic layers, a total detrital respiration could be estimated as 88.3 ± 42.4 g C m^{-2} yr^{-1} or 882.961 ± 423.748 t km^{-2} yr^{-1} (range: 459.213–1,306.710 t km^{-2} yr^{-1}). The inverse solution estimated a detrital respiration of 532.192 t km^{-2} yr^{-1}.

Export

The fraction of the organic carbon that is not returned to the water column but is buried and preserved within the sediment represents the export of detritus. Silverberg et al. (2000) estimated a burial flux of particulate organic carbon between 0.46 and 0.53 mol C m^{-2} yr^{-1} at the Anticosti Gyre and Cabot Strait stations, respectively. This represents a detrital export close to 5.9 ± 0.6 g C m^{-2} yr^{-1} or 5.94 x 10^{1} ± 0.59 x 10^{1} t km^{-2} yr^{-1}. The inverse solution estimated a detrital export of 5.65 x 10^{1} t km^{-2} yr^{-1}.

Data synthesis

Data about biomass, export (here equal to commercial catch), production, and consumption are summarized in Tables 18 and 19.

Table 18. Observed biomass and export for each group used as input parameters for modelling for the 2000–2002 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Mysticeti	0.298	0.132	0.166	0.430					
Odontoceti	0.038	0.016	0.022	0.054	**2.10×10^{-4}**	9.04×10^{-5}	1.46×10^{-4}	2.74×10^{-4}	2.12×10^{-4}
Harp and hooded seals	0.148	0.002	0.146	0.149	2.25×10^{-2}	2.12×10^{-2}	**1.27×10^{-3}**	**4.36×10^{-2}**	5.04×10^{-3}
Grey and harbour seals	0.041	0.002	0.040	0.044	**3.06×10^{-7}**	5.30×10^{-7}	0	9.18×10^{-7}	3.53×10^{-7}
Seabirds	0.004	0.002[b]	0.002	0.006	3.35×10^{-4}	1.49×10^{-4}[c]	**1.86×10^{-4}**	**4.84×10^{-4}**	2.25×10^{-4}
Large cod	0.615	0.067	0.542	0.674	6.50×10^{-2}	4.20×10^{-3}	6.24×10^{-2}	**6.94×10^{-2}**	7.00×10^{-2}
Small cod	0.119	0.037	0.078	0.150					
Large Green. halibut	0.228	0.017	0.214	0.247	**8.05×10^{-3}**	2.55×10^{-3}	6.07×10^{-3}	9.70×10^{-3}	8.01×10^{-3}
Small Green. halibut	1.596	0.413	1.190	2.015					
Amer. plaice	0.336	0.266	0.082	0.613	**2.01×10^{-3}**	9.34×10^{-4}	1.23×10^{-3}	3.04×10^{-3}	2.30×10^{-3}
Flounders	0.063	0.047	0.023	0.115	**4.57×10^{-3}**	3.38×10^{-5}	4.54×10^{-3}	4.60×10^{-3}	4.56×10^{-3}
Skates	0.074	0.046	0.044	0.127	**7.64×10^{-4}**	2.74×10^{-4}	5.39×10^{-4}	1.07×10^{-3}	7.48×10^{-4}
Redfish	1.069	0.130	0.925	1.178	**7.39×10^{-3}**	6.61×10^{-4}	6.90×10^{-3}	8.14×10^{-3}	7.34×10^{-3}
Large demersals	0.148	0.092	0.073	0.250	**3.23×10^{-3}**	7.71×10^{-5}	3.15×10^{-3}	3.30×10^{-3}	3.23×10^{-3}
Small demersals	0.504	0.630	0.059	0.950					
Capelin	45.141	63.724	0.071	90.211	**2.94×10^{-2}**	2.12×10^{-2}	7.14×10^{-3}	4.94×10^{-2}	2.76×10^{-2}
Large pelagics	0.011	0.011	0.002	0.023	**3.21×10^{-6}**	5.56×10^{-6}	0	9.63×10^{-6}	3.41×10^{-6}
Pisci. small pel. feeders	0.524	0.290	0.320	0.729	**6.82×10^{-2}**	4.63×10^{-2}	1.76×10^{-2}	1.08×10^{-1}	6.73×10^{-2}

Table 18. Cont.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Plank. small pel. feeders	1.153	0.055	1.087	1.197	**1.25×10^{-1}**	6.56×10^{-3}	1.17×10^{-1}	1.29×10^{-1}	1.25×10^{-1}
Female shrimp	0.946	0.207	0.717	1.122	**1.43×10^{-1}**	1.71×10^{-2}	1.22×10^{-1}	1.57×10^{-1}	1.45×10^{-1}
Male shrimp	0.617	0.127	0.476	0.721	**9.39×10^{-2}**	2.14×10^{-2}	7.61×10^{-2}	1.13×10^{-1}	9.22×10^{-2}
large crabs	3.351	3.916	0.991	5.710	**8.25×10^{-2}**	7.17×10^{-3}	7.78×10^{-2}	9.06×10^{-2}	8.29×10^{-2}
Small crabs	0.426	0.576	0.037	0.816					
Echinoderms	88.000	34.365	63.700	112.300					
Molluscs	49.750	10.819	42.100	57.400	**3.56×10^{-3}**	1.09×10^{-3}	2.47×10^{-3}	4.65×10^{-3}	3.51×10^{-3}
Polychaetes	11.200	0.990	10.500	11.900					
Other benthic invertebrates	6.350	2.051	4.900	7.800					
Large zooplankton	7.135	0.236	6.937	7.396					
Small zooplankton	70.742	3.366	68.437	74.605					
Phytoplankton	15.302	7.851	8.872	24.052					
Detritus	132.608	113.440	61.630	222.058	5.94×10^{1}	0.59×10^{1}	**5.35×10^{1}**	**6.53×10^{1}**	5.65×10^{1}

[a]: Export was mainly the catch (including the commercial fishery and anthropogenic mortality such as hunting, etc.). For detritus, export was loss of detritus buried as sediment.
[b]: calculated as $B_X * CV(B_Y)_{mean}$ with $CV(B_Y)_{mean}$ = 51%, the average of all coefficients of variation for observed biomass except those estimated for seals.
[c]: calculated as $Exp_X * CV(Exp_Y)_{mean}$ with $CV(Exp_Y)_{mean}$ = 44%, the average of all coefficients of variation for observed export.

Table 19. Observed production and consumption used as input parameters for modelling for the 2000–2002 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface. Means and SDs were calculated on the two extreme values.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Mysticeti	0.020	0.009	**0.011**	**0.029**	0.012	1.451	0.832	**0.863**	**2.040**	1.501
Odontoceti	0.006	0.002	**0.003**	**0.008**	0.003	0.432	0.209	**0.284**	**0.580**	0.338
Harp and hooded seals	0.014	0.004	**0.011**	**0.016**	0.013	1.015	0.478	**0.677**	**1.353**	1.299
Grey and harbour seals	0.006	0.004	**0.003**	**0.008**	0.003	0.365	0.285	**0.164**	**0.567**	0.298
Seabirds	**0.0011**	0.0008[a]	0.0003	0.0019	0.0013	0.309	0.280	**0.111**	**0.507**	0.254
Large cod	0.327	0.156	**0.216**	**0.438**	0.216	2.167	1.560	**1.064**	**3.270**	1.065
Small cod	0.071	0.022	**0.047**	**0.090**	0.087	0.456	0.362	**0.200**	**0.713**	0.398
Large Green. halibut	0.029	0.002	**0.026**	**0.031**	0.029	0.319	0.128	**0.228**	**0.409**	0.233
Small Green. halibut	0.798	0.257	**0.476**	**1.209**	0.478	6.840	7.428	**1.587**	**12.092**	1.608
Amer. plaice	0.100	0.077	**0.019**	**0.226**	0.223	1.600	1.788	**0.336**	**2.865**	2.165
Flounders	0.017	0.009	**0.009**	**0.028**	0.027	0.170	0.151	**0.063**	**0.277**	0.132
Skates	0.017	0.010	**0.010**	**0.028**	0.023	0.219	0.206	**0.074**	**0.365**	0.075
Redfish	0.141	0.017	**0.123**	**0.155**	0.147	5.230	5.885	**1.069**	**9.392**	1.145
Large demersals	0.033	0.018	**0.018**	**0.053**	0.052	0.461	0.443	**0.148**	**0.775**	0.251
Small demersals	0.212	0.265	**0.025**	**0.400**	0.396	2.295	2.532	**0.504**	**4.086**	2.653
Capelin	27.114	38.273	**0.049**	**54.176**	4.233	1243.174	1757.735	**0.268**	**2486.080**	22.010
Large pelagics	0.004	0.004	**0.001**	**0.009**	0.008	0.091	0.113	**0.011**	**0.171**	0.042
Pisci. small pel. feeders	0.168	0.122	**0.082**	**0.255**	0.254	1.885	1.872	**0.561**	**3.208**	1.088

Table 19. Cont.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Plank. small pel. feeders	0.357	0.009	**0.346**	**0.369**	0.365	8.766	10.715	**1.189**	**16.342**	2.499
Female shrimp	1.062	0.680	**0.581**	**1.542**	1.163	7.079	5.006	**3.540**	**10.619**	6.620
Male shrimp	0.688	0.428	**0.386**	**0.991**	0.886	4.588	3.244	**2.294**	**6.882**	3.975
Large crabs	0.753	0.674	**0.277**	**1.230**	1.070	6.611	8.046	**0.922**	**12.300**	9.922
Small crabs	0.149	0.193	**0.013**	**0.286**	0.286	1.449	1.989	**0.048**	**2.855**	2.849
Echinoderms	60.023	81.777	**19.110**	**134.760**	19.101	780.517	1013.732	**63.700**	**1497.333**	69.057
Molluscs	73.793	134.613	**29.470**	**219.842**	29.500	1270.461	1657.780	**98.233**	**2442.689**	126.412
Polychaetes	29.184	28.258	**11.445**	**51.408**	22.376	304.675	376.923	**38.150**	**571.200**	117.158
Other benthic invertebrates	17.833	16.345	**8.085**	**31.200**	11.021	186.808	226.074	**26.950**	**346.667**	87.608
Large zooplankton	17.740	11.198	**9.822**	**25.658**	19.784	118.266	83.627	**59.133**	**177.399**	73.299
Small zooplankton	448.766	145.952	**369.331**	**575.738**	443.417	1116.599	959.493	**438.135**	**1795.063**	1070.721
Phytoplankton	2185.476	1107.451	**1078.025**	**3292.927**	1159.113					
Detritus										

[a]: Calculated as P_X*$CV(P_Y)_{mean}$ with $CV(P_Y)_{mean}$ = 69%, the average of all coefficients of variation for observed production.

DISCUSSION

The present data set was used to construct models of the northern Gulf of St. Lawrence for the 2000–2002 period. Two other reports have been completed for the same area for the mid-1980s (1985–1987: groundfish pre-collapse period) and the mid-1990s (1994–1986: groundfish post-collapse period) (Morisette et al. 2003; Savenkoff et al. 2004b). The time periods were determined after the analysis of biomass fluctuations for the key fish species of the northern Gulf system (i.e., cod and redfish). Also, these time periods were chosen based on the availability of reliable information for these species.

The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence one has in them). The strengths and weaknesses of these inputs have to be judged. There are two levels of uncertainties in all mass-balance models. One level is which components (boxes and flows in the mass-balance models) to include in the starting configuration; the other level is the uncertainty of what the starting values should be for the minimum number of components that constrains the parameter estimation step.

Uncertainty in the input data

Ecosystem modelling requires the collection of a considerable amount of information. The modelling results described here were influenced by several areas of uncertainty for different groups at the lower and higher trophic levels. The quality of input data was variable. Catch estimates of commercial species are considered quite reliable although there is indirect but reliable evidence for non-negligible misreporting (non-reported landings and discards at sea) (Fréchet 1991; Hurtubise et al. 1992; Palmer and Sinclair 1997). Uncertainty also occurs for the catch estimate of small Greenland halibut, which was assumed to be null. However, this could be biased since there seemed to be a large by-catch of this species in the shrimp fishery in 1997–1999 (Orr et al. 2000) even though no information is available for the northern Gulf area. Biomass estimates for several other model compartments (seals, seabirds, herring, mackerel, crabs) were based on data from other surveys or population models. In other cases, biomass was based on densities reported for other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates) or was estimated by initial models to meet predator demands (small demersal feeders).

Very little is known about fish and invertebrate production and consumption in the Gulf of St. Lawrence. For most model compartments, total mortality was estimated as catch plus biomass multiplied by natural mortality. In these cases, a fixed rate of natural mortality was assumed based on life-history considerations, literature reports, or expert opinion. It was also necessary to use empirical data from other areas and/or time frames (e.g., capelin, shrimp), or less specific information (e.g., pelagic feeders, benthic invertebrates) for production and consumption estimates.

Further uncertainties with diet data resulted from assuming that the diet of a key species is representative of the functional group to which it belongs, or from attributing the “unidentified prey” part in stomach content analyses in proportion to the different identified groups in the stomachs. The uncertainties remaining in the understanding of the ecosystem may be due to the use of incorrect values because no data exist or to the confidence limits being too large. They may result from an inaccurate aggregation of species within one functional group or from

unknown mechanisms occurring in the ecosystem. Overall, even though the model is not a perfect representation of reality, it is probably as good as it can be with the information available.

Strengths and weaknesses of the modelling efforts

Among the multispecies models, inverse models are static-flow models that provide a "snapshot" of the system at one moment in time and use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem. The use of upper and lower limits to constrain the majority of input values (production, consumption, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent.

However, due to the fact that our empirical databases and scientific understanding of ecological processes will always be incomplete (underdetermined system: the number of flows to be solved [n = 467 in this case] exceeds the number of independent mass balance relations [m = 166]), flow network solutions are not unique. Moreover, mass-balance models estimate a very large number of parameters, and it is possible that the relatively limited data available are insufficient to constrain these parameters. Also, even though most of the data are good estimates for the 4RS ecosystem during the 2000–2002 period, some input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters from the northern Gulf ecosystem. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. Where one modelling approach compromises or simplifies portions of the system, another may provide a realistic and precise representation of the same parts of the system. In this study, by randomly perturbing data inputs, we constructed a set of balanced solutions and we used the mean of these 31 random perturbations. The estimated flows fall inside our a priori constraints (once the data are perturbed) and therefore are reasonable "middle ground" descriptions.

CONCLUSION

This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence. The model enabled us to bring together wide-ranging data concerning this ecosystem. The model provides an overall view of the ecosystem, identifies general robust patterns, and shows where the uncertainties in the food web occur, which could be examined in future studies. Inverse modelling was useful in constraining observations into a coherent picture, but it remains that the results are sensitive to some choices we made regarding the modelling structure and that other equivalent solutions are possible since the number of flows to be solved exceeds the number of independent mass balance relations (i.e., the system is underdetermined). Progress is still needed to refine our understanding of the structure of ecosystems in the Gulf of St. Lawrence as well as in other areas of the world.

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See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

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