Input data and parameter estimates
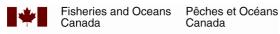# for ecosystem models
of the lower St. Lawrence Estuary (2008–2010)

Claude Savenkoff

2012

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Input data and parameter estimates for ecosystem models
of the lower St. Lawrence Estuary (2008–2010)

by

Claude Savenkoff

Direction des Sciences
Pêches et Océans Canada
Institut Maurice-Lamontagne
C.P. 1000, 850, route de la Mer
Mont-Joli, Québec, Canada G5H 3Z4

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ABSTRACT

Savenkoff, C. 2012. Input data and parameter estimates for ecosystem models of the lower St. Lawrence Estuary (2008–2010). Can. Tech. Rep. Fish. Aquat. Sci. 2999: vii+150 pp.

Mass-balance models were used to reconstruct trophic flows through the lower St. Lawrence Estuary ecosystem for the 2008–2010 period. The whole-system model is divided into 41 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of the 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 comparison.

RÉSUMÉ

Savenkoff, C. 2012. Input data and parameter estimates for ecosystem models of the lower St. Lawrence Estuary (2008–2010). Can. Tech. Rep. Fish. Aquat. Sci. 2999: vii+150 pp.

Des modèles d'équilibre de masse ont été utilisés pour représenter les flux trophiques de l'écosystème de l'estuaire maritime du Saint-Laurent pour la période 2008–2010. L'écosystème a été divisé en 41 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 la modélisation. Les paramètres estimés par la modélisation inverse sont également montrés pour comparaisons.

INTRODUCTION

Mass-balance models have been constructed using inverse methodology for the northern Gulf of St. Lawrence for 1985–1987, 1994–1996, 2000–2002, and 2003–2005 to describe the structure and function of the ecosystem for each time period (Morissette et al. 2003, Savenkoff et al. 2004a, 2005, 2009). We adapted the previous modelling structure to the lower St. Lawrence Estuary ecosystem (a subarea of NAFO division 4T) to make an overall description of community structure, trophic interactions, and the effects of fishing and predation on the vertebrate and invertebrate communities of the ecosystem during the 2008–2010 period.

Usable information exists on most of the benthic and pelagic communities of the lower Estuary. However, there is no overall description of ecosystem functioning and no comprehensive synthesis has been made between all compartments or functional groups. Food web modelling is an ideal way to describe such an ecosystem by creating an overview of its trophic network. The fists step was to collect and analyse basic data for the different studied groups. Based on these data, an ecosystem model was then constructed. This report presents the data and input parameters gathered to develop mass-balance models for the ecosystem of the lower St. Lawrence Estuary by using inverse methodology during the 2008–2010 period. The objective of this report is to describe the data sources, data modifications and assumptions made during parameterisation of the models. 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 estimated values from this final solution are presented here, along with the input parameters, to facilitate comparisons between inputs and outputs of inverse modelling. The work described in this report is part of the Quebec Region Ecosystem Research Initiative (ERI), a national program to enhance scientific research that was designed to contribute to progress on the ecosystem-based management (EBM) in Canada (MPO 2007).

MATERIAL AND METHODS

<u>Study area</u>

The study covers the lower St. Lawrence Estuary, a part of the Northwest Atlantic Fisheries Organization (NAFO) division 4T, an area equivalent to 6,407 km^2 (Fig. 1). The lower Estuary is also one of the Canadian Ecosystem Research Initiative locations and has been identified as an Ecologically and Biologically Significant Area (EBSA) within the Large Ocean Management Area (LOMA) (DFO 2007, Savenkoff et al. 2007a). The lower St. Lawrence Estuary (LSLE) is an elongated channel with an average length, width, and depth of 200 km, 40 km, and 300 m, respectively. The LSLE has low surface salinities due to freshwater input from the St. Lawrence and Saguenay rivers and is characterized by intense vertical mixing and upwelling (Therriault and Lacroix 1976, Greisman and Ingram 1977).

The nearshore region (depth < 37 m) was excluded from the model because it is not covered by annual summer bottom-trawl surveys and because exchanges between the infra-littoral and offshore zones are still poorly understood. Hence, diadromous fish (e.g., American

eel *Anguilla rostrata*) and infra-littoral species were not included in this study. The period covered by this analysis covers the 2008–2010 period. We used this time period because in 2008, four new coastal strata were added to the initial 1990 sampling protocol in order to include the depths between 37 and 183 m (Bourdages et al. 2010).

Figure 1. Map of the Estuary and Gulf of St. Lawrence showing the 200 m isobath.

Functional groups

Based on data availability and the ecological and commercial significance of the species, the food web of the LSLE was depicted by 41 compartments representing the main pelagic, demersal, and benthic species found in the area (Table 1). We distinguished seven marine mammal groups, one seabird group, seventeen fish groups, fourteen invertebrate groups, one phytoplankton group, and one detritus group (Table 1).

Table 1. Functional groups used in modelling for the 2008–2010 period.

Group Name	Main species
Blue whales	*Balaenoptera musculus*
Other mysticetes or baleen whales	Fin whale *Balaenoptera physalus*, minke whale *Balaenoptera acutorostrata*, humpback whale *Megaptera novaeangliae*
Beluga whales	Beluga whale *Delphinapterus leucas*
Other odontocetes or toothed whales	Common porpoise *Phocoena phocoena*
Harbour seals	*Phoca vitulina*
Grey seals	*Halichoerus grypus*
Harp seals	*Pagophilus groenlandica*
Seabirds	Double-crested cormorant *Phalacrocorax auritus*, ring-billed gull *Larus delawarensis*, herring gull *L. argentatus*, great black-backed gull *L. marinus*, common tern *Sterna hirundo*, Arctic tern *S. paradisaea*, black guillemot *Cepphus grylle*, northern gannet *Morus bassanus*, black-legged kittiwake *Rissa tridactyla*, common murre *Uria aalge*, razorbill *Alca torda*, Atlantic puffin *Fratercula arctica*, Leach's storm-petrel *Oceanodroma leucorhoa*
Large Atlantic cod ($\geq$ 35 cm)	*Gadus morhua*
Small Atlantic cod ($<$ 35 cm)	*Gadus morhua*
Large Greenland halibut ($\geq$ 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut ($<$ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	Witch flounder *Glyptocephalus cynoglossus*, yellowtail flounder *Limanda ferruginea*, winter flounder *Pseudopleuronectes americanus*
Skates	Thorny skate *Amblyraja radiata*, smooth skate *Malacoraja senta*
Atlantic halibut	*Hippoglossus hippoglossus*
Redfish	*Sebastes fasciatus, S. mentella*
Black dogfish	*Centroscyllium fabricii*
White hake	*Urophycis tenuis*

Table 1. Cont.

Group Name	Main species
Large demersal feeders	Large eelpouts (genus *Lycodes* spp.), marlin-spike *Nezumia bairdii*, common lumpfish *Cyclopterus lumpus*, longfin hake *Urophycis chesteri*, haddock *Melanogrammus aeglefinus*, monkfish *Lophius americanus*, wrymouth *Cryptacanthodes maculatus*, sea raven *Hemitripterus americanus*, and their juveniles
Small demersal feeders	Atlantic hagfish *Myxine glutinosa*, shorthorn sculpin *Myoxocephalus scorpius*, fourbeard rockling *Enchelyopus cimbrius*, moustache sculpin *Triglops murrayi*, snakeblenny *Lumpenus lampretaeformis*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, daubed shanny *Leptoclinus maculatus*, snailfishes (Liparidae), Atlantic soft pout *Melanostigma atlanticum*, Atlantic poacher *Leptagonus decagonus*, and their juveniles
Large pelagic feeders	Silver hake *Merluccius bilinearis*, spiny dogfish *Squalus acanthias*, pollock *Pollachius virens*, and their juveniles
Capelin	*Mallotus villosus*
Herring	Atlantic herring *Clupea harengus*
Small pelagic feeders	White barracudina *Arctozenus risso*, Arctic cod *Boreogadus saida*, Atlantic argentine *Argentina silus*, sand lance *Ammodytes* spp., other mesopelagics
Squid	Northern shortfin squid *Illex illecebrosus*
Shrimp	Northern shrimp *Pandalus borealis*, striped shrimp *P. montagui*, pink glass shrimp *Pasiphaea multidentata*, Arctic argid *Argis dentata*, Greenland shrimp *Eualus macilentus*
Large crabs (> 45 mm CW)	Snow crab *Chionoecetes opilio*, other non-commercial species (e.g., toad crabs *Hyas* spp.)
Small crabs (≤ 45 mm CW)	Snow crab *Chionoecetes opilio*, rock crab *Cancer irroratus*, other non-commercial species (e.g., toad crabs *Hyas* spp.)
Echinoderms	Heart urchin *Brisaster fragilis*, brittle star *Ophiura robusta*, sea urchin *Strongylocentrotus pallidus*, sea stars, sand dollar *Echinarachnius parma*
Molluscs	Stimpson clam *Spisula polynyma*, sea scallop *Placopecten magellanicus*, other Pectinidae, whelks *Buccinum* spp., wedgeclam *Mesodesma deauratum*, propeller clam *Cyrtodaria siliqua*

Table 1. Cont.

Group Name	Main species
Polychaetes	*Exogene hebes*, *Heteromastus filiformis*, *Lumbrinereis latreilli*, *Nephtys ciliata*
Other benthic invertebrates	Miscellaneous crustaceans, sea anemones, nematodes, other meiofauna
Large euphausiids	*Meganyctiphanes norvegica*
Small euphausiids	*Thysanoessa raschii*, *T. inermis*
Large hyperiid amphipods	*Themisto libellula*
Other macrozooplankton	Chaetognaths (mainly *Sagitta elegans*, *Pseudosagitta maxima*, and *Eukrohnia hamata*), mysids (mainly *Boreomysis artica*, *Mysis mixta*, and *Erythrops erythrophthalma*), small hyperiid amphipods (*Themisto gaudichaudi*, *T. abyssorum*, *T. compressa*), cnidarians (mainly *Aglantha digitalis*, *Dimophyes arctica*, and *Obelia* spp.), ctenophores (mainly *Beroe* spp.), molluscs (gastropoda, mainly *Clione limacina* and *Limacina helicina*), decapod larvae, polychaetes (mainly *Tomopteris* spp.), tunicates > 5 mm, ichthyoplankton
Surface mesozooplankton (0–100 m depth; active component)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton
Deep mesozooplankton (100–320 m depth; inactive component, i.e., in diapause)	Copepods (*Calanus finmarchicus* and *C. hyperboreus*)
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *Chaetoceros* spp., *Fragilariopsis oceanica*, *F. cylindrus*, *Leptocylindrus minimus*, *Thalassiosira bioculata*, *T. nordenskioeldii*, *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)

Some compartments such as pelagic feeders and demersal feeders are composite groups, where the species were aggregated on the basis of similarity in size and ecological role. Cod *Gadus morhua* and Greenland halibut *Reinhardtius hippoglossoides* were each separated into two

groups based on diet, size at first capture in fisheries, and 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 treat juveniles and adults separately for other fish species. Crabs were also separated into small ($\leq$ 45 mm carapace width CW) and large crabs (> 45 mm CW) based on important differences in diet and vulnerability to predation (in particular cannibalism; crab prey ranged in size between 3.9 and 48.8 mm CW) and minimal carapace width of adult snow crabs (40 mm CW) (Lovrich and Sainte-Marie 1997). Only large crabs are recruited to the fishery and consist exclusively of male snow crab, *Chionoecetes opilio* $\geq$ 95 mm CW. In order to reproduce the diapause behaviour and population dynamics of calanoid copepods, the main mesozooplankton species present in the LSLE, mesozooplankton was divided into two groups: surface-water (0–100 m depth; active component) and deep-water (100–320 m depth; inactive component, i.e., in diapause) mesozooplankton. Indeed, there is a spatial separation of development stages influenced by the estuarine two-layer circulation, with an export of early copepodite stages in the surface layer renewed by an advection of the overwintering stage C5 from the adjacent northwest Gulf of St. Lawrence (GSL) in the deeper waters during summer (Plourde et al. 2001, 2003).

<u>Collecting the data</u>

Biomass, production, consumption, diet composition, and fishery landings or anthropogenic mortality (export) were needed for each group to estimate the magnitude of trophic fluxes using inverse modelling. 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 study period 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.

<u>Biomass</u>

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant for the 2008–2010 period. The biomass of each functional group was obtained either directly or estimated from similar ecosystems when it was not available for the studied area. This parameter is expressed in biomass per surface unit (i.e., tons wet weight km^{-2}).

Data on biomass of fishes and macroinvertebrates are collected each summer in the Estuary and the northern Gulf of St. Lawrence from the Department of Fisheries and Oceans Canada (DFO) multi-species bottom-trawl survey using a Campelen trawl aboard the CCGS *Teleost* (2004–2010) (see Bourdages et al. 2007 for more details on the protocol). The sampling strategy consisted of a stratified random sampling in depth-based strata (Doubleday 1981). Weighted

means were calculated to estimate the biomass in the area using the *PACES* (*Programme d'Analyse des Campagnes d'Échantillonnage Stratifiées*) software (Bourdages 2001). These survey estimates were not converted to catchability-adjusted biomass since the previous catchability coefficients estimated from Harley and Myers (2001) and Savenkoff et al. (2004a) were not related to the new vessel/trawl used. Biomass estimates obtained from the surveys are considered as minimal values given that the nearshore region (depth < 37 m) is not covered and that some species may not be properly sampled (low catchability, e.g., pelagic species).

Biomass estimates for several other model compartments were based on data from other surveys (blue whales: photo-identified blue whale data sets collected by the Mingan Island Cetacean Study MICS; other cetaceans: Trans North Atlantic Sighting Surveys; seals: aerial visual surveys; zooplankton and phytoplankton: Atlantic Zone Monitoring Progra) and population models (seabirds, crabs). In other cases, biomass was based on densities reported from other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates) or was estimated by initial diagnostic assays of the model to meet predator demands (large and small demersal feeders, capelin *Mallotus villosus*, herring *Clupea harengus*, large and small pelagic feeders, squid).

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

Catch

Annual landings for harvested species were estimated from zonal interchange file format (ZIFF) databases (MPO, unpublished data) updated from related Canadian Science Advisory Secretariat science advisory reports. The study area, the lower St. Lawrence Estuary, included NAFO subdivisions 4Tp and 4Tq. By-catches in the shrimp and Greenland halibut fisheries were examined from the at-sea observer database (BIOREX Company for the Estuary data). The annual coverage by observers is around 5%. For by-catch, we used area equivalent to 4,525 km^2 (standard area; DFO 2002) and 4,260 km^2 (deep strata of the summer scientific surveys; B. Bernier, Maurice Lamontagne Institute, pers. comm.), repectively, for the shrimp and Greenland halibut fisheries.

Since the 2010 landing data were not yet available. Hence, mean, standard deviation, minimum, and maximum values for catch were calculated based only on the point estimates for the first two years (i.e., error in the estimates themselves was not included in these standard deviations).

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 eventually consumed, fished, or lost to other mortality) during the model period. In this study, it was assumed that there was no year-to-year change in biomass over the 2008–2010 time period (low coefficients of variation of biomass CVs) and that

emigration was zero. Thus production in this model is the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. Production is a flux expressed as 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, based on a modified catch curve analysis of the survey data, were available only for large cod, American plaice, and white hake. An estimate of production was then obtained by multiplying biomass by the annual mortality rate A (A = 1 - e^{-Z}, with Z being the instantaneous mortality rate according to Ricker 1980). For most other model compartments, total mortality or production was assumed to be equivalent to the biomass multiplied by natural mortality (M) plus catch (Allen 1971). In these cases, a fixed natural mortality rate was assumed based on life-history considerations (FishBase; Froese and Pauly 2002), 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 from a variety of methods (e.g., seals) or based on a range of reported values for other areas (e.g., benthic invertebrates).

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1992). 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 or estimated using FishBase (Froese and Pauly 2002), 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 (e.g., seals). 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 ≥ 1).

Diet composition

Diet matrices were constructed using field data (% contribution in mass to diet) from the study area whenever possible. However, these data do not exist for some species, in which case 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 potential prey 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 were a large number of such values (88 of 487 flows) for the 2008–2010 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 the Food and Agriculture Organization (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 2002). The natural mortality and the Q/B ratio of different species were thus determined using FishBase (Life-history tool in the species table) based on water temperature, maximum species length, mean species mass, the aspect ratio of the caudal fin of fish, and the general diet composition.

Model structure

This work applies the inverse methodology proposed by Vézina and Platt (1988) for planktonic food webs and adapted by Savenkoff et al. (2004b, 2007a) for whole ecosystem networks. 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. 2004b). These models 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 (objective least-square criterion) both the sum of squared flows (and thus the total sum of energy flows through the food web) and the sum of squared residual errors (i.e., minimizes the imbalances between inputs and outputs) consistent with the constraints (Vézina and Platt 1988). Inverse methods provide a powerful tool to estimate ecosystem flows using limited data and straightforward mass balance and metabolic constraints.

In the inverse approach, we use local measurements (e.g., landings), information on the trophic structure of the ecosystem (e.g., diet composition), and measurements of specific processes (e.g., production and consumption) to reconstruct the interactions and to estimate flows (in t km^{-2} yr^{-1}; see Appendix 1) such as respiration, egestion, predation, or mortality due to factors other than fishing or predation for each functional group. Ecosystem inverse modelling is based on combining compartmental mass balance equations with data equations and eco-physiological constraints on the energy flows (Savenkoff et al. 2004b). The mass balance equations specify that, for each consumer group, the sum of inflows (consumption) is balanced by the sum of outflows (production, respiration, and egestion), a net change in the biomass variable (ΔBi), and a residual term (ε) (Appendix 2). We assumed that there was no change in biomass ($\Delta Bi = 0$) during the

studied time period and that net migration was zero (migration out of or into the study area, food intake of predators that are not part of the system, etc.) (steady-state assumption). Also, production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed other mortality causes). Other mortality causes include natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004b), unsuspected migration, or other processes not accounted for in the model. The general mass-balance equation for individual compartments can be written as:

(1) Consumption – respiration – egestion – fishing mortality – predation – other mortality = 0 + ε

The equations calculated for this study were not exactly balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero. These differences are here termed the residuals, which are represented by the error term ε. The residual for each compartmental mass-balance, if it is not equal to zero, corresponds to an annual change in biomass.

For mesozooplankton, the mass-balance equation was modified to account for the diapause behaviour and population dynamics of calanoid copepods. Indeed, a part of the surface-water active population overwinters in deep waters to form the passive component in diapause (Plourde et al. 2001, 2003). Therefore, a flow from surface mesozooplankton (output) to deep mesozooplankton (input) was added to the two mass-balance equations (Appendix 2). Also, we introduced a metabolic loss to represent the marked seasonal decrease in mean body dry weight during winter without corresponding changes in prosome length (Plourde et al. 2003) (Appendix 2). The minimum dry weight of the different development stages was observed in April and May (no data in winter months). The difference in dry weight between the two periods represented an increase of 70% in body weight of stages C6f and C5, and 50% in stage C4 during summer (Plourde et al. 2003).

For phytoplankton and detritus, the general mass-balance equation was simplified (Appendix 2). For the phytoplankton group, production must balance the sum of the outputs (phytoplankton respiration, 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). Because bacteria were considered part of this functional group, detritus is assumed to respire.

For zooplankton, phytoplankton, and detritus groups, we also introduced in the mass-balance equation an "advection" term, a residual inflow or outflow required, if necessary, to balance the models in order to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990) (Appendix 2).

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 into the model the observations 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 generally included values from the system (e.g., landings [catches]; Appendix 2). 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%) (Appendix 2). For the data equation, the mean calculated directly from the lower and upper limit range or the value available only as a point estimate was used in modelling. Also, the equations calculated for the specified values (data equations) were not reproduced exactly and the differences between observed inputs and estimated flows are represented by the residual erm ε (Appendix 2). Inverse modelling could thus find a solution that was not necessarily balanced (not in steady state). This yielded 212 (41 mass balances and 171 specified flows) equations (Appendix 2) that had to be solved for 646 unknown flows (Appendix 1).

This system was strongly underdetermined (e.g., the number of flows to be solved exceeded the number of independent mass balance relations), so additional constraints were needed to incorporate general eco-physiological knowledge into the model (Appendix 3). Each flow was taken to be non-negative, and flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements (Appendix 3). 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, 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 zooplankton groups (between 50 and 90%). For certain flows (production, consumption, other diet proportions with higher SD values [e.g., > 0.6%], export for detritus, etc.), minimum and maximum values were incorporated as constraints (Appendix 3). To facilitate comparisons with other ecosystem models, we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is used in the system through predation or fishing mortality. 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). Note that (1-EE) represents the natural mortality other than predation or other mortality causes (MO). In all, 1729 constraints were added to the 212 mass balance relations, leading to a system of 1941 equations and inequalities to be solved for the 646 unknown flows. The model was coded as a set of MATLAB[TM] scripts, including routines from the Optimization Toolbox[TM] and supporting Excel[TM] spreadsheets.

The choice of weights for each mass balance equation (called row weights) and for each unknown flow (column weights) is an important part of the solution process. In this study, the variances of the observed data were used as the row weights and the variances of the estimated flows as the column weights. We used the inverse of the variances in the weighting scheme, which limited the influence of large uncertainties on the solution. The weighting scheme has two effects: (1) it introduces a prior hypothesis about the relative sizes of the unknown flows, and (2) it limits the influence of large uncertainties on the solution, e.g., the weighted optimal fits were largely determined by the parts of the ecosystem about which we know the most. For each

predation flow, we used the weighting scheme defined by Savenkoff et al. (2004b) to reduce numerical instability and give less weight to predation equations compared to other mass-balance equations in the solution. Indeed, there was a large number (88 of 487) of proportion of prey u in diet (by mass) of consumer y values that were low (< 0.1%) or equal to 0% (representing a trophic relation between prey and predator in other ecosystems or another time period). This gave less weight to predation equations, allowing greater differences between initial and final estimates of diet proportions and reducing numerical instability.

To find a solution, we used the minimum norm (MN) inversion (the parsimony principle) that seeks to minimize both the sum of squared energy flows (thus the total sum of flows through the food web) and squared residual errors ε (minimizes the imbalances between inputs and outputs), that are consistent with the constraints. Mass-balance models are deterministic and require many input parameters, some of which may be poorly known or adapted from other ecosystems. To explore the effects of uncertainty on the model results, a perturbation analysis was carried out once the initial balanced solution was obtained. We randomly perturbed each term by up to its standard deviation in order to represent the true uncertainties of the input data. Assuming uniform distribution, each x_i term was thus replaced by $x_i + rn\, SD_i$, where rn is a randomly chosen real number between -1 and 1 and the inverse analysis was recalculated each time (Savenkoff et al. 2007b). The final solution is always the mean of one solution without perturbation (the "initial solution") and 30 iterations with random perturbations of the input data (to a maximum of their standard deviations). This number is a compromise between limitations in computing time (one week for 31 balanced and ecologically realistic random perturbations) and statistical significance. The estimated values from this final solution are presented in Appendix 4.

First modelling runs

Based on first inverse modelling runs, initial production values (and thus biomass) for several groups (large and small demersal feeders, capelin, herring, large and small pelagic feeders, squid) seemed to be too low to meet predator demands.

For the zooplankton, phytoplankton, and detritus groups, an "advection" term – a required residual inflow or outflow – was added in the mass-balance equation if necessary to balance the models in order to reproduce the passive transport of organisms by the estuarine circulation (Appendix 2). However, without information to constrain these advection terms, they were all equal to zero in the modelling runs.

RESULTS: DATA COLLECTING AND SYNTHESIS

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

Cetaceans: mysticetes and odontocetes (Claude Savenkoff, Jean-François Gosselin, Marie-Hélène Truchon, Lena Measures, and Véronique Lesage; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

The 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). In the Estuary, minke (*Balaenoptera acutorostrata*), blue (*Balaenoptera musculus*), humpback (*Megaptera novaeangliae*), and fin (*Balaenoptera physalus*) whales are the most abundant species among the large and medium whales (J.-F. Gosselin, Institut Maurice-Lamontagne, unpublished data). The beluga whale (*Delphinapterus leucas*) is the most abundant of the small odontocetes in the Estuary, although harbour porpoise (*Phocoena phocoena*) also occur in this area. Other cetaceans, like white-sided dolphins (*Lagenorhynchus acutus*) and white-beaked dolphins (*Lagenorhynchus albirostris*) may occur occasionally in the lower Estuary (Lesage et al. 2007).

Among the cetaceans, the beluga is the only permanent resident of the Estuary or Gulf of St. Lawrence (reviewed in Lesage et al. 2007). Although some individuals of blue whales and other rorqual whales are known to occur in the waters of the St. Lawrence system throughout the year, these species are considered as seasonal visitors, coming into the study area mainly for feeding purposes.

Based on diet and body mass, cetaceans were first separated into two groups: the mysticetes (baleen whales) and the odontocetes (toothed whales). Among mysticetes, blue whale was considered separately from the other species to estimate potential competition with this species in the study area. Beluga whales and other odontocetes were also separated into two groups.

Biomass

Data on cetacean abundance for the St. Lawrence Estuary was obtained as part of the 2007 Trans North Atlantic Sighting Survey (TNASS) effort in eastern Canada (Lawson and Gosselin 2009). The cetacean survey in the St. Lawrence Estuary covered 12,071 km^2, so we used this survey area to calculate the parameters for this group instead of the value usually used for the other groups (the sampling area for the lower Estuary). Abundance estimates for this zone, uncorrected for availability and perception biases, were 38 minke whales (upper and lower limits of the 95% confidence interval, 95% CI: 8–217 animals), 8 fin whales (95% CI: 1–43 ind.), 14 humpback whales (95% CI: 0–38 ind.), 210 harbour porpoises (95% CI: 29–1,527 ind.), and 885 beluga whale (95% CI: 344–1,615 ind.) (J.-F. Gosselin, Institut Maurice-Lamontagne, unpublished data). No other species were observed in this stratum during the 2007 survey, preventing an estimation of their abundance. Given their relatively low abundance in the northwest Atlantic (Sears and Calambokidis 2002, Lesage et al. 2007), only 17 blue whales (*Balaenoptera musculus*) were seen during the entire 2007 Canadian survey (Lawson and Gosselin 2009). However, based on the longest photo-identified blue whale data sets collected by the Mingan Island Cetacean Study (MICS), Comtois et al. (2010) estimated that the number of distinct photo-identified animals per year ranged between 18 and 46 individuals in the 2005–2007 time period in the lower Estuary (mean: 30 individuals).

Mean body mass taken from the review of Lesage et al. (2007) was 5.5 t for minke whales, 31.5 t for fin whales, 27.5 t for humpback whales, 100.0 t for blue whales, 0.05 t for harbour porpoises, and 0.6 t for beluga whales. Based on the previous information on abundance, body mass, and area, we estimated mean biomass values of 3,000 tons or 0.249 ± 0.119 t km^{-2} for blue whales, 846 tons or 0.070 ± 0.031 t km^{-2} for other mysticetes, 531 tons or 0.044 ± 0.013 t km^{-2} for belugas, and 11 tons or 0.001 ± 0.001 t km^{-2} for other odontocetes. Biomass estimates for species other than blue whales are underestimates as they are uncorrected for animals diving at the time of the survey and those at the surface but undetected by observers.

Anthropogenic activities associated with marine mammal mortality

The nature of anthropogenic activities underlying marine mammal mortalities was assessed from a study examining stranding events recorded in the Estuary and northwestern Gulf of St. Lawrence from 1994 to 2008 for evidence of anthropogenic signs (M.-H. Truchon, L. Measures, and J.-C. Brêthes, Institut Maurice-Lamontagne and Université du Québec à Rimouski, unpublished data). Of 1590 stranding events (1994 to 2008), 192 involved anthropogenic activities, including fishery entanglement (48%), ship collision (19%), gunshot (16%), probable illegal hunting (13%), and severe injuries (5%). These records include six species of large cetaceans, three species of small cetaceans, and four species of seals. Overall, anthropogenic incidents on marine mammals were mostly reported during summer, probably due to seasonality in human activities (e.g., recreational activities, intense maritime traffic, most fisheries, etc.), probability of carcass detection, and presence of species in the study area. Anthropogenic incidents on marine mammals significantly increased over years (M.-H. Truchon, L. Measures, and J.-C. Brêthes, Institut Maurice-Lamontagne and Université du Québec à Rimouski, unpublished data).

For the 2003–2008 period, 17 cetacean mortalities related to anthropogenic interactions have been reported in the Estuary. Two minke whale mortalities were associated with entanglement in fishing gear while one fin whale mortality was related to ship collision. For odontocetes, three beluga and one harbour porpoise died from ship collision while 10 harbour porpoise mortalities were caused by other anthropogenic incidents, probably illegal hunting.

Based on the previous information on abundance, body mass, and area (12,071 km^2), we estimated lethal anthropogenic incidents of 3.52×10^{-3} t km^{-2} yr^{-1} for other mysticetes, 1.49×10^{-4} t km^{-2} yr^{-1} for belugas, 4.83×10^{-5} t km^{-2} yr^{-1} for other odontocetes, and none for blue whales. We used the coefficients of variation for biomass (44%, 29%, and 98%, respectively, for other mysticetes, belugas, and other odontocetes; see below) to estimate the standard deviations for anthropogenic mortality. The final solution of inverse modelling (hereafter termed "inverse solution") estimated anthropogenic mortality values of $3.52 \times 10^{-3} \pm 8.85 \times 10^{-4}$ t km^{-2} yr^{-1} for other mysticetes, $1.57 \times 10^{-4} \pm 2.32 \times 10^{-5}$ t km^{-2} yr^{-1} for belugas, and $3.85 \times 10^{-5} \pm 2.48 \times 10^{-5}$ t km^{-2} yr^{-1} for other odontocetes.

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 minke whales was estimated to be 0.074 yr^{-1} (mean value; Tanaka 1990). Other values were estimated by Ohsumi (1979) for minke whales (0.090 yr^{-1}), fin whales (0.040 yr^{-1}), humpback whales (0.070 yr^{-1}), and odontocetes (i.e., dolphins; mean value: 0.149 yr^{-1}). After weighting according to the biomass of each species in the present study, we estimated a natural mortality of 0.063 yr^{-1} for blue whales and other mysticetes and 0.149 yr^{-1} for belugas and other odontocetes. No catch has been reported for blue whales while minimum anthropogenic mortalities were 3.52 x 10^{-3} t km^{-2} yr^{-1} for other mysticetes, 1.49 x 10^{-4} t km^{-2} yr^{-1} for belugas, and 4.83 x 10^{-5} t km^{-2} yr^{-1} for odontocetes, based on beach-cast carcasses. We used the coefficients of variation for biomass (48%, 44%, 29%, and 98%, respectively, for blue whales, other mysticetes, belugas, and other odontocetes) to estimate the standard deviations for production. This resulted in a total production of 0.016 ± 0.008 t km^{-2} yr^{-1} (range: 0.009–0.024 t km^{-2} yr^{-1}) for blue whales, 0.008 ± 0.003 t km^{-2} yr^{-1} (range: 0.004–0.022 t km^{-2} yr^{-1}) for other mysticetes, 0.007 ± 0.002 t km^{-2} yr^{-1} (range: 0.003–0.012 t km^{-2} yr^{-1}) for belugas, and 0.0002 ± 0.0002 t km^{-2} yr^{-1} (range: 0.0001–0.0010 t km^{-2} yr^{-1}) for other odontocetes. The inverse solution estimated a production of 0.011 ± 0.002 t km^{-2} yr^{-1} (P/B of 0.04 yr^{-1}) for blue whales, 0.006 ± 0.002 t km^{-2} yr^{-1} (P/B of 0.08 yr^{-1}) for other mysticetes, 0.0028 ± 0.0001 t km^{-2} yr^{-1} (P/B of 0.06 yr^{-1}) for belugas, and 0.0001 ± 0.0001 t km^{-2} yr^{-1} (P/B of 0.10 yr^{-1}) for other odontocetes.

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). Mean body mass of each cetacean species was estimated from Lesage et al. (2007). We also used the coefficients of variation for biomass to estimate the standard deviations for consumption.

Assuming a residence time of 180 days for blue whales and other mysticetes, this gives a mean annual consumption of 0.447 ± 0.215 t km^{-2} yr^{-1} (range: 0.268–0.686 t km^{-2} yr^{-1}) for blue whales and 0.177 ± 0.074 t km^{-2} yr^{-1} (range: 0.018–0.774 t km^{-2} yr^{-1}) for other mysticetes. 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 values (0.016 and 0.008 t km^{-2} yr^{-1}, respectively) and the GE limits, we obtained other consumption ranges of 1.575 to 15.749 t km^{-2} yr^{-1} for blue whales and 0.796 to 7.962 t km^{-2} yr^{-1} for other mysticetes. The value based on the lower GE limit (0.1%) was not realistic, being at least 10 times higher than the consumption value based on daily ration. So the resulting consumption range was 0.268 to 1.575 t km^{-2} yr^{-1} (mean consumption value: 0.922 ± 0.924 t km^{-2} yr^{-1}) for blue whales and 0.018 to 0.796 t km^{-2} yr^{-1} (mean consumption value: 0.407 ± 0.551 t km^{-2} yr^{-1}) for other mysticetes. The inverse

solution estimated a consumption of 1.170 ± 0.668 t km^{-2} yr^{-1} (Q/B: 4.71 yr^{-1}) for blue whales and 0.589 ± 0.167 t km^{-2} yr^{-1} (Q/B: 8.40 yr^{-1}) for other mysticetes.

Assuming a residence time of 180 days for harbour porpoises and 365 days for beluga whales (permanent resident), the mean annual consumption was estimated at 0.447 ± 0.131 t km^{-2} yr^{-1} (range: 0.174–0.815 t km^{-2} yr^{-1}) for belugas and 0.008 ± 0.007 t km^{-2} yr^{-1} (range: 0.001–0.055 t km^{-2} yr^{-1}) for other odontocetes. 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 values (0.007 and 0.0002 t km^{-2} yr^{-1}, respectively) and the GE limits, we obtained other consumption ranges of 0.670 to 6.704 t km^{-2} yr^{-1} for belugas and 0.019 to 0.186 t km^{-2} yr^{-1} for other odontocetes. The value based on the lower GE limit was not realistic, so the resulting consumption range was 0.174 to 0.815 t km^{-2} yr^{-1} (mean consumption value: 0.494 ± 0.454 t km^{-2} yr^{-1}) for belugas and 0.001 to 0.055 t km^{-2} yr^{-1} (mean consumption value: 0.028 ± 0.038 t km^{-2} yr^{-1}) for other odontocetes. The inverse solution estimated a consumption value of 0.282 ± 0.017 t km^{-2} yr^{-1} (Q/B: 6.40 yr^{-1}) for belugas and 0.010 ± 0.005 t km^{-2} yr^{-1} (Q/B: 10.82 yr^{-1}) for other odontocetes.

Diet composition

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 made up at least 75% of consumed mass. If other prey were reported, remaining consumption was divided equally among them. Based on Bundy et al. (2000) for the Newfoundland–Labrador Shelf, the following diets for mysticetes were used in the analysis:

- Humpback whales: capelin, euphausiids, small pelagics (mainly sand lance), and squid (adapted from Mitchell 1973 and Bundy et al. 2000);
- Fin whales: capelin, euphausiids, and small pelagics (mainly sand lance) (adapted from Mitchell 1975, Sutcliffe and Brodie 1977, and Bundy et al. 2000);
- Minke whales: capelin, small cod, euphausiids, herring, and squid (adapted from Mitchell 1974, Horwood 1990, and Bundy et al. 2000).

The overall proportion of each prey item by mass was weighted according to the consumption of each cetacean species to obtain the resulting diet of the other mysticetes group. Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of the resulting diet were capelin, small pelagics, and large and small euphausiids (85.7% of the diet; Table 2).

Blue whales are specialist feeders and consume almost exclusively euphausiids worldwide (Yochem and Leatherwood 1985, Sears and Calambokidis 2002). In the North Atlantic, their main prey items are the euphausiids *Thysanoessa inermis*, *T. longicaudata*, *T. raschii*, and *Meganyctiphanes norvegica*. In the North Pacific, blue whales feed mainly on the euphausiids *Euphausia pacifica*, *T. spinifera*, *T. inermis*, *T. longipes*, *T. raschii*, and *Nematoscelis megalops*, but other prey species from the genus *Calanus* and pelagic red crab have been reported (Yochem and Leatherwood 1985, Schoenherr 1991, Fiedler et al. 1998). All these potential food items were accounted for in the final diet composition (Table 2). Due to the lack of information on

zooplankton species identification, the diet proportions for macrozooplankton and mesozooplankton were redistributed in the resulting diet according to the biomass proportion of each zooplankton species.

For beluga whales, we used the diet reported by Smith et al. (2011). The prey proportions were estimated from occurrence of species in the diet of beluga collected mainly at the Banc de Manicouagan in 1938–1939 (Vladykov 1946) and in various areas of the Estuary and northern Gulf of St. Lawrence through beluga strandings in 1989–2008. How closely these data reflect the true diet of the population, in terms of species composition and relative contribution to the consumed biomass, is unknown. Occurrences for recent diet were based on a very small sample size (n = 19), while those from the 1930s were from an area no longer used by St. Lawrence beluga (Smith et al. 2011). Using these occurrences as a proxy for abundance in the diet and mean body wet weight for each prey species, we estimated prey proportions by mass. Large and small demersals, cod, herring, and squid would constitute the main prey items in beluga diet (Table 3). For harbour porpoises, we used the diets estimated by Fontaine et al. (1994) in the Estuary and the northern Gulf of St. Lawrence, by Gannon et al. (1998) in the Gulf of Maine, and by Recchia and Read (1989) from the Bay of Fundy. The main prey items of the resulting diet were herring, large pelagics, capelin, and small pelagics (Table 3).

Table 2. Diet compositions (%) of blue whales and other mysticetes (baleen whales) used in modelling. Est: diet estimates from 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.

Prey	Blue whales					Other mysticetes				
	Mean	±SD	Min	Max	Est	Mean	±SD	Min	Max	Est
Large cod										
Small cod						1.6	2.9	**0.0**	**5.0**	0.0
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Atlantic halibut										
Redfish										
Black dogfish										
White hake										
Large demersals										
Small demersals										
Capelin						65.0	21.7	**37.5**	**75.0**	64.0
Large pelagics										
Herring						4.8	6.5	**0.0**	**12.5**	0.2
Small pelagics						7.6	5.0	**0.0**	**10.0**	0.2
Squid						3.4	2.5	**0.0**	**5.0**	0.0
Shrimp										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.										
Large euphausiids	44.4	2.3	**0.0**	**100.0**	35.1	6.1	8.1	**1.7**	**16.3**	11.6
Small euphausiids	50.6	2.7	**0.0**	**100.0**	59.1	7.0	9.2	**2.0**	**18.6**	15.2
Large hyperiid amp.	**0.1**	0.1	0.0	0.2	0.1	**0.1**	0.2	0.0	0.4	0.1
Other macrozoop.	2.4	2.4	**0.0**	**4.8**	2.2	4.4	5.8	**1.2**	**11.7**	8.6
Surface mesozoop.	2.5	2.5	**0.0**	**5.0**	3.5	**0.0**	0.0	0.0	0.0	0.0
Deep mesozoop.	**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	210.0	100.0	100.0		42.5	154.4	100.0
TRN	6					11				

Table 3. Diet compositions (%) of belugas and other odontocetes (toothed whales) used in modelling. Est: diet estimates from 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.

Prey	Belugas					Other odontocetes				
	Mean	±SD	Min	Max	Est	Mean	±SD	Min	Max	Est
Large cod	7.1	10.2	**0.0**	**14.4**	12.1	**0.1**	0.2	0.0	0.3	0.1
Small cod	7.1	10.2	**0.0**	**14.4**	10.4	**0.1**	0.2	0.0	0.3	0.1
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders	1.2	1.7	**0.0**	**2.4**	2.4	**0.0**	0.0	0.0	0.0	0.0
Skates	2.7	3.9	**0.0**	**5.6**	5.6					
Atlantic halibut										
Redfish	2.9	4.2	**0.0**	**5.9**	1.1	2.3	3.2	**0.0**	**5.9**	3.3
Black dogfish										
White hake	8.5	12.2	**0.0**	**17.2**	1.7	4.5	7.0	**0.0**	**12.6**	4.1
Large demersals	15.8	7.2	**2.7**	**21.0**	20.8	4.5	7.0	**0.0**	**12.6**	4.3
Small demersals	12.7	8.3	**3.5**	**18.7**	18.6	**0.0**	0.1	0.0	0.1	0.0
Capelin	4.2	6.0	**0.0**	**8.4**	8.4	13.4	23.2	**0.0**	**40.2**	36.7
Large pelagics	4.1	5.9	**0.0**	**8.3**	0.2	13.9	12.3	**0.0**	**23.3**	0.2
Herring	13.5	18.4	**0.7**	**26.7**	5.0	43.8	17.8	**26.6**	**62.1**	38.0
Small pelagics	3.5	4.8	**0.2**	**7.0**	4.5	11.1	13.5	**1.9**	**26.6**	12.5
Squid	11.0	4.9	**0.1**	**14.6**	0.1	5.5	7.9	**0.0**	**14.6**	0.0
Shrimp	0.5	0.8	**0.0**	**1.1**	1.1					
Small crabs										
Echinoderms										
Molluscs	**0.1**	0.1	0.0	0.2	0.1					
Polychaetes	**0.0**	0.1	0.0	0.1	0.0					
Other bent. inver.	5.0	4.0	**2.3**	**7.9**	7.9	**0.6**	0.6	0.0	1.0	0.6
Large euphausiids						**0.0**	0.0	0.0	0.0	0.0
Small euphausiids										
Large hyperiid amp.										
Other macrozoop.										
Surface mesozoop.										
Deep mesozoop.										
Phytoplankton										
Detritus										
Total	100.0		9.5	174.0	100.0	100.0		28.5	199.6	100.0
TRN	17					14				

Seals (Claude Savenkoff, Véronique Lesage, Marie-Hélène Truchon, Lena Measures, and Mike Hammill; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

Four species of pinnipeds occur in the Estuary and the Gulf of St. Lawrence: harp seals (*Pagophilus groenlandica*), grey seals (*Halichoerus grypus*), hooded seals (*Cystophora cristata*), and harbour seals (*Phoca vitulina*). Harbour and grey seals are the most abundant pinnipeds in the Estuary during summer (Robillard et al. 2005). Harp seals and hooded seals are normally found in Arctic waters at that time of the year. They migrate to the Labrador and Newfoundland area and the Gulf of St. Lawrence, including the St. Lawrence Estuary, beginning in late November to forage and to breed during winter (Sergeant 1976, Hammill et al. 1997, DFO 2010a). Although most of the animals have left the St. Lawrence by early summer, some harp seal concentrations may still be observed in the Estuary and northern Gulf in late June (V. Lesage, Institut Maurice-Lamontagne, pers. comm.). Hooded seals appear more solitary outside of the reproductive period when in Canadian waters and few observations are reported beyond springtime. Therefore, hooded seals were excluded from the analyses.

Harbour seals (weight = 70–90 kg) are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Although total population size and its relative distribution remain highly uncertain, the St. Lawrence might support approximately 4000–5000 harbour seals, which is a third of the total population, of which approximately 75–80% would occur in the Gulf of St. Lawrence (Robillard et al. 2005, Lesage et al. 2007). Recent studies based on aerial surveys of haul out sites indicate that harbour seals are more numerous in the lower Estuary and along the south shore than in the upper Estuary or the Saguenay River or along the north shore (Robillard et al. 2005). Harbour seals are permanent residents of the Estuary (Lesage et al. 2007).

The grey seal is larger than the harbour seal (weight = 150–350 kg). Major breeding colonies in eastern Canada are located on Sable Island, on the eastern shore of Canada (including Hay Island and other small colonies along coastal Nova Scotia), and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977, Thomas et al. 2007). After breeding, both juveniles and adults disperse widely over eastern Canada. Both Sable Island and southern Gulf of St. Lawrence grey seals occupy the Estuary and Gulf during the ice-free period, but the number of individuals present during that period, although in the thousands, remains uncertain (Robillard et al. 2005). In the Estuary, the largest aggregations are observed at Île-aux-Fraises the Bic archipelago, and along the north shore of the lower St. Lawrence Estuary between the Betsiamites River mouth and Baie-Comeau (Robillard et al. 2005, Lesage et al. 2007).

The harp seal (weight = 130–140 kg) is the most abundant pinniped in Atlantic Canada and usually summers in the Canadian Arctic or northwest Greenland before returning south to overwinter in Atlantic Canada (DFO 2010a). 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).

Biomass

The abundance and distribution of harbour seals and grey seals in the St. Lawrence Estuary were assessed using seven aerial visual surveys of the Estuary, including three in June (1995, 1996, 2000) and four in August (1994–1997) (Robillard et al. 2005). The August 1994 survey was excluded from the present analyses since the limits of the study area were less extensive to the east. In general, harbour seals were seen more frequently than grey seals. However, grey seals generally formed larger aggregations than harbour seals (Robillard et al. 2005). Harbour seal counts at haul-out sites ranged from 410 to 723 individuals in the St. Lawrence Estuary while a total of 244 to 723 grey seals were counted at haul-out sites. Applying correction factors (e.g., haul-out behaviour controlled principally by tides, pupping season) to the most recent counts resulted in absolute abundance estimates of 811–1252 harbour seals in 1997 (August) and 721–858 animals in 2000 (June) (Robillard et al. 2005), thus a range of 721–1252. No equivalent correction factors are available for grey seals since abundance is usually determined through pup counts on the ice or land during the pupping season (Hammill et al. 1998, Bowen et al. 2003). Consequently, we used the 244–723 range for grey seals. Depending on the survey year and season, and excluding the 1994 survey, 58–71% of the harbour seals and 78–92% of the grey seals were observed in the lower Estuary (Robillard et al. 2005). Applying these factors resulted in abundance ranges of 418 to 889 harbour seals and 190 to 665 grey seals for the 1995–2000 time period. For harp seals, we used 0 to 300 animals in the lower Estuary as guesstimates for lower and upper limits of abundance.

Mean body mass was 80 kg for harbour seals, 250 kg for grey seals, and 135 kg for harp seals (Lesage et al. 2007). Based on the previous information on abundance, body mass, and area (lower Estuary survey: 6,840 km^2), we estimated mean biomass ranges of 0.005 to 0.010 t km^{-2} for harbour seals, 0.007 to 0.024 t km^{-2} for grey seals, and 0.000 to 0.006 t km^{-2} for harp seals for the 1995–2000 period. To calculate biomass in the 2008–2010 period, we used a population growth rate for each seal group from an updated version of the population model of Hammill and Stenson (2000). For harp seals, we used a population growth rate of 2.0% in 2001–2004 and 3.0% in 2005–2010. We used a population growth rate of 4.7% and 5.7%, respectively, in 2001–2010 for grey and harbour seals. Harp seal biomass was adjusted for residence time (25% or three months). The resulting biomass was 0.011 ± 0.003 t km^{-2} (range: 0.008 to 0.018 t km^{-2}) for harbour seals, 0.022 ± 0.010 t km^{-2} (range: 0.010 to 0.039 t km^{-2}) for grey seals, and 0.001 ± 0.001 t km^{-2} (range: 0.000 to 0.002 t km^{-2}) for harp seals.

Catch

We used seal mortalities related to anthropogenic interactions reported in the Estuary for the 2003–2008 period (M.-H. Truchon, L. Measures, and J.-C. Brêthes; Institut Maurice-Lamontagne and Université du Québec à Rimouski, unpublished data). Mortalities are therefore underestimates given that only reported animals are compiled (a lot of animals die without reported observations). Of eight seal mortalities due to anthropogenic factors, two were associated with entanglement in fishing gears (two harbour seals), five with gunshot (two harbour seals, two grey seals, and one harp seal), and one with severe injury events (one harp seal). For Québec's North Shore (including the Estuary), there was also harvest data for harp and grey seals

in the 2008–2010 period (M. Hammill, Institut Maurice-Lamontagne, unpublished data). Mortalities ranged between 248 to 2,190 for harp seals and 0 to 5 for grey seals.

Based on the previous information on abundance, body mass, and area (12,071 km^2 for the Estuary and 115,930 km^2 for Québec's North Shore region; i.e., the whole scientific survey area in the Estuary and northern Gulf), we estimated anthropogenic mortality ranges of 2.89 x 10^{-4} to 2.55 x 10^{-3} t km^{-2} yr^{-1} for harp seals (mean: 1.07 x 10^{-3} ± 1.28 x 10^{-3} t km^{-2} yr^{-1}), 2.16 x 10^{-6} to 4.14 x 10^{-5} t km^{-2} yr^{-1} for grey seals (mean: 1.81 x 10^{-5} ± 2.06 x 10^{-5} t km^{-2} yr^{-1}), and 0 to 2.65 x 10^{-5} t km^{-2} yr^{-1} for harbour seals (mean: 8.84 x 10^{-6} ± 1.53 x 10^{-5} t km^{-2} yr^{-1}). For harp seals, mortality through total removals was reduced by 25% (see biomass section) to account for the summer season only. This resulted in a mortality range of 7.22 x 10^{-5} to 6.38 x 10^{-4} t km^{-2} yr^{-1} for harp seals (mean: 2.67 x 10^{-4} ± 3.21 x 10^{-4} t km^{-2} yr^{-1}). The mean mortality value for harp seals is greater than the mean production value (9.06 x 10^{-5} t km^{-2} yr^{-1}; see below), so we used mortality ranges rather than mean value in modelling. The inverse solution estimated anthropogenic mortality values of 7.44 x 10^{-5} ± 2.39 x 10^{-6}, 2.28 x 10^{-5} ± 9.02 x 10^{-6}, and 1.12 x 10^{-5} ± 6.86 x 10^{-6} t km^{-2} yr^{-1} for harp, grey, and harbour seals, respectively.

Production

The P/B ratio for each group was estimated by dividing the pup biomass by the population biomass (minimum value) for the study area as reported in an updated version of the population model of Hammill and Stenson (2000). The P/B ratios were 0.073 yr^{-1} for harp seals, 0.101 yr^{-1} for grey seals, and 0.071 yr^{-1} for harbour seals for the 2008–2010 period. Multiplying these P/B ratios by minimum and maximum biomass values for each species resulted in production ranges of 0.0000 to 0.0001 t km^{-2} yr^{-1} for harp seals, 0.0010 to 0.0039 t km^{-2} yr^{-1} for grey seals, and 0.0005 to 0.0013 t km^{-2} yr^{-1} for harbour seals.

Production was also estimated by adding the annual mass gain for each age class in the population to the mass of pups. Mass at age for harp seals was obtained from Chabot and Stenson (2002). An updated version of the population model of Hammill and Stenson (2000) provided the information for grey and harbour seals. This resulted in production ranges of 0.0000 to 0.0002 t km^{-2} yr^{-1} for harp seals, 0.0016 to 0.0061 t km^{-2} yr^{-1} for grey seals, and 0.0012 to 0.0029 t km^{-2} yr^{-1} for harbour seals.

Finally, the resulting upper and lower limit ranges were 0.0000 to 0.0002 t km^{-2} yr^{-1} (mean: 0.0001 ± 0.0001 t km^{-2} yr^{-1}) for harp seals, 0.0010 to 0.0061 t km^{-2} yr^{-1} (mean: 0.0029 ± 0.0023 t km^{-2} yr^{-1}) for grey seals, and 0.0005 to 0.0029 t km^{-2} yr^{-1} (mean: 0.0013 ± 0.0010 t km^{-2} yr^{-1}) for harbour seals. The inverse solution estimated production values of 0.0001 ± 0.0000 t km^{-2} yr^{-1} (P/B = 0.08 yr^{-1}) for harp seals, 0.0016 ± 0.0007 t km^{-2} yr^{-1} (P/B = 0.07 yr^{-1}) for grey seals, and 0.0006 ± 0.0001 t km^{-2} yr^{-1} (P/B = 0.05 yr^{-1}) for harbour seals.

Consumption

The Q/B for each seal species was estimated at 4.26 yr^{-1}, 3.80 yr^{-1}, and 4.00 yr^{-1}, respectively, for harp, grey, and harbour seals from an updated version of the consumption model of Hammill and Stenson (2000). Multiplying these Q/B ratios by minimum and maximum biomass values for each species resulted in consumption ranges of 0.000 to 0.008 t km^{-2} yr^{-1} for harp seals, 0.038 to 0.146 t km^{-2} yr^{-1} for grey seals, and 0.030 to 0.072 t km^{-2} yr^{-1} for harbour seals.

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 values (0.0001, 0.0029, and 0.0013 t km^{-2} yr^{-1}, respectively) and the GE limits, we obtained other consumption ranges of 0.009 to 0.091 t km^{-2} yr^{-1} for harp seals, 0.288 to 2.882 t km^{-2} yr^{-1} for grey seals, and 0.133 to 1.327 t km^{-2} yr^{-1} for harbour seals. The value based on the lower GE limit (0.1%) was not realistic, being at least 11 times higher than the consumption value based on Q/B ratios. So the resulting consumption range was 0.000 to 0.009 t km^{-2} yr^{-1} (mean consumption value: 0.005 ± 0.006 t km^{-2} yr^{-1}) for harp seals, 0.038 to 0.288 t km^{-2} yr^{-1} (mean consumption value: 0.163 ± 0.177 t km^{-2} yr^{-1}) for grey seals, and 0.030 to 0.133 t km^{-2} yr^{-1} (mean consumption value: 0.082 ± 0.072 t km^{-2} yr^{-1}) for harbour seals. The inverse solution estimated consumption values of 0.008 ± 0.003 t km^{-2} yr^{-1} (Q/B = 8.66 yr^{-1}) for harp seals, 0.160 ± 0.057 t km^{-2} yr^{-1} (Q/B = 7.22 yr^{-1}) for grey seals, and 0.060 ± 0.010 t km^{-2} yr^{-1} (Q/B = 5.32 yr^{-1}) for harbour seals.

Diet composition

Diet data from the study area during the 2008–2010 period were unavailable for seals, so data from other areas and time periods were used instead. For harp seals, diet information was available for pups (n = 166), juveniles (i.e., age 1–4; n = 73), and adults (n = 21) in the northern Gulf during 1998–2001 (M. Hammill, unpublished data). The different diet proportions of the final diet were weighted by the biomass proportion of each class in the northern Gulf for the 2006–2010 period (4.4%, 13.2%, and 82.3%, respectively, for pups, juveniles, and adults). According to these diets, the main prey species were, in order of importance, Atlantic cod, Atlantic herring, and shrimp based on mass contribution (69.2% of total diet; Table 4).

For grey seals, diet information was available for pups (n = 1), juveniles (i.e., age 1–4; n = 11), and adults (n = 24) in the northern Gulf in 2004 and 2006 (M. Hammill, unpublished data). The different diet proportions of the overall grey seal diet were weighted by the biomass proportion of each class (4%, 6%, and 90%, respectively, for pups, juveniles, and adults) in the study area. We also used diet information based on seals collected between 1999 and 2004 on the south coast of Newfoundland (NAFO division 3Ps; n = 13) and between 1998 and 2004 in the Gulf of St. Lawrence and around Newfoundland (NAFO divisions 3Pn and 4R; n = 21) (Stenson and Hammill, unpublished data). The different prey proportions of the final diet were weighted by the number of analyzed stomach content in each area. According to these studies, the main prey species of grey seals were small pelagic feeders, herring, Atlantic cod, and small demersals based on mass contribution (72.3% of the diet; Table 4).

The harbour seal diet composition was examined for two inshore habitats of Atlantic Canada (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, large pelagics (pollock *Pollachius virens*), and Atlantic cod based on mass contribution. We obtained upper and lower limits resulting from these different diet studies. The resulting diet composition of harbour seals is shown in Table 5.

Table 4. Diet compositions (%) of harp and grey seals used in modelling. Est: diet estimates from 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 seals					Grey seals				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	10.2	7.4	**0.0**	**31.7**	12.8	9.8	8.0	**0.0**	**38.5**	0.7
Small cod	15.5	8.4	**0.0**	**49.4**	10.8	9.8	8.0	**0.0**	**38.5**	0.4
Large Green. halibut	0.7	1.2	**0.0**	**4.4**	2.0	0.8	1.4	**0.0**	**7.0**	2.9
Small Green. halibut	0.7	1.2	**0.0**	**4.4**	1.8	0.8	1.4	**0.0**	**7.0**	1.9
American plaice	0.7	1.2	**0.0**	**4.4**	2.3	1.2	2.5	**0.0**	**16.1**	6.5
Flounders	0.7	1.2	**0.0**	**4.4**	2.5	3.0	7.7	**0.0**	**54.3**	22.3
Skates						1.9	9.5	**0.0**	**46.4**	39.8
Atlantic halibut						0.8	1.3	**0.0**	**5.9**	3.1
Redfish	1.8	1.7	**0.0**	**12.1**	1.3	2.0	6.7	**0.0**	**32.8**	0.0
Black dogfish										
White hake	**0.1**	0.2	0.0	1.3	0.1	**0.0**	0.0	0.0	0.0	0.0
Large demersals	2.6	2.4	**0.0**	**12.8**	1.2	5.9	5.8	**0.0**	**30.3**	0.3
Small demersals	3.7	3.4	**0.0**	**20.4**	2.9	8.7	10.2	**0.0**	**56.7**	0.4
Capelin	3.7	2.6	**0.0**	**18.2**	9.5	4.4	10.2	**0.0**	**51.8**	8.7
Large pelagics	5.4	5.8	**0.0**	**22.4**	0.0	4.8	4.8	**0.0**	**19.6**	0.0
Herring	25.6	17.6	**3.8**	**83.4**	7.9	20.6	20.7	**2.1**	**74.3**	2.1
Small pelagics	6.5	5.5	**0.1**	**28.8**	2.3	23.3	21.1	**0.0**	**97.1**	0.0
Squid	**0.0**	0.1	0.0	0.8	0.0	0.3	0.9	**0.0**	**4.5**	0.0
Shrimp	17.8	19.5	**0.0**	**72.3**	20.5	1.6	5.1	**0.0**	**18.6**	10.8
Small crabs	**0.0**	0.0	0.0	0.0	0.0	**0.1**	0.5	0.0	2.3	0.1
Echinoderms										
Molluscs	0.2	0.7	**0.0**	**2.4**	1.6					
Polychaetes										
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large euphausiids	2.0	5.9	**0.0**	**18.3**	10.2					
Small euphausiids	2.0	5.9	**0.0**	**18.3**	10.2					
Large hyperiid amp.	**0.0**	0.1	0.0	0.9	0.0					
Other macrozoop.	**0.1**	0.6	0.0	4.7	0.1	**0.0**	0.0	0.0	0.0	0.0
Surface mesozoop.										
Deep mesozoop.										
Phytoplankton										
Detritus										
Total	100.0		3.9	415.6	100.0	100.0		2.1	601.5	100.0
TRN	23					21				

Table 5. Diet composition (%) of harbour seals used in modelling. Est: diet estimates from 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.

Prey	Harbour seals				
	Mean	± SD	Min	Max	Est
Large cod	6.2	12.4	**3.7**	**21.2**	20.7
Small cod	3.4	6.5	**1.9**	**11.2**	7.0
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders	2.1	11.2	**0.0**	**15.8**	15.8
Skates	0.8	1.8	**0.0**	**2.7**	2.7
Atlantic halibut					
Redfish	0.9	0.7	**0.0**	**0.9**	0.4
Black dogfish					
White hake	3.4	23.5	**0.0**	**33.2**	1.8
Large demersals	1.9	1.3	**0.0**	**1.9**	1.0
Small demersals	7.4	5.9	**0.0**	**8.3**	5.1
Capelin	6.0	6.9	**0.0**	**9.8**	8.9
Large pelagics	13.9	43.6	**0.0**	**61.7**	0.1
Herring	26.9	21.1	**12.0**	**41.8**	15.9
Small pelagics	5.7	23.1	**0.0**	**32.7**	7.0
Squid	14.8	42.4	**0.0**	**60.0**	0.0
Shrimp	5.9	6.8	**0.0**	**13.4**	13.0
Small crabs	**0.4**	0.5	0.0	1.0	0.4
Echinoderms					
Molluscs	**0.2**	0.3	0.0	0.5	0.2
Polychaetes					
Other bent. inver.	**0.1**	0.2	0.0	0.3	0.1
Large euphausiids					
Small euphausiids					
Large hyperiid amp.					
Other macrozoop.					
Surface mesozoop.					
Deep mesozoop.					
Phytoplankton					
Detritus					
Total	100.0		17.6	316.3	100.0
TRN	17				

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*), herring gull (*Larus argentatus*), ring-billed gull (*Larus delawarensis*), great black-backed gull (*Larus marinus*), black guillemot (*Cepphus grylle*), common tern (*Sterna hirundo*), and Arctic tern (*Sterna paradisaea*). 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*).

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 the Estuary and the Gulf of St. Lawrence. 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). 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 the Gulf of St. Lawrence, population estimates (Table 6) were calculated as follows (G. Chapdelaine, unpublished data; Working Group on Seabird Ecology 1999):

(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 estimate of the total number of seabird breeding pairs in the Gulf of St. Lawrence is about 368,669 or 1.2×10^6 individuals as the total population of birds using the area (TPA) (Working Group on Seabird Ecology 1999). The seabird guild is dominated by black-legged kittiwake (22.5% of TPA), but their biomass represents only 9.2% of total seabird biomass. The northern gannet dominates the seabird biomass total with 33.6% and represents 11.2% of TPA. Herring gulls, common guillemots, and double-crested cormorants are the next most important seabirds with 13.5%, 11.4%, and 11.9%, respectively, of TPA, and they represent 14.2%, 11.0%, and 16.2% of the total seabird biomass. The total biomass estimate for the whole 4RST bird inventory area is 859 t or 0.004 t km^{-2}.

Other information about these species was based on a study for the North Atlantic (Barrett et al. 2006). These authors estimated a seabird biomass of 2100 t or 0.002 t km^{-2} in the Gulf of St Lawrence and Scotian Shelf (total area: 10^6 km^2). Accordingly, the mean biomass density for the study area was thus 0.003 ± 0.001 t km^{-2} (range: 0.002 to 0.004 t km^{-2}).

Table 6. Approximate period of occupation, population size, average body mass, and biomass for the main species of seabirds that breed within the study area 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

Catch/anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the the Gulf of St. Lawrence: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). 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 caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounted to 1×10^{-3} t km^{-2} per year in the Newfoundland–Labrador Shelf. On the basis of information for seabirds from the previous study (Bundy et al. 2000), we estimated a catch rate (0.08 yr^{-1}; 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 lower Estuary. It totalled 2.55×10^{-4} t km^{-2} yr^{-1} of seabirds being removed annually from

the study area through anthropogenic mortality (range: 1.75 x 10^{-4} to 3.35 x 10^{-4} t km^{-2} yr^{-1}). The inverse solution estimated a catch of 1.92 x 10^{-4} ± 6.42 x 10^{-5} t km^{-2} yr^{-1}.

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}, representing a P/B of 0.28 yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.31 yr^{-1}. When the biomass values and the two previous P/B ratios were used, we obtained a production range of 0.0006 to 0.0012 t km^{-2} yr^{-1} (production = 0.0009 ± 0.0003 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.0009 ± 0.0002 t km^{-2} yr^{-1}, representing a P/B of 0.30 yr^{-1}.

Consumption

Estimated food Q/B for seabirds in the northern Gulf is 126.18 yr^{-1} (Chapdelaine, unpublished data). Based on the study of Barrett et al. (2006) for the North Atlantic, we estimated another Q/B of 122.38 yr^{-1}. We obtained another Q/B of 51.05 yr^{-1} based on on previous ecosystem models for the northern Gulf. When the biomass values and the three previous Q/B ratios were used, we obtained a consumption range of 0.107 to 0.507 t km^{-2} yr^{-1}.

Based on the previous mean production (0.0009 t km^{-2} yr^{-1}) for seabirds and the minimum and maximum GE limits (0.1–1%; Christensen and Pauly 1992), we obtained consumption values of 0.089 and 0.892 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.089 and 0.892 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.399 ± 0.381 t km^{-2} yr^{-1}. The inverse model's solution was a consumption of 0.111 ± 0.087 t km^{-2} yr^{-1}, representing a Q/B of 36.20 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 (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. There is no diet data available for Leach's storm-petrel, kittiwakes, murres, razorbills, or Atlantic puffins from the Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). We also used the diet compositions estimated by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; ducks, piscivorous birds, and planktivorous birds). Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. Based on these different studies, we estimated the diet composition of seabirds used in modelling for the study area (Table 7). The most important prey items of the resulting diet of seabirds were capelin, small pelagics, and molluscs (72.6% of the diet; Table 7).

Table 7. Diet composition (%) of seabirds used in modelling. Est: diet estimates from 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**	0.3	0.0	0.6	0.2
Large Green. halibut					
Small Green. halibut	**0.2**	0.4	0.0	0.8	0.2
American plaice	**0.2**	0.4	0.0	0.8	0.2
Flounders	**0.2**	0.4	0.0	0.8	0.2
Skates	**0.2**	0.4	0.0	0.8	0.2
Atlantic halibut					
Redfish					
Black dogfish					
White hake	**0.0**	0.0	0.0	0.1	0.0
Large demersals	**0.1**	0.4	0.0	0.9	0.1
Small demersals	4.0	6.6	**0.0**	**16.9**	0.3
Capelin	35.2	34.2	**0.0**	**79.3**	29.5
Large pelagics	**0.0**	0.0	0.0	0.1	0.0
Herring	0.8	0.8	**0.0**	**2.0**	0.0
Small pelagics	22.4	24.6	**0.0**	**58.2**	0.2
Squid	0.3	0.7	**0.0**	**1.7**	0.0
Shrimp	**0.4**	0.6	0.0	1.4	0.4
Small crabs					
Echinoderms					
Molluscs	15.0	36.7	**0.0**	**90.0**	26.7
Polychaetes					
Other bent. inver.	1.9	4.0	**0.0**	**10.0**	2.7
Large euphausiids	6.2	13.3	**0.0**	**33.2**	13.4
Small euphausiids	7.1	15.2	**0.0**	**37.9**	16.8
Large hyperiid amp.	**0.1**	**0.3**	0.0	0.7	0.1
Other macrozoop.	4.4	9.6	**0.0**	**23.8**	7.4
Surface mesozoop.	**0.1**	**0.3**	0.0	0.8	0.1
Deep mesozoop.	0.7	1.4	**0.0**	**3.6**	0.9
Phytoplankton					
Detritus					
Total	100.0		0.0	364.5	100.0
TRN	22				

Atlantic cod (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

Northern Gulf of St. Lawrence cod (NAFO divisions 3Pn and 4RS) undertake an extensive annual migration (DFO 2010b). In winter, they are found off southwestern (3Pn) and southern Newfoundland (3Ps) at depths of more than 366 m. In April and May, they migrate towards the Port au Port Peninsula, on the west coast of Newfoundland (division 4R), where spawning begins. During the summer, fish continue their migration and disperse in the coastal zones, along the west coast of Newfoundland (division 4R) and towards Québec's middle and lower North Shore (division 4S).

Cod landings in the northern Gulf of St. Lawrence exceeded 100,000 tonnes in 1983 (DFO 2010b). Landings declined continuously until 1993. The fishery was under moratorium from 1994 to 1996. It reopened in 1997 and catches and TACs have varied between 3,000 to 7,500 tonnes since, except in 2003 when the fishery was closed again. Currently, it is the only Atlantic coast cod stock where the directed fishery is only conducted with fixed gears (longlines, gillnets, and hand lines) (DFO 2010b).

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.

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 2008–2010 period. Length-frequency data from each year were extrapolated to the whole area using the *PACES* (*Programme d'Analyse des Campagnes d'Échantillonnage Stratifiées*) software to obtain an estimate of cod abundance for this zone (Bourdages 2001). 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 2008–2010 period of 610 t or 0.09 t km^{-2} (SD = 0.06 t km^{-2}; range = 0.03–0.14 t km^{-2}) and 313 t or 0.05 t km^{-2} (SD = 0.03 t km^{-2}; range = 0.02–0.08 t km^{-2}) for large and small cod, respectively.

Catch

Landings for large cod (age 4+) were taken from zonal interchange file format (ZIFF) databases (MPO, unpublished data). Mean catch of large cod was 0.1 t or 7.65 x 10^{-6} ± 1.08 x 10^{-5} t km^{-2} yr^{-1}. For the small cod group, a by-catch value from the shrimp fishery was estimated at 10 t or 1.55 x 10^{-3} ± 1.21 x 10^{-3} t km^{-2} yr^{-1} (J. Gauthier and L. Savard, Maurice Lamontagne Institute,

unpublished data). The inverse solution estimated catch values of $9.05 \times 10^{-6} \pm 5.23 \times 10^{-6}$ and $1.58 \times 10^{-3} \pm 7.52 \times 10^{-4}$ t km^{-2} yr^{-1}, respectively, for large and small cod groups.

Production

Direct estimates of total mortality (Z), based on a modified catch curve analysis of the survey data, were available for large cod (mean value = 1.06 yr^{-1}; Sinclair 2001). This instantaneous rate was then converted into real mortality rate (A = 0.65 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 (0.65 yr^{-1}) is equal to the P/B ratio of cod in 2008–2010 (Allen 1971). The production range was from 0.02 to 0.09 t km^{-2} yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated another mean P/B ratio of 0.39 yr^{-1} (production range: 0.01 to 0.05 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 0.38 yr^{-1} (DFO 2010b). We obtained a production range of 0.01 to 0.05 t km^{-2} yr^{-1}. Combining the three methods resulted in a production range of 0.01 to 0.09 t km^{-2} yr^{-1} (mean: 0.04 ± 0.03 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.05 ± 0.01 t km^{-2} yr^{-1}, resulting in a P/B of 0.55 yr^{-1}.

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M) plus catch. Natural mortality for small cod was assumed to be 0.6 yr^{-1}. Based on previous biomass and catch values for small cod, we estimated a production range of 0.01 to 0.05 t km^{-2} yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.75 yr^{-1} (production range: 0.02 to 0.06 t km^{-2} yr^{-1}). Combining the two methods resulted in a mean annual production of 0.03 ± 0.02 t km^{-2} yr^{-1} (range: 0.01 to 0.06 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.06 ± 0.00 t km^{-2} yr^{-1}, representing a P/B value of 1.22 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 = 2.34 yr^{-1} from Pauly 1989 in Froese and Pauly 2002) as well as in the Gulf of St. Lawrence (Q/B = 1.96 yr^{-1} from Waiwood et al. 1980; Q/B = 2.03 yr^{-1} from previous ecosystem models for the northern Gulf). Finally, we estimated a Q/B of 3.10 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 38–63 cm length size with corresponding mass values based on our length–mass relationships). Combining the different Q/B ratios resulted in a consumption range between 0.07 and 0.44 t km^{-2} yr^{-1}. Based on the previous mean production (0.04 t km^{-2} yr^{-1}) for large cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.15 and 0.45 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1 or Q ≥ B x 1), we used 0.09 t km^{-2} yr^{-1} instead of the lowest value (0.07 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 0.09 and 0.45 t km^{-2} yr^{-1}, corresponding to a mean

consumption of 0.27 ± 0.25 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.18 ± 0.05 t km^{-2} yr^{-1}, representing a Q/B of 1.91 yr^{-1}.

Two studies were first 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 3.25 yr^{-1} (Waiwood et al. 1980) and 2.56 yr^{-1} (Grundwald and Koster 1994). Based on previous ecosystem models for the northern Gulf, we estimated another mean Q/B ratio of 3.38 yr^{-1}. Finally, we estimated a Q/B of 7.65 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 8–33 cm length size with corresponding mass values based on our length–mass relationships). This corresponded to a consumption range between 0.06 and 0.61 t km^{-2} yr^{-1} combining the different Q/B ratios. Based on the previous mean production (0.03 t km^{-2} yr^{-1}) for small cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.11 and 0.34 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.06 and 0.61 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.28 ± 0.25 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.26 ± 0.09 t km^{-2} yr^{-1}, representing a Q/B of 5.37 yr^{-1}.

Diet composition

Stomach content data for large cod from the lower Estuary were available, but were few in number from 2000 to 2007 (n = 12) and for the studied period (n = 59) (D. Chabot, unpublished data). These two diets were used to construct the upper and lower limit constraints in inverse modelling for this group. The most important prey items of large cod were shrimp, small demersal feeders (e.g., snakeblenny *Lumpenus lampretaeformis*), and capelin (83.9% of the diet; Table 8).

For small cod, we also used the diets for the 2000–2007 (n = 5) and 2008–2010 (n = 72) periods to constrain inverse models (D. Chabot, unpublished data). The most important prey items of small cod were shrimp, other macrozooplankton, and large hyperiid amphipods (79.1% of the diet; Table 8).

Table 8. Diet compositions (%) of large and small cod used in modelling. Est: diet estimates from 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.

Prey	Large cod (> 35 cm)					Small cod (≤ 35 cm)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders	1.6	1.4	**0.0**	**2.0**	1.3					
Skates										
Atlantic halibut										
Redfish										
Black dogfish										
White hake										
Large demersals	4.4	3.7	**0.0**	**5.2**	0.0	2.7	2.1	**0.0**	**2.9**	0.0
Small demersals	13.9	11.9	**0.0**	**16.8**	0.1	3.6	2.7	**0.0**	**3.9**	0.3
Capelin	10.6	9.0	**0.0**	**12.8**	7.4					
Large pelagics										
Herring										
Small pelagics	**0.5**	0.4	0.0	0.6	0.5					
Squid										
Shrimp	59.4	13.3	**56.2**	**75.0**	71.2	67.8	26.5	**32.8**	**70.2**	50.0
Small crabs	**2.1**	0.1	2.1	2.2	2.1	2.1	1.6	**0.0**	**2.2**	0.5
Echinoderms										
Molluscs	1.0	0.9	**0.0**	**1.2**	0.4					
Polychaetes						**0.3**	0.2	0.0	0.3	0.3
Other bent. inver.	**0.2**	0.1	0.0	0.2	0.2	4.9	3.7	**0.0**	**5.2**	2.3
Large euphausiids	1.6	2.2	**1.1**	**4.2**	2.1	4.0	10.7	**3.0**	**18.2**	12.3
Small euphausiids	1.4	2.6	**0.8**	**4.5**	3.3	3.3	11.9	**2.2**	**19.0**	11.3
Large hyperiid amp.	0.4	1.8	**0.0**	**2.5**	2.1	5.1	7.8	**4.4**	**15.3**	12.2
Other macrozoop.	2.8	7.5	**1.0**	**11.6**	9.4	6.3	6.3	**5.7**	**14.7**	10.8
Surface mesozoop.						**0.0**	0.0	0.0	0.0	0.0
Deep mesozoop.						**0.0**	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		61.3	138.7	100.0	100.0		48.0	152.0	100.0
TRN	13					12				

Greenland halibut (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)

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 2010c). Greenland halibut are generally found in the channels of the Gulf of St. Lawrence at depths ranging between 130 and 500 m. Juveniles dominate the Estuary and north of Anticosti. Spawning takes place primarily in winter, from January to March (DFO 2010c).

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 declined at the beginning of the 1990s and are now around 3,000–4,000 t (DFO 2010c).

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 (size of pre-recruits to the fishery: 40–43 cm; DFO 2010c). Greenland halibut greater than 40 cm in length are equivalent to fish aged six years and older (Brodie 1991).

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 2008–2010 period. Length-frequency data from each year were extrapolated to the whole 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 2008–2010 period of 6,416 t or 1.00 t km^{-2} (SD = 0.12 t km^{-2}; range = 0.87–1.11 t km^{-2}) and 10,813 t or 1.69 t km^{-2} (SD = 0.14 t km^{-2}; range = 1.57–1.84 t km^{-2}) for large and small Greenland halibut, respectively.

Catch

According to the ZIFF databases, the mean annual landing of large Greenland halibut during the 2008–2010 period was 315 t or $4.82 \times 10^{-2} \pm 1.14 \times 10^{-3}$ t km^{-2} yr^{-1}. For the small Greenland halibut group, a by-catch value from the shrimp and Greenland halibut fisheries was estimated at 8 t or $1.29 \times 10^{-3} \pm 2.93 \times 10^{-4}$ t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice Lamontagne Institute, unpublished data). The inverse solution estimated catch values of $4.84 \times 10^{-2} \pm 4.79 \times 10^{-4}$ and $1.27 \times 10^{-3} \pm 1.55 \times 10^{-4}$ t km^{-2} yr^{-1}, respectively, for large and small Greenland halibut groups.

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 = 0.33 yr^{-1}) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 66 cm along with a water temperature of 3°C (DFO surveys; unpublished data). When the biomass and catch values were used, we obtained a production range of 0.34 to 0.42 t km^{-2} yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.19 yr^{-1} (production range: 0.17 to 0.21 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.17 to 0.42 t km^{-2} yr^{-1} (mean: 0.28 ± 0.11 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.26 ± 0.04 t km^{-2} yr^{-1}, representing a P/B of 0.26 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. When the biomass and catch values were used, we obtained a production range of 0.63 to 1.10 t km^{-2} yr^{-1}. We obtained another production range of 0.51 to 0.59 t km^{-2} yr^{-1} based on a mean P/B of 0.32 yr^{-1} from previous ecosystem models for the northern Gulf. The resulting lower and upper production limits were 0.51 and 1.10 t km^{-2} yr^{-1}, corresponding to a mean production of 0.74 ± 0.22 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.52 ± 0.02 t km^{-2} yr^{-1}, representing a P/B of 0.31 yr^{-1}.

Consumption

A Q/B ratio (1.66 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 (2.40 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish having a mean mass of 693.72 g and a mean length of 42.8 cm (mean characteristics of the large Greenland halibut group) at 3ºC (DFO, groundfish survey database, unpublished data). We estimated a Q/B of 1.10 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 43–73 cm length size with corresponding mass values based on our length–mass relationships). Based on previous ecosystem models for the northern Gulf, we estimated another mean Q/B ratio of 1.05 yr^{-1}. When the biomass values and the previous Q/B ratios were used, we obtained a consumption range of 0.91 to 2.67 t km^{-2} yr^{-1} for large Greenland halibut. Based on the previous mean production (0.28 t km^{-2} yr^{-1}) for large Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.95 and 2.85 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.91 and 2.85 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.84 ± 1.06 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.90 ± 0.04 t km^{-2} yr^{-1}, representing a Q/B of 0.90 yr^{-1}.

Q/B values for small Greenland halibut were obtained from five different sources. Using the mean daily consumption of 5-year-old Greenland halibut (< 40 cm) (Chumakov and Podrazhanskaya 1986), the Q/B ratio was 4.43 yr^{-1}. A Q/B estimate of 3.20 yr^{-1} was obtained from FishBase (Froese and Pauly 2002) for fish having a mean mass of 169.27 g and a mean length of 25.4 cm (mean characteristics of the small Greenland halibut group) at 3ºC (DFO,

groundfish survey database, unpublished data). A third estimate (Q/B: 2.66 yr^{-1}) was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a). We estimated a Q/B of 5.09 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 18–38 cm length size with corresponding mass values based on our length–mass relationships). Finally, we estimated another mean Q/B ratio of 1.38 yr^{-1} based on previous ecosystem models for the northern Gulf. When the minimum and maximum biomass values and the previous Q/B ratios were used, we obtained a consumption range of 2.16 to 9.36 t km^{-2} yr^{-1} for small Greenland halibut. Based on the previous mean production (0.74 t km^{-2} yr^{-1}) for small Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.69 and 11.03 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 1.69 and 11.03 t km^{-2} yr^{-1}, corresponding to a mean consumption of 6.06 ± 4.83 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.74 ± 0.16 t km^{-2} yr^{-1}, representing a Q/B of 1.03 yr^{-1}.

Diet composition

Stomach content data for large Greenland halibut from the lower Estuary were available, but were few in number for the studied period (n = 40) (D. Chabot, unpublished data). We also used data for the 2000–2007 period (n = 563) in the study area to construct the upper and lower limit constraints in inverse modelling (D. Chabot, unpublished data). The most important prey items were small demersals (e.g., fourbeard rockling, Atlantic soft pout), shrimp, large demersals (e.g., marlin-spike, lycodes spp.), and small pelagics (72.9% of the diet; Table 9).

For small Greenland halibut, we used the stomach content data for the 2000–2007 (n = 902) and 2008–2010 (n = 209) periods from the lower Estuary to constrain the models (D. Chabot, unpublished data). The most important prey items were other macrozooplankton, shrimp, capelin, large hyperiid amphipods, and small demersals (e.g., Atlantic soft pout) (81.3% of the diet; Table 9).

Table 9. Diet compositions (%) of large and small Greenland halibut used in modelling. Est: diet estimates from 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.

Prey	Large Greenland halibut (> 40 cm)					Small Greenland halibut (≤ 40 cm)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	4.2	3.2	**0.0**	**4.5**	2.0	2.7	2.4	**0.0**	**3.3**	0.0
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Atlantic halibut										
Redfish	4.5	3.4	**0.0**	**4.8**	0.3					
Black dogfish										
White hake										
Large demersals	12.1	3.5	**6.7**	**16.6**	10.7	5.5	9.2	**0.5**	**16.1**	0.5
Small demersals	34.9	8.3	**27.2**	**45.8**	29.1	11.3	7.2	**6.4**	**19.6**	6.4
Capelin	6.1	4.6	**0.0**	**6.5**	6.5	16.2	4.0	**15.1**	**20.8**	19.7
Large pelagics										
Herring										
Small pelagics	8.1	6.1	**0.0**	**8.6**	1.4	2.8	1.5	**1.2**	**3.3**	1.2
Squid										
Shrimp	17.9	14.4	**16.6**	**37.0**	37.0	17.7	11.3	**14.7**	**30.7**	28.2
Small crabs	**0.8**	0.6	0.0	0.8	0.8					
Echinoderms	**0.1**	0.0	0.1	0.1	0.1	0.2	0.7	**0.0**	**1.0**	0.7
Molluscs	**0.8**	0.6	0.0	0.8	0.8	**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 euphausiids	1.0	0.8	**0.0**	**1.1**	1.1	4.0	1.7	**2.0**	**4.4**	4.2
Small euphausiids	0.8	0.6	**0.0**	**0.9**	0.9	3.5	1.8	**1.5**	**4.0**	3.8
Large hyperiid amp.	1.3	1.0	**0.0**	**1.4**	1.4	15.3	10.9	**2.7**	**18.2**	12.7
Other macrozoop.	7.5	5.3	**0.5**	**8.0**	7.9	20.9	16.1	**2.3**	**25.2**	22.7
Surface mesozoop.										
Deep mesozoop.										
Phytoplankton										
Detritus										
Total	100.0		51.1	137.0	100.0	100.0		46.5	146.5	100.0
TRN	16					14				

<u>American plaice</u>

Background

American plaice (*Hippoglossoides platessoides*) 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. 2001). It has been exploited in NAFO divisions 4RST 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. However, yearly landings have since declined to around 100 t in recent years.

Biomass

Annual biomass estimates for American plaice were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. Mean biomass was estimated at 1,160 t or 0.18 t km^{-2} (SD = 0.02 t km^{-2}; range: 0.17–0.21 t km^{-2}) for American plaice.

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 15.2 t or 2.33 x 10^{-3} ± 3.15 x 10^{-4} t km^{-2} yr^{-1} for American plaice. These landings included by-catch values from the shrimp and Greenland halibut fisheries of 2.4 t or 3.68 x 10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 2.30 x 10^{-3} ± 1.50 x 10^{-4} t km^{-2} yr^{-1} for American plaice.

Production

Direct estimates of total mortality (Z) were available for American plaice. A Z of 0.54 (and then A = P/B = 0.42 yr^{-1} according to Ricker 1980) was estimated for American plaice in the southern Gulf (MPO 2008). Based on previous ecosystem models for the northern Gulf, we estimated another mean P/B ratio of 0.42 yr^{-1} while Bundy (2004) estimated a value of 0.23 yr^{-1} for the eastern Scotian Shelf. When the biomass and catch values were used, we obtained production ranges of 0.04 to 0.09 t km^{-2} yr^{-1}. Production was also estimated by multiplying biomass by natural mortality (M) plus catch. Natural mortality was assumed at 0.22 yr^{-1} (Pitt 1982, FishBase with a maximal length of 53 cm along with a water temperature of 3°C; Froese and Pauly 2002) for American plaice. We obtained production ranges of 0.04 to 0.05 t km^{-2} yr^{-1} when the biomass and catch values were used. Combining the different methods resulted in a mean annual production of 0.06 ± 0.02 t km^{-2} yr^{-1} (range: 0.04–0.09 t km^{-2} yr^{-1}). The inverse

solution estimated a production for American plaice of 0.05 ± 0.01 t km^{-2} yr^{-1}, resulting in a P/B of 0.29 yr^{-1}.

Consumption

For American plaice, FishBase provided an initial Q/B estimate (Froese and Pauly 2002). The Q/B value obtained in this way was 3.50 yr^{-1} for American plaice having a mean mass of 110.36 g and a mean length of 20.3 cm (mean characteristics; DFO, groundfish survey database, unpublished data) at 3°C. 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 1.24 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 4.67 yr^{-1} (assuming that feeding is constant throughout the year). In the eastern Scotian Shelf, the Q/B ratio for American plaice was estimated at 1.20 yr^{-1} (Bundy 2004) while we obtained a Q/B ratio of 2.91 yr^{-1} based on previous ecosystem models for the northern Gulf. When the biomass values and the previous Q/B ratios were used, we obtained a consumption range of 0.20 to 0.98 t km^{-2} yr^{-1} for American plaice. Based on the previous mean production (0.06 t km^{-2} yr^{-1}) for American plaice and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.18 and 0.55 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.18 and 0.98 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.48 ± 0.37 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.23 ± 0.12 t km^{-2} yr^{-1} for American plaice, representing a Q/B of 1.26 yr^{-1}.

Diet composition

Diet data from the lower Estuary during the 2008–2010 period were unavailable for American plaice, so studies from other areas and time periods were used instead. We used the diet compositions found by Bundy (2004) for the eastern Scotian Shelf (1999–2000; n = 727), by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997) to construct the upper and lower limit constraints in inverse modelling. Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of American plaice were small euphausiids, other benthic invertebrates, polychaetes, large euphausiids, capelin, small pelagics, and other macrozooplankton (77.2% of the diet; Table 10).

Table 10. Diet composition (%) of American plaice used in modelling. Est: diet estimates from 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.

Prey	American plaice				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	**0.0**	0.0	0.0	0.1	0.0
Large Green. halibut					
Small Green. halibut	**0.0**	0.0	0.0	0.1	0.0
American plaice	**0.1**	0.0	0.0	0.1	0.1
Flounders	**0.1**	0.1	0.0	0.1	0.1
Skates					
Atlantic halibut					
Redfish	**0.0**	0.0	0.0	0.1	0.0
Black dogfish					
White hake					
Large demersals	**0.2**	0.3	0.0	0.5	0.2
Small demersals	0.9	1.4	**0.0**	**2.8**	0.0
Capelin	10.2	12.2	**0.0**	**25.8**	4.6
Large pelagics					
Herring					
Small pelagics	9.7	9.1	**0.0**	**26.8**	0.0
Squid	**0.0**	0.1	0.0	0.1	0.0
Shrimp	7.8	9.6	**0.0**	**18.8**	3.9
Small crabs	1.8	1.9	**0.0**	**5.6**	0.5
Echinoderms	7.7	4.3	**0.0**	**31.1**	13.9
Molluscs	4.0	2.5	**0.0**	**51.4**	15.8
Polychaetes	11.9	7.9	**0.0**	**21.0**	9.5
Other bent. inver.	12.9	1.6	**0.0**	**38.5**	16.0
Large euphausiids	11.4	8.8	**0.9**	**34.4**	16.4
Small euphausiids	13.0	10.0	**1.1**	**39.3**	9.1
Large hyperiid amp.	**0.3**	0.2	0.0	0.8	0.3
Other macrozoop.	8.2	6.3	**0.7**	**24.7**	9.8
Surface mesozoop.	**0.0**	0.0	0.0	0.2	0.0
Deep mesozoop.	**0.0**	0.0	0.0	0.9	0.0
Phytoplankton					
Detritus					
Total	100.0		2.7	322.9	100.0
TRN	22				

<u>Flounders (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)</u>

Background

In previous northern Gulf models, the flounder group consisted 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.

During the 2008–2010 period, the key species of the flounder group is witch flounder, mainly because of its high biomass (100% of total flounder biomass) and commercial significance. The other species were also present in the study area or the northern Gulf, but at other time periods and in fewer numbers.

Biomass

Annual biomass estimates for flounders were obtained using *PACES* to analyze research survey data from the whole area during the 2008–2010 period. Total biomass in the study area for witch flounder was directly computed with *PACES* (no catch for the other species in the studied period). Mean biomass was estimated at 1,383 t or 0.21 t km^{-2} (SD = 0.05 t km^{-2}; range: 0.15–0.25 t km^{-2}) for flounders.

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 1.5 t or $2.29 \times 10^{-4} \pm 3.37 \times 10^{-5}$ t km^{-2} yr^{-1} for flounders. These landings included mainly by-catch values from the shrimp and Greenland halibut fisheries of 1.4 t or 2.14×10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $2.27 \times 10^{-4} \pm 1.66 \times 10^{-5}$ t km^{-2} yr^{-1} for flounders.

Production

There was no information available on production or total mortality (Z) of flounders within the study area. Production was estimated by multiplying biomass by natural mortality (M) plus catch. Natural mortality of flounders was estimated at 0.20 yr^{-1} from FishBase with a maximal length of 52 cm along with a water temperature of 3°C (Froese and Pauly 2002). When the biomass and catch values were used, we obtained a production range of 0.03 to 0.05 t km^{-2} yr^{-1}.

Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.41 yr^{-1} for flounders (production range: 0.06 to 0.10 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.03 to 0.10 t km^{-2} yr^{-1} for flounders (production = 0.07 ± 0.03 t km^{-2} yr^{-1}). The production estimated by the inverse solution was 0.06 ± 0.01 t km^{-2} yr^{-1} (P/B = 0.30 yr^{-1}) for flounders.

Consumption

Consumption estimates for the flounder group (i.e., witch flounder) were derived from different sources (Table 11).

Table 11.   Q/B ratios (yr^{-1}) for flounders in different regions of the northwest Atlantic. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Witch flounder	3.70	FishBase: 80.83 g and 21.3 cm
	3.25	Laurinolli et al. (2004)[a]
All flounders	1.89	Previous northern Gulf ecosystems

[a]: Daily consumption values for 8–53 cm length size with corresponding mass values based on our length–mass relationships.

When the biomass values were used, this resulted in a total consumption range of 0.29 to 0.92 t km^{-2} yr^{-1}. Based on the previous mean production (0.07 t km^{-2} yr^{-1}) for flounders and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.22 and 0.66 t km^{-2} yr^{-1}, respectively. The resulting lower and upper consumption limits were thus 0.22 and 0.92 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.52 ± 0.33 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.26 ± 0.14 t km^{-2} yr^{-1} for flounders, representing a Q/B of 1.22 yr^{-1}.

Diet composition

Stomach content data for flounders from the lower Estuary were available, but were few in number for the studied period (n = 102) (D. Chabot, unpublished data). We also used data for the 2000–2009 period (n = 15) in the northern Gulf of St. Lawrence to construct the upper and lower limit constraints in inverse modelling (D. Chabot, unpublished data). The most important prey items were polychaetes and large euphausiids (78.4% of the diet; Table 12).

Table 12. Diet composition (%) of flounders used in modelling. Est: diet estimates from 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.

| Prey | Flounders | | | | |
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Herring					
Small pelagics					
Squid					
Shrimp	1.9	1.5	**0.0**	**2.2**	1.3
Small crabs					
Echinoderms					
Molluscs	**0.1**	0.1	0.1	0.1	0.1
Polychaetes	66.7	24.4	**62.2**	**96.7**	78.5
Other bent. inver.	2.9	1.9	**0.6**	**3.2**	1.4
Large euphausiids	11.7	9.5	**0.0**	**13.4**	8.4
Small euphausiids	2.4	1.9	**0.0**	**2.7**	1.4
Large hyperiid amp.	1.8	1.4	**0.0**	**2.0**	1.1
Other macrozoop.	4.9	3.4	**0.7**	**5.5**	3.0
Surface mesozoop.	2.5	1.6	**0.5**	**2.8**	1.9
Deep mesozoop.	5.2	3.1	**1.4**	**5.8**	3.0
Phytoplankton					
Detritus					
Total	100.0		65.4	134.6	100.0
TRN	10				

Skates (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

The skate group included mainly two species: the thorny skate (*Amblyraja radiata*), considered here as the key species for the group (84.3% of total skate biomass) and the smooth skate (*Malacoraja senta*; 10.8% of total skate biomass). Other skate species are often unidentified (4.9% of total skate biomass), and another species, the winter skate (*Leucoraja ocellata*), was also present in the studied area but at other time periods and in low numbers. 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.

Biomass

Annual biomass estimates for skates were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. Total biomass in the study area for each skate species was directly computed and results were summed. The mean biomass was estimated at 3,549 t or 0.55 t km^{-2} (SD = 0.08 t km^{-2}; range: 0.47–0.61 t km^{-2}) for skates.

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 19.7 t or 3.01 x 10^{-3} ± 8.68 x 10^{-4} t km^{-2} yr^{-1} for skates. These landings included mainly by-catch values from the shrimp and Greenland halibut fisheries of 19.3 t or 2.95 x 10^{-3} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 3.11 x 10^{-3} ± 3.38 x 10^{-4} t km^{-2} yr^{-1} for skates.

Production

There was no information available on production or total mortality (Z) of skates within the study area. Production was estimated by multiplying biomass by natural mortality (M) plus catch. Natural mortality was assumed to range between 0.21 yr^{-1} (Simon and Frank 1995), 0.24 yr^{-1} (FishBase for smooth skate with a maximal length of 53 cm along with a water temperature of 3°C; Froese and Pauly 2002), and 0.55 yr^{-1} (FishBase for thorny skate with a maximal length of 57 cm along with a water temperature of 3°C; Froese and Pauly 2002) for skates. When the

biomass and catch values were used, we obtained a production range of 0.10 to 0.34 t km^{-2} yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.27 yr^{-1} for skates (production range: 0.12 to 0.16 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.10 to 0.34 t km^{-2} yr^{-1} for skates (production: 0.18 ± 0.08 t km^{-2} yr^{-1}). The production value estimated by the inverse solution was 0.14 ± 0.03 t km^{-2} yr^{-1} (P/B = 0.25 yr^{-1}) for skates.

Consumption

For skates, consumption estimates were derived from different sources (Table 13).

Table 13. Q/B ratios (yr^{-1}) for skates in different regions of the northwest Atlantic. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Thorny skate	2.70	FishBase: 393.13 g and 28.1 cm
	2.37	Dolgov (1997)[a]
	2.87	Vinter (1989)
	5.67	Laurinolli et al. (2004)[b]
Smooth skate	3.00	FishBase: 220.22 g and 28.5 cm
	7.67	Laurinolli et al. (2004)[c]
All skates	1.29	Previous northern Gulf ecosystems

[a]: Estimated annual consumption from the Barents Sea (Dolgov 1997) was divided by mean biomass, resulting in an annual Q/B ratio of 2.37 yr^{-1} for our study area.
[b]: Daily consumption values for 13–58 cm length size with corresponding mass values based on our length–mass relationships.
[c]: Daily consumption values for 13–53 cm length size with corresponding mass values based on our length–mass relationships.

When the annual biomass values for skates and previous Q/B ratios were used, this resulted in a total consumption range of 0.60 to 4.68 t km^{-2} yr^{-1}. Based on the previous mean production (0.18 t km^{-2} yr^{-1}) for skates and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.60 and 1.79 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.60 and 4.68 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.92 ± 1.93 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.61 ± 0.04 t km^{-2} yr^{-1} for skates, representing a Q/B of 1.10 yr^{-1}.

Diet composition

Stomach content data for skates from the lower Estuary were available for the studied period (thorny skate, n = 68; smooth skate, n = 43; D. Chabot, unpublished data). Since the number of analyzed stomachs was low, we also used stomach content data from 2000 to 2007 (thorny skate, n = 49; smooth skate, n = 62; D. Chabot, unpublished data) to construct the upper and lower limit constraints in inverse modelling for this group. The different diet proportions of the overall diet were weighted by the biomass proportion of each skate species (87% and 13%, respectively, for thorny and smooth skates) in the study area. The most important prey items in the resulting diet of skates were shrimp, small demersals, small crabs, and large euphausiids (80.5% of the diet; Table 14).

Table 14. Diet composition (%) of skates used in modelling. Est: diet estimates from 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.

| Prey | Skates | | | | |
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals					
Small demersals	11.4	9.1	**6.1**	**18.9**	6.1
Capelin					
Large pelagics					
Herring					
Small pelagics	4.3	5.3	**0.0**	**7.5**	0.0
Squid					
Shrimp	49.6	14.1	**38.0**	**58.0**	53.0
Small crabs	10.1	2.9	**8.1**	**12.1**	8.6
Echinoderms	**0.0**	0.0	0.0	0.0	0.0
Molluscs	**0.4**	0.5	0.0	0.7	0.4
Polychaetes	0.9	1.5	**0.0**	**2.1**	1.6
Other bent. inver.	**0.4**	0.2	0.3	0.5	0.4
Large euphausiids	9.3	6.2	**5.3**	**14.1**	13.2
Small euphausiids	3.0	0.8	**2.5**	**3.7**	3.2
Large hyperiid amp.	**2.6**	0.3	2.4	2.8	2.6
Other macrozoop.	5.9	5.0	**3.0**	**10.0**	8.8
Surface mesozoop.	**0.9**	0.2	0.7	1.0	0.9
Deep mesozoop.	**1.2**	0.6	0.7	1.5	1.2
Phytoplankton					
Detritus					
Total	100.0		67.0	133.0	100.0
TRN	14				

Atlantic halibut (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

Atlantic halibut (*Hippoglossus hippoglossus*) of NAFO divisions 4RST can be found throughout the Estuary and Gulf of St. Lawrence. In the northern Gulf, the species is more abundant in the Esquiman, Laurentian, and Anticosti channels, at depths of 200 m and greater (DFO 2009). In the southern Gulf, the greatest concentrations occur in shallower waters (at depths less than 100 m), near the Miscou Bank, north of Prince Edward Island, northwest of Cape Breton, and around the Îles-de-la-Madeleine. Atlantic halibut grows fast. The annual average growth rate in the Gulf was evaluated at 7.5–8.5 cm per year. Male and female growth rates are comparable. However, it was observed that females reach a larger maximum size than males. The size at sexual maturity for female halibut from the Gulf stock was recently measured at 130 cm (commercial size $\geq$81 cm) (DFO 2009). The diet of smaller halibut (<30 cm) is mostly made up of invertebrates, whereas larger size halibut are more piscivorous. Halibut landings, which were around 650 t in the early 1960s, hit a record low in 1982 at 91 t. Until 1995, they seldom exceeded the threshold of 300 t, which is equivalent to the TAC established in 1988. From 1996 to 2003, landings ranged between 230 and 320 t and then exceeded 400 t in 2004, and reached a level comparable to that of the early 1970s (500 t) in the whole 4RST area (DFO 2009).

Biomass

Annual biomass estimates for Atlantic halibut were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. The mean biomass was estimated at 462 t or 0.07 t km^{-2} (SD = 0.04 t km^{-2}; range: 0.05–0.12 t km^{-2}) for Atlantic halibut.

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 4.6 t or $7.11 \times 10^{-4} \pm 1.65 \times 10^{-4}$ t km^{-2} yr^{-1} for Atlantic halibut. These landings included by-catch values from the shrimp and Greenland halibut fisheries of 1.8 t or 2.81×10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $7.15 \times 10^{-4} \pm 7.45 \times 10^{-5}$ t km^{-2} yr^{-1} for Atlantic halibut.

Production

There was no information available on production or total mortality (Z) of Atlantic halibut within the study area. Production was estimated by multiplying biomass by natural mortality (M) plus catch. Natural mortality was assumed to be 0.17 yr^{-1} for Atlantic halibut (FishBase with a

maximal length of 135 cm along with a water temperature of 3°C; Froese and Pauly 2002). When the biomass and catch values were used, we obtained a production range of 0.009 to 0.021 t km^{-2} yr^{-1} for Atlantic halibut (production: 0.013 ± 0.006 t km^{-2} yr^{-1}). The production value estimated by the inverse solution was 0.014 ± 0.005 t km^{-2} yr^{-1} (P/B = 0.19 yr^{-1}).

Consumption

For Atlantic halibut, FishBase provided an initial Q/B estimate (Froese and Pauly 2002) of 1.50 yr^{-1} for Atlantic halibut having a mean mass of 5,836.00 g and a mean length of 68.4 cm (mean characteristics; DFO, groundfish survey database, unpublished data) at 3°C. We estimated another Q/B of 3.25 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 28–68 cm length size with corresponding mass values based on our length–mass relationships). When the biomass values and the two previous Q/B ratios were used, we obtained a consumption range of 0.07 to 0.38 t km^{-2} yr^{-1} for Atlantic halibut. Based on the previous mean production (0.013 t km^{-2} yr^{-1}) for Atlantic halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.04 and 0.13 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1 or Q ≥ B x 1), we used 0.07 t km^{-2} yr^{-1} instead of the lowest value (0.04 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were thus 0.07 and 0.38 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.23 ± 0.22 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.07 ± 0.00 t km^{-2} yr^{-1} for Atlantic halibut, representing a Q/B of 1.01 yr^{-1}.

Diet composition

Stomach content data for Atlantic halibut from the lower Estuary were available, but were few in number for 2000 to 2007 (n = 23) and for the studied period (n = 11) (D. Chabot, unpublished data). We used these two diets to construct the upper and lower limit constraints in inverse modelling for this group. The most important prey items of Atlantic halibut were herring, small demersal feeders, and large demersal feeders (e.g., Lycodes spp.) (74.2% of the diet; Table 15).

Table 15. Diet composition (%) of Atlantic halibut used in modelling. Est: diet estimates from 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.

| Prey | Atlantic halibut | | | | |
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut	7.7	6.3	**1.7**	**10.6**	10.6
American plaice					
Flounders					
Skates	6.5	14.2	**0.0**	**20.1**	20.1
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals	15.4	5.9	**12.7**	**21.0**	14.3
Small demersals	14.2	7.2	**10.9**	**21.0**	11.5
Capelin					
Large pelagics					
Herring	44.7	24.7	**21.0**	**56.0**	21.3
Small pelagics					
Squid					
Shrimp	4.2	4.8	**2.0**	**8.8**	8.8
Small crabs	1.1	2.1	**0.2**	**3.1**	3.1
Echinoderms					
Molluscs	1.6	1.7	**0.0**	**2.3**	2.3
Polychaetes					
Other bent. inver.	3.5	3.7	**0.0**	**5.2**	4.7
Large euphausiids	1.1	2.3	**0.0**	**3.3**	3.3
Small euphausiids					
Large hyperiid amp.					
Other macrozoop.	**0.1**	**0.1**	0.0	0.1	0.1
Surface mesozoop.					
Deep mesozoop.					
Phytoplankton					
Detritus					
Total	100.0		48.5	151.5	100.0
TRN	11				

Redfish (Claude Savenkoff and Denis Chabot; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

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 in 1995 in the Gulf of St. Lawrence (Gascon 2003). The different redfish species were aggregated in the present study since species identification is not feasable during the summer scientific surveys (Dutil et al. 2006).

Biomass

Annual biomass estimates for redfish were obtained using *PACES* software to analyze research survey data from the study area during the 2008–2010 period. The average annual biomass was estimated at 231 t or 0.04 t km^{-2} (SD = 0.02 t km^{-2}; range: 0.02–0.06 t km^{-2}) for redfish.

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 1.0 t or 1.59 x 10^{-4} t km^{-2} yr^{-1} for redfish (SD = 4.41 x 10^{-5} t km^{-2} yr^{-1}). These landings included mainly by-catch values from the shrimp and Greenland halibut fisheries of 0.9 t or 1.40 x 10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 1.65 x 10^{-4} ± 2.23 x 10^{-5} t km^{-2} yr^{-1} for redfish.

Production

Information on production and total mortality (Z) of redfish was lacking. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality (M) plus the catch (Allen 1971). Natural mortality (M) for redfish was assumed to range between 0.20 yr^{-1} (Bundy 2004) and 0.25 yr^{-1} (FishBase for a maximal length of 32 cm along with a water temperature of $3^{o}C$; Froese and Pauly 2002). When the biomass and catch values were used, we obtained a production range between 0.004 and 0.016 t km^{-2} yr^{-1}. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.16 yr^{-1} (production range: 0.003 to 0.010 t

km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.003 to 0.016 t km^{-2} yr^{-1} (mean: 0.007 ± 0.005 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.015 ± 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.42 yr^{-1} for redfish.

Consumption

FishBase was used to estimate the Q/B ratio of redfish assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in a Q/B ratio of 3.80 yr^{-1} for fish having a mean mass of 72.70 g and a mean length of 15.7 cm (mean characteristics; DFO, groundfish survey database, unpublished data). 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 6.00 yr^{-1} for fingerlings down to around 1.30 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 1.49 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, resulting in a Q/B ratio of 2.41 yr^{-1}. On the Newfoundland–Labrador Shelf, the Q/B ratio for redfish was estimated at 1.70 yr^{-1} (Pitcher et al. 2002) while we obtained a Q/B ratio of 1.09 yr^{-1} based on previous ecosystem models for the northern Gulf. Finally, we estimated a Q/B of 5.10 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 8–33 cm length size with corresponding mass values based on our length–mass relationships). When the biomass values and the previous Q/B ratios were used, we obtained a consumption range of 0.02 to 0.33 t km^{-2} yr^{-1} for redfish. Based on the previous mean production (0.007 t km^{-2} yr^{-1}) for redfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.02 and 0.07 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1 or Q ≥ B x 1), we used 0.04 t km^{-2} yr^{-1} instead of the lowest value (0.02 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 0.04 and 0.33 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.18 ± 0.20 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.08 ± 0.03 t km^{-2} yr^{-1} for redfish, representing a Q/B of 2.30 yr^{-1}.

Diet composition

Stomach content data for redfish from the lower Estuary were unavailable for the studied period. We used data for the 1993–1999 period in both the lower Estuary (n = 46) and the northern Gulf of St. Lawrence (n = 2393) to construct the upper and lower limit constraints in inverse modelling (D. Chabot, unpublished data). The most important prey items of the resulting diet of redfish were shrimp, other macrozooplankton, and capelin (77.6% of the diet; Table 16).

Table 16. Diet composition (%) of redfish used in modelling. Est: diet estimates from 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.

Prey	Redfish				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish	2.5	1.8	**0.0**	**2.5**	0.0
Black dogfish					
White hake					
Large demersals	1.7	1.2	**0.0**	**1.8**	0.0
Small demersals	1.9	1.4	**0.0**	**1.9**	0.0
Capelin	18.1	13.0	**0.0**	**18.4**	11.9
Large pelagics					
Herring					
Small pelagics	2.1	1.5	**0.0**	**2.2**	0.0
Squid					
Shrimp	36.6	14.2	**16.8**	**36.9**	23.0
Small crabs					
Echinoderms					
Molluscs	**0.0**	0.0	0.0	0.0	0.0
Polychaetes					
Other bent. inver.	1.0	0.7	**0.0**	**1.0**	0.3
Large euphausiids	3.3	14.8	**2.9**	**23.8**	16.0
Small euphausiids	2.4	17.6	**1.9**	**26.8**	18.1
Large hyperiid amp.	5.2	3.7	**0.0**	**5.3**	2.9
Other macrozoop.	23.0	6.9	**22.8**	**32.6**	26.8
Surface mesozoop.	1.0	0.7	**0.0**	**1.0**	0.7
Deep mesozoop.	1.3	0.9	**0.0**	**1.3**	0.1
Phytoplankton					
Detritus					
Total	100.0		44.4	155.6	100.0
TRN	14				

Black dogfish

Background

Black dogfish (*Centroscyllium fabricii*) is a small deep–dwelling shark with a short and heavily set body (Gascon 1996). They are distributed along the slopes of the Atlantic Ocean basin ranging from Greenland down to Cape Hatteras, possibly Florida and into the Gulf of Mexico (Kulka 2006). Black dogfish are a bathydemersal species resident in waters as shallow as 300 m but generally found in water deeper than 500 m. Black dogfish are concentrated in the Laurentian Channel, into Hermitage Channel, and near the St. Pierre Bank.

Within the Laurentian Channel, the relative abundance fluctuated at low levels during the 1970s and 1980s, increased rapidly and stabilized through the mid-1990s, after which it has declined and possibly became stable (Kulka 2006). Ovoviviparous (embryos develop inside eggs that are retained within the mother's body until they are ready to hatch), black dogfish exhibit a highly structured distribution with a degree of separation by life stage. Large pregnant females migrate to shallow waters in the Laurentian Channel where pupping occurs. The young migrate into deeper waters of the channel where as they mature, they migrate out of the Laurentian Channel in to the slope waters. They may migrate significant distances to the Labrador Shelf. Black dogfish are primarily by-catch in Greenland halibut, crab, redfish, monkfish, and witch flounder fisheries (Gascon 1996).

Biomass

Annual biomass estimates for black dogfish were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. The mean biomass was estimated at 872 t or 0.14 t km^{-2} (SD = 0.14 t km^{-2}; range = 0.02–0.29 t km^{-2}).

Catch

According to the ZIFF databases, the mean annual landing during the 2008–2010 period was 0.6 t or 9.29 x 10^{-5} t km^{-2} yr^{-1} for black dogfish (SD = 1.32 x 10^{-5} t km^{-2} yr^{-1}). These landings included mainly by-catch values from the Greenland halibut fishery of 0.6 t or 9.28 x 10^{-5} t km^{-2} yr^{-1} (B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 9.25 x 10^{-5} ± 7.54 x 10^{-6} t km^{-2} yr^{-1} for black dogfish.

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 black dogfish (M = 0.20 yr^{-1}) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 70 cm along with a water temperature of 3°C (DFO, groundfish survey database, unpublished data). When the biomass and catch values were used, we obtained a mean production of 0.028 ± 0.028 t km^{-2} yr^{-1} (range: 0.004–0.059 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.033 ± 0.013 t km^{-2} yr^{-1}, representing a P/B of 0.24 yr^{-1}.

Consumption

A Q/B ratio (2.20 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish having a mean mass of 1002.26 g and a mean length of 58.9 cm at 3ºC (DFO, groundfish survey database, unpublished data). When the annual biomass values and the previous Q/B ratio were used, we obtained a consumption range of 0.04 to 0.65 t km^{-2} yr^{-1} for black dogfish. Based on the previous mean production (0.028 t km^{-2} yr^{-1}) for black dogfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.09 and 0.28 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1 or Q ≥ B x 1), we used 0.14 t km^{-2} yr^{-1} instead of the lowest value (0.04 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were thus 0.14 and 0.65 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.39 ± 0.36 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.14 ± 0.00 t km^{-2} yr^{-1}, representing a Q/B of 1.02 yr^{-1}.

Diet composition

Diet data from the studied area during the 2008–2010 period were unavailable for black dogfish, so studies from other areas and time periods were used instead. We used the diet compositions estimated by González et al. (2007) for the divisions 3NO (The Grand Banks) and 3M (Flemish Cap) of the northwest Atlantic (see their Table 3). Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. Overall, the most important prey items of black dogfish, in percent mass of stomach content, were shrimp, other macrozooplankton (mainly Scyphozoa), small demersals, redfish, and other benthic invertebrates (90.7% of the diet; Table 17).

Table 17. Diet composition (%) of black dogfish used in modelling. Est: diet estimates from 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.

Prey	Black dogfish				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish	8.5	5.6	**4.4**	**12.3**	4.5
Black dogfish					
White hake					
Large demersals					
Small demersals	9.4	2.1	**7.7**	**10.7**	9.1
Capelin					
Large pelagics					
Herring					
Small pelagics	2.9	4.0	**0.0**	**5.6**	0.2
Squid	**1.8**	0.1	1.7	1.8	1.8
Shrimp	43.9	1.1	**42.5**	**44.0**	44.0
Small crabs					
Echinoderms	0.7	1.0	**0.0**	**1.5**	1.5
Molluscs					
Polychaetes	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.	5.4	7.3	**0.2**	**10.5**	10.5
Large euphausiids	1.8	0.8	**1.2**	**2.3**	2.3
Small euphausiids	2.1	0.9	**1.4**	**2.7**	2.7
Large hyperiid amp.	**0.0**	0.0	0.0	0.0	0.0
Other macrozoop.	**23.5**	0.5	22.8	23.6	23.5
Surface mesozoop.	**0.0**	0.0	0.0	0.0	0.0
Deep mesozoop.	**0.1**	0.1	0.0	0.1	0.1
Phytoplankton					
Detritus					
Total	100.0		81.8	115.1	100.0
TRN	11				

<u>White hake</u>

Background

White hake (*Urophycis tenuis*) is a large demersal fish that occurs in continental waters of the western Atlantic Ocean (Scott and Scott 1988). They occur from southern Labrador and the Grand Bank southward to North Carolina, occasionally straying to deep waters off Florida (Musick 1974). In the southern Gulf, white hake are largely found on soft bottom habitats with water temperatures of 5–11°C (DFO 2005). White hake are highly fecund, having several million eggs per female. In the southern Gulf, male and female white hake reach sexual maturity at different sizes (at about 41 cm and 44 cm respectively) and at ages of 2 to 5 years (DFO 2005). Spawning commences in the southern Gulf in early June and peaks in the second half of the same month (DFO 2005). It seems that there are at least two different stock components in the southern Gulf, one occupying shallow inshore areas in summer, principally the Northumberland Strait area (the "Strait" component) and another occupying deep water along the Laurentian Channel in summer (the "Channel" component) (DFO 2005).

White hake are exploited throughout their geographical range by seasonal fisheries, but the most important directed fishery for this species has occurred in the southern Gulf of St. Lawrence (NAFO division 4T) (DFO 2005). The fishery for white hake in NAFO division 4T has historically been the third or fourth most important groundfish fishery in the southern Gulf, with annual landings that averaged 5,675 t from 1960–1994 (DFO 2005). Directed fishing for white hake has been closed in the southern Gulf since 1995 and daily by-catch limits have been imposed on fisheries targeting other species (DFO 2005).

Biomass

Annual biomass estimates for white hake were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. The mean biomass was estimated at 78 t or 0.012 t km^{-2} (SD = 0.006 t km^{-2}; range = 0.006–0.018 t km^{-2}).

Catch

According to the ZIFF databases, the mean annual landing of white hake during the 2008–2010 period was 1.6 t or $2.49 \times 10^{-4} \pm 5.47 \times 10^{-5}$ t km^{-2} yr^{-1}. These landings included by-catch values from the shrimp and Greenland halibut fisheries of 1.0 t or 1.51×10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $2.56 \times 10^{-4} \pm 2.80 \times 10^{-5}$ t km^{-2} yr^{-1} for white hake.

Production

Direct estimates of total mortality (Z) were available for white hake. Hurlbut and Poirier

(2001) estimated Z values of 0.75 to 2 between 1995 and 2001 in the Southern Gulf of St. Lawrence while Bundy and Simon (2005) estimated that total mortality of white hake on the Scotian Shelf has increased to 1.0 in 1995. In the 2000s, total mortality ranged between 0.8 and 1.0, which represented the range used in the present study. The instantaneous mortality rates (Z) were then converted into real mortality rates (A: 0.55–0.63 yr^{-1}; $A = 1 - e^{-Z}$; Ricker 1980). Since we assumed a steady state (no year-to-year change in biomass), total mortality A is equal to the P/B ratio of white hake in 2008–2010 (Allen 1971). The annual production estimates ranged between 0.003 and 0.011 t km^{-2} yr^{-1}. We obtained other production estimates assuming that production was equivalent to biomass multiplied by natural mortality (M) plus catch. Natural mortality for white hake (M = 0.55 yr^{-1}) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 59 cm along with a water temperature of $3^{o}C$. When the biomass and catch values were used, we obtained a production range of 0.003 to 0.010 t km^{-2} yr^{-1}. Combining the two methods resulted in a production range of 0.003 to 0.011 t km^{-2} yr^{-1} (mean production: 0.007 ± 0.003 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.007 ± 0.003 t km^{-2} yr^{-1}, representing a P/B of 0.61 yr^{-1}.

Consumption

A Q/B ratio (3.10 yr^{-1}) was first estimated from Pauly (1989; see FishBase, Froese and Pauly 2002). We estimated another Q/B of 6.94 yr^{-1} from the study of Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy (daily consumption values for 18–58 cm length size with corresponding mass values based on our length–mass relationships). When the biomass values and the two previous Q/B ratios were used, we obtained a consumption range of 0.02 to 0.12 t km^{-2} yr^{-1} for white hake. Based on the previous mean production (0.007 t km^{-2} yr^{-1}) for white hake and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.02 and 0.07 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.02 and 0.12 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.06 ± 0.05 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.03 ± 0.01 t km^{-2} yr^{-1}, representing a Q/B of 2.41 yr^{-1}.

Diet composition

Diet data from the studied area during the 2008–2010 period were unavailable for white hake, so studies from other areas and time periods were used instead. We used the diet compositions estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s; white hake in large demersal feeders, n = 1,618) and by Bundy (2004) for the eastern Scotian Shelf (1980–1985; white hake in large demersal piscivores, n = 104). Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. Overall, the most important prey items of white hake, in percent mass of stomach content, were small pelagics and large pelagic feeders (75.3% of the diet; Table 18).

Table 18. Diet composition (%) of white hake used in modelling. Est: diet estimates from 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.

Prey	White hake				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	**0.3**	0.4	0.0	0.6	0.3
Large Green. halibut					
Small Green. halibut	**0.3**	0.4	0.0	0.7	0.3
American plaice	**0.6**	0.0	0.0	0.7	0.6
Flounders	**0.9**	0.4	0.0	1.2	0.9
Skates					
Atlantic halibut					
Redfish	6.4	9.0	**0.0**	**12.7**	3.1
Black dogfish					
White hake	**0.2**	0.3	0.0	0.4	0.2
Large demersals	3.2	4.5	**0.0**	**6.3**	3.0
Small demersals	1.9	1.2	**0.1**	**19.5**	7.9
Capelin					
Large pelagics	30.8	43.6	**0.0**	**61.6**	0.1
Herring	2.1	0.9	**0.0**	**2.9**	1.2
Small pelagics	44.5	58.7	**0.0**	**93.3**	4.5
Squid	0.5	0.6	**0.0**	**0.9**	0.0
Shrimp	5.1	4.2	**0.0**	**28.6**	24.7
Small crabs	**0.3**	0.5	0.0	71.3	0.3
Echinoderms					
Molluscs					
Polychaetes	2.2	3.0	**0.0**	**57.7**	52.1
Other bent. inver.	**0.8**	0.2	0.0	8.1	0.8
Large euphausiids	**0.0**	0.0	0.0	0.5	0.0
Small euphausiids	**0.0**	0.0	0.0	0.6	0.0
Large hyperiid amp.	**0.0**	0.0	0.0	0.0	0.0
Other macrozoop.	**0.0**	0.0	0.0	0.4	0.0
Surface mesozoop.					
Deep mesozoop.					
Phytoplankton					
Detritus					
Total	100.0		0.1	368.1	100.0
TRN	20				

<u>Large demersal feeders</u>

Background

     The large demersal feeders are mainly made up of large eelpouts (genus: Lycodes; 82.9% of total biomass), marlin-spike (*Nezumia bairdii*; 14.1%), common lumpfish (*Cyclopterus lumpus*; 1.7%), longfin hake (*Urophycis chesteri*; 1.2%), their juveniles, and other large demersal species also present in the studied area but few in number (0.1%). On average, Vahl's eelpout (*Lycodes vahlii*) and Laval eelpout (*Lycodes lavalaei*) accounted for 84% and 16%, respectively, of total biomass of large eelpouts. Information was very limited for most of these species in the studied area.

Biomass

     For the large demersal feeders, biomass was calculated from scientific research survey data using the *PACES* software from the study area during the 2008–2010 period. The biomasses of all species were summed to obtain an estimate for the group. The mean biomass for the large demersal feeders was estimated to be 397 t or 0.062 t km^{-2} (SD = 0.020 t km^{-2}; range: 0.047–0.085 t km^{-2}). In fact, based on initial inverse modelling runs (see the following production section), the previous values seemed too low to meet predator demands. Hence these values were increased for large demersal feeders (0.339 ± 0.413 t km^{-2}; range: 0.047–0.632 t km^{-2}).

Catch

     According to the ZIFF databases, the mean annual landing of large demersals was 8.9 t or 1.36 x 10^{-3} t km^{-2} yr^{-1} (SD = 1.13 x 10^{-4} t km^{-2} yr^{-1}) for the 2008–2010 period. These landings included mainly by-catch values from the shrimp and Greenland halibut fisheries of 8.6 t or 1.31 x 10^{-3} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 1.35 x 10^{-3} ± 5.63 x 10^{-5} t km^{-2} yr^{-1} for large demersal feeders.

Production

     Information on production and total mortality (Z) of 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 range between 0.27 and 0.36 yr^{-1} (Table 19). When the biomass and catch values for the large demersal group were used, we obtained a production range of 0.014 to 0.032 t km^{-2} yr^{-1}. Finally, we estimated a mean P/B ratio of 0.24 yr^{-1} for large demersals from previous ecosystem models in the northern Gulf (production range of 0.011 to 0.020 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.011 to 0.032 t km^{-2} yr^{-1} (mean production: 0.019 ± 0.007 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 0.192 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit (mean production: 0.102 ± 0.128 t km^{-2} yr^{-1}). The maximum production value was related to a biomass value of 0.632 t km^{-2} (see the previous biomass section). The inverse solution estimated a production of 0.188 ± 0.012 t km^{-2} yr^{-1}, representing a P/B of 0.55 yr^{-1} for large demersal feeders.

Table 19. Natural mortality (M; yr^{-1}) for different large demersal feeders estimated using FishBase (Froese and Pauly 2002). Maximum length (cm) observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	M	Maximum length
Longfin hake	0.32	35.0
Vahl's eelpout	0.30	38.0
Laval eelpout	0.27	44.0
Lumpfish	0.36	37.0
Marlin-spike	0.36	32.0

Consumption

For the large demersal feeders, consumption estimates were derived from different sources (Table 20).

Table 20. Q/B ratios (yr^{-1}) for large demersal feeders. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean mass and length observed during the DFO surveys (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Lumpfish	2.60	FishBase: 472.83 g and 18.4 cm
Longfin hake	3.10	FishBase: 186.20 g and 29.2 cm
Marlin-spike	4.80	FishBase: 21.90 g and 18.5 cm
Vahl's eelpout	(4.10)	FishBase: 51.14 g and 21.9 cm
	(1.86)	Laurinolli et al. (2004)[a]
	2.98[b]	Mean
Laval eelpout	4.40	FishBase: 35.22 g and 17.6 cm
Large demersal feeders	1.53	Previous northern Gulf ecosystems

[a]: Daily consumption values for the 13–38 cm length size with corresponding mass values based on our length–mass relationships.
[b]: Mean of Vahl's eelpout's values.

The Q/B ratios ranged between 1.53 and 4.80 yr^{-1} (Table 20). When the minimum and maximum biomass values for large demersals were used, total consumption ranged from 0.072 to

3.032 t km^{-2} yr^{-1}. Based on the previous mean production (0.102 t km^{-2} yr^{-1}) for large demersals and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.339 and 1.018 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.072 and 3.032 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.552 ± 2.093 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.725 ± 0.244 t km^{-2} yr^{-1} for large demersals, representing a Q/B of 2.14 yr^{-1}.

Diet composition

Stomach content data for large demersal feeders from the lower Estuary were available in 2001 only (large eelpouts, n = 32; D. Chabot, unpublished data). Since the number of analyzed stomachs was low, we also used stomach content data from the northern Gulf in 2001 (large eelpouts, n = 31; marlin-spike, n = 99; D. Chabot, unpublished data). Finally, we used the diet compositions estimated by Bowman et al. (2000) for the Scotian Shelf (longfin hake) and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; lumpfish) to construct the upper and lower limit constraints in inverse modelling for this group. Due to the lack of information on zooplankton species identification in Bowman et al. (2000) and Pitcher et al. (2002), the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species in the present analysis. The different diet proportions of the overall diet were weighted by the biomass proportion of each species (83%, 14%, 2%, and 1%, respectively, for large eelpouts, marlin-spike, lumpfish, and longfin hake) in the study area. The most important prey items of the resulting diet of large demersals were other macozooplankton, echinoderms, large euphausiids, molluscs,# and polychaetes (71.9% of the diet; Table 21).

Table 21. Diet composition (%) of large demersal feeders used in modelling. Est: diet estimates from 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.

| Prey | Large demersal feeders | | | | |
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals					
Small demersals					
Capelin	0.2	7.1	**0.0**	**10.0**	6.3
Large pelagics					
Herring	**0.0**	0.4	**0.0**	**0.6**	0.0
Small pelagics	**0.0**	0.4	**0.0**	**0.6**	0.0
Squid	**0.0**	0.1	**0.0**	**0.2**	0.0
Shrimp	1.1	4.0	**0.0**	**5.7**	3.9
Small crabs					
Echinoderms	16.1	15.2	**0.3**	**21.7**	4.4
Molluscs	12.7	21.4	**0.0**	**30.2**	7.7
Polychaetes	12.2	15.0	**0.0**	**21.2**	4.3
Other bent. inver.	9.0	8.5	**0.0**	**12.1**	3.7
Large euphausiids	12.7	15.8	**5.4**	**27.8**	12.6
Small euphausiids	8.2	18.5	**5.6**	**31.7**	24.1
Large hyperiid amp.	4.4	12.3	**0.0**	**17.5**	7.2
Other macrozoop.	18.1	15.5	**8.4**	**30.4**	20.8
Surface mesozoop.	2.4	3.2	**0.0**	**4.5**	3.1
Deep mesozoop.	2.7	3.9	**0.0**	**5.5**	1.2
Phytoplankton					
Detritus	0.0	0.7	**0.0**	**1.0**	0.6
Total	100.0		19.8	220.7	100.0
TRN	16				

Small demersal feeders

Background

The small demersal feeders include Atlantic hagfish (*Myxine glutinosa*; 54.8% of total biomass), fourbeard rockling (*Enchelyopus cimbrius*; 26.5%), Atlantic poacher (*Leptagonus decagonus*; 3.8%), daubed shanny (*Leptoclinus maculatus*; 3.3%), snakeblenny (*Lumpenus lampretaeformis*; 3.0%), Atlantic soft pout (*Melanostigma atlanticum*; 2.5%), snailfishes (Liparidae; 1.7%), Arctic staghorn sculpin (*Gymnocanthus tricuspis*; 1.6%), moustache sculpin (*Triglops murrayi*; 0.6%), shorthorn sculpin (*Myoxocephalus scorpius*; 0.3%), their juveniles, and other small demersal species also present in the studied area but few in number (1.9%). Unfortunately, little is known about these species and only scant information from the study area was available.

Biomass

For the small demersal feeders, biomass was calculated from scientific research survey data using the *PACES* software from the study area during the 2008–2010 period. The biomasses of all species were summed to obtain an estimate for the group. The mean biomass for the small demersal feeders was estimated to be 1,411 t or 0.22 t km^{-2} (SD = 0.08 t km^{-2}; range: 0.16–0.31 t km^{-2}). However, based on initial inverse modelling runs (see the following production section), the previous values seemed too low to meet predator demands. Hence these values were increased for small demersal feeders (0.58 ± 0.60 t km^{-2}; range: 0.16–1.00 t km^{-2}).

Catch

There is no direct fishery for species in the small demersal feeder group. However, by-catch information was available for the study period. The by-catch values from the shrimp and Greenland halibut fisheries were estimated at 13.9 t or 2.12 x 10^{-3} ± 6.86 x 10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 2.20 x 10^{-3} ± 2.99 x 10^{-4} t km^{-2} yr^{-1} for small demersal feeders.

Production

Information on production and total mortality (Z) of small 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 range between 0.23 and 0.63 yr^{-1} (Table 22). When the biomass and catch values for small demersal feeders were used, we obtained a production range of 0.039 to 0.195 t km^{-2} yr^{-1} for the group. Finally, we estimated a mean P/B ratio of 0.69 yr^{-1} for small demersals from previous ecosystem models in the northern

Gulf (production range of 0.110 to 0.211 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.039 to 0.211 t km^{-2} yr^{-1} (mean production: 0.115 ± 0.060 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 0.527 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit (mean production: 0.283 ± 0.345 t km^{-2} yr^{-1}). The maximum production value was related to a biomass value of 1.009 t km^{-2} (see the previous biomass section). The inverse solution estimated a production of 0.526 ± 0.002 t km^{-2} yr^{-1}, representing a P/B of 0.90 yr^{-1} for small demersal feeders.

Table 22. Natural mortality (M; yr^{-1}) for different small demersal feeders estimated using FishBase (Froese and Pauly 2002). Maximum length (cm) observed during the DFO survey (Nozères et al. 2010) and a temperature of 3°C were used.

Species	M		Maximum length	
Atlantic hagfish	0.25		48.1	
Shorthorn sculpin	0.23		41.1	
Fourbeard rockling	0.40		29.8	
Moustache sculpin	0.54		16.5	
Snakeblenny	0.37		40.2	
Arctic staghorn sculpin	0.34		23.2	
Daubed shanny	0.52		17.5	
Snailfish (Liparidae)	0.59[a]		15.4[a]	
Blacksnout seasnail		(0.65)		(12.9)
Variegated snailfish		(0.45)		(21.6)
Sea tadpole		(0.59)		(14.6)
Lowfin snailfish		(0.66)		(12.6)
Atlantic soft pout	0.63		13.3	
Atlantic poacher	0.45		21.5	

[a]: Mean of the values of each Liparidae species.

Consumption

Consumption estimates for small demersal feeders were derived from different sources (Table 23).

Table 23. Q/B ratios (yr^{-1}) for small demersal species. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (Nozères et al. 2010) and a temperature of 3°C were used.

Species	Q/B		Reference
Atlantic hagfish		(4.00)	FishBase: 57.24 g and 35.3 cm
	(2.59 and 4.79)		Martini et al. (1996)
	3.79[a]		Mean
Shorthorn sculpin	2.70		FishBase: 404.74 g and 28.0 cm
Fourbeard rockling	4.20		FishBase: 43.09 g and 20.8 cm
Moustache sculpin	5.50		FishBase: 11.58 g and 11.4 cm
Snakeblenny	4.70		FishBase: 24.27 g and 28.4 cm
Arctic staghorn sculpin	4.20		FishBase: 41.63 g and 14.8 cm
Daubed shanny	6.20		FishBase: 6.23 g and 12.6 cm
Atlantic soft pout	7.00		FishBase: 3.45 g and 10.5 cm
Atlantic poacher	5.10		FishBase: 17.55 g and 16.9 cm
Snailfish (Liparidae)	4.75[b]		Mean
Blacksnout seasnail		(4.70)	FishBase: 24.39 g and 9.3 cm
Variegated snailfish		(4.20)	FishBase: 45.88 g and 12.6 cm
Sea tadpole		(5.30)	FishBase: 14.39 g and 10.5 cm
Lowfin snailfish		(4.80)	FishBase: 21.74 g and 12.1 cm
Small demersal feeders	2.98		Previous northern Gulf ecosystems

[a]: Mean of Atlantic hagfish's values.
[b]: Mean of the values of each Liparidae species.

The Q/B ratios ranged between 2.70 and 7.00 yr^{-1} (Table 23). When the minimum and maximum biomass values for small demersals were used, total consumption ranged from 0.433 to 7.061 t km^{-2} yr^{-1}. Based on the previous mean production (0.283 t km^{-2} yr^{-1}) for small demersals and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.942 and 2.826 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.433 and 7.061 t km^{-2} yr^{-1}, corresponding to a mean consumption of 3.747 ± 4.687 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.061 ± 1.029 t km^{-2} yr^{-1} for small demersals, representing a Q/B of 3.53 yr^{-1}.

Diet composition

Stomach content data for small demersal feeders from the lower Estuary were available in 2001 only (Atlantic soft pout, n = 56; D. Chabot, unpublished data). Since the number of analyzed stomachs was low, we also used stomach content data from the northern Gulf in 2001 (Atlantic soft pout, n = 135; sculpins, n = 26; snailfish (Liparidae) n = 15; D. Chabot, unpublished data). All these diets were used to construct the upper and lower limit constraints in inverse modelling for this group. The different diet proportions of the overall diet were weighted

by the biomass proportion of each species (37%, 37%, and 25%, respectively, for Atlantic soft pout, sculpins, and snailfish) in the study area. The most important prey items of the resulting diet of small demersals were small crabs, other macrozooplankton, deep mesozooplankton, and shrimp (87.7% of the diet; Table 24).

Table 24. Diet composition (%) of small demersal feeders used in modelling. Est: diet estimates from 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 demersal feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish	0.5	1.0	**0.0**	**1.4**	0.0
Black dogfish					
White hake					
Large demersals					
Small demersals	0.6	1.1	**0.0**	**1.5**	0.0
Capelin					
Large pelagics					
Herring					
Small pelagics					
Squid					
Shrimp	9.4	25.4	**0.0**	**35.9**	15.3
Small crabs	32.5	61.9	**0.0**	**87.5**	0.3
Echinoderms					
Molluscs	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	0.4	0.8	**0.0**	**1.2**	0.5
Other bent. inver.	1.1	1.8	**0.0**	**2.5**	0.8
Large euphausiids	0.6	1.1	**0.0**	**1.5**	0.9
Small euphausiids	0.6	1.2	**0.0**	**1.7**	1.0
Large hyperiid amp.	3.1	4.7	**0.0**	**6.7**	2.4
Other macrozoop.	24.9	38.9	**0.0**	**55.0**	32.5
Surface mesozoop.	5.3	12.4	**0.0**	**17.5**	13.3
Deep mesozoop.	20.8	58.3	**0.0**	**82.5**	33.1
Phytoplankton					
Detritus					
Total	100.0		0.0	295.0	100.0
TRN	13				

Large pelagic feeders

Background

The large pelagic feeders generally include silver hake (*Merluccius bilinearis*), spiny dogfish (*Squalus acanthias*), pollock (*Pollachius virens*), and their juveniles. For the present study, the only abundant large pelagic feeder was silver hake (100% of biomass); based on the summer scientific surveys, the other two species were also present in the studied area, but at other time periods. However, commercial landings and by-catch values of spiny dogfish have been reported from the shrimp and Greenland halibut fisheries for the study period. Pelagic fishes are less vulnerable to bottom trawling. However, despite their low catchability, several species were regularly caught in the annual scientific research surveys (e.g., capelin, Atlantic mackerel, Atlantic herring, and other large and small pelagic groups) and could thus be included in our analyses.

Biomass

For the large pelagic feeders, biomass was calculated from scientific research survey data using the *PACES* software from the study area during the 2008–2010 period. The mean biomass for the large pelagic feeders (i.e., silver hake) was estimated to be 9 t or 0.001 t km^{-2} (SD = 0.001 t km^{-2}; range: 0.000–0.002 t km^{-2}).

Catch

According to the ZIFF databases, landings for large pelagic feeders were 1.5 t or 2.23×10^{-4} t km^{-2} yr^{-1} (SD = 4.10×10^{-5} t km^{-2} yr^{-1}). These landings included mainly by-catch values of both silver hake and spiny dogfish from the shrimp and Greenland halibut fisheries of 1.5 t or 2.23×10^{-4} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $2.28 \times 10^{-4} \pm 2.17 \times 10^{-5}$ t km^{-2} yr^{-1}.

Production

There was no information on specific production or total mortality (Z) values for the large pelagic feeders in the study area. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality (M) was estimated at 0.68 yr^{-1} for silver hake from FishBase (Froese and Pauly 2002) and a maximal length of 35.2 cm along with a water temperature of 3°C (Nozères et al. 2010). For spiny dogfish, a natural mortality of 0.17 yr^{-1} was obtained from FishBase (Froese and Pauly 2002) and a maximal length of 88.3 cm along with a water temperature of 3°C (Nozères et al. 2010). When the annual biomass and catch values for the large pelagic group were used, we obtained a production range of 3.0×10^{-4} to 0.002 t km^{-2} yr^{-1}. Finally, we estimated two P/B ratios for large

pelagics from previous ecosystem models in the northern Gulf (0.51 yr^{-1}) and for silver hake based on Bundy (2004) for the the Scotian Shelf (0.94 yr^{-1}) (production range: 1.5 x 10^{-4} to 0.002 t km^{-2} yr^{-1}). Combining the different methods resulted in a production range of 1.5 x 10^{-4} to 0.002 t km^{-2} yr^{-1} (mean production: 0.001 ± 0.001 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.001 ± 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.96 yr^{-1}.

Consumption

For the large pelagic feeders, consumption estimates were derived from different sources (Table 25).

Table 25. Q/B ratios (yr^{-1}) for large pelagic feeders.

Species	Q/B	Reference
Spiny dogfish	(4.77)	Pauly (1989)
	(4.75)	Wetherbee and Cortès (2004)
	(2.50)	Tanasichuck et al. (1991)
	(2.70)	Jones and Geen (1977)
	3.68[a]	Mean
Silver hake	(3.85 and 4.26)	Pauly (1989)
	(7.87)	Durbin et al. (1983)
	(11.32)	Edwards and Bowman (1979)
	(7.60)	Cohen and Grosslein (1981)
	(14.36)	Laurinolli et al. (2004)[b]
	(7.88)	Waldron (1988)
	8.16[c]	Mean
Large pelagic feeders	2.74	Previous northern Gulf ecosystems

[a]: Mean of spiny dogfish's values.
[b]: Daily consumption values for the 8–33 cm length size with corresponding mass values based on our length–mass relationships.
[c]: Mean of silver hake's values.

When the annual biomass values for the large pelagic group and the different Q/B ratios were used, total consumption ranged from 0.0007 to 0.034 t km^{-2} yr^{-1}. Based on the mean production (0.001 t km^{-2} yr^{-1}) for the large pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.003 and 0.010 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1 or Q ≥ B x 1), we used 0.0015 t km^{-2} yr^{-1} instead of the lowest value (0.0007 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 0.0015 and 0.034 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.018 ± 0.023 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.005 ± 0.002 t km^{-2} yr^{-1} for the large pelagic feeders, representing a Q/B ratio of 3.55 yr^{-1}.

Diet composition

Diet data from the studied area during the 2008–2010 period were unavailable for the large pelagic feeders (i.e., silver hake), so studies from other areas and time periods were used instead. We used the diet compositions estimated by Bundy (2004) for the eastern Scotian Shelf (1999–2000; large silver hake, n = 33; and small silver hake, n = 474) to construct the upper and lower limits used as constraints in inverse modelling for this group. Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of the resulting diet of large pelagics were capelin, small pelagics, shrimp, large and small euphausiids, and other macrozooplankton (85.1% of the diet; Table 26).

Table 26. Diet composition (%) of large pelagic feeders used in modelling. Est: diet estimates from 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.

Prey	Large pelagic feeders				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	0.9	0.8	**0.0**	**1.1**	0.1
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					
Atlantic halibut					
Redfish	**0.0**	0.0	0.0	0.0	0.0
Black dogfish					
White hake					
Large demersals	4.8	4.2	**0.0**	**5.9**	0.5
Small demersals	**0.1**	0.1	0.1	0.2	0.1
Capelin	30.3	24.7	**1.7**	**36.6**	20.5
Large pelagics	5.8	2.9	**2.4**	**6.5**	2.4
Herring	3.0	2.5	**0.2**	**3.7**	0.4
Small pelagics	16.7	7.0	**8.6**	**18.5**	9.2
Squid	**0.0**	0.1	0.0	0.2	0.0
Shrimp	14.7	38.6	**4.9**	**59.5**	41.8
Small crabs	**0.0**	0.0	0.0	0.0	0.0
Echinoderms					
Molluscs					
Polychaetes	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.	**0.1**	0.2	0.0	0.3	0.1
Large euphausiids	8.2	1.0	**7.9**	**9.4**	8.6
Small euphausiids	9.3	1.2	**9.0**	**10.7**	9.7
Large hyperiid amp.	**0.2**	0.0	0.2	0.2	0.2
Other macrozoop.	5.9	0.7	**5.7**	**6.7**	6.2
Surface mesozoop.					
Deep mesozoop.					
Phytoplankton					
Detritus					
Total	100.0		40.6	159.4	100.0
TRN	19				

<u>Capelin</u>

Background

Capelin (*Mallotus villosus*) is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. In the northeast Atlantic, capelin occur in waters near Russia (Barents Sea), Norway, Iceland, and Greenland. In the northwest Atlantic, it is found along the coasts of Labrador and Newfoundland, on the Grand Banks, and in the Estuary and Gulf of St. Lawrence (DFO 2008). Further south, capelin are also found in the eastern portion of the Scotian Shelf and occasionally in the Bay of Fundy.

Spawning is preceded by intense migration towards the coast and occurs inter-tidally on beaches and in deeper waters (DFO 2008). In the first case, capelin literally "roll" on the sandy or fine gravel beaches. Spawning essentially occurs at water temperatures of 6–10°C and is more predominant at night. The eggs, which are reddish in colour and approximately 1 mm in diameter, attach to the substrate. The incubation period varies according to ambient temperature, lasting for approximately 15 days at 10°C. Upon hatching, larvae quickly adopt a planktonic existence and remain near the surface until the arrival of winter. The most significant growth period occurs during the first year. Males are longer than females, with maximum lengths rarely above 210 mm. Capelin can spawn at age 2 years, and nearly 100% of males die following reproduction (DFO 2008).

The species is exploited commercially in some areas and is probably the most important forage fish of the northern Gulf of St. Lawrence (Savenkoff et al. 2007b).

Biomass

Annual biomass estimates of capelin were obtained from the scientific surveys for the 2008–2010 period using the *PACES* software. This resulted in a mean annual biomass estimate of 15,372 t or 2.395 ± 1.764 t km^{-2} (range: 0.745 to 4.253 t km^{-2}). However, note that the capelin biomass was only a gross approximation (catchability of capelin is unknown and likely variable from year to year for the bottom trawl used on the groundfish survey; in addition, the bottom trawl is very inefficient for estimating the relative abundance/biomass of pelagic species).

Catch

According to the ZIFF databases, the average annual capelin landing for the 2008–2010 period in the study area was 38.4 t or $5.87 \times 10^{-3} \pm 8.85 \times 10^{-4}$ t km^{-2} yr^{-1}. These landings included by-catch values from the shrimp fishery of 2.5 t or 3.81×10^{-4} (J. Gauthier and L. Savard, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $5.82 \times 10^{-3} \pm 4.99 \times 10^{-4}$ t km^{-2} yr^{-1} for capelin.

Production

Production of capelin was assumed to be equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was estimated to range between 0.60 yr^{-1}, to reflect the biology of this short-lived species (F. Grégoire, Maurice-Lamontagne Institute, pers. comm.) and in agreement with the study of Blanchard et al. (2002) in the Barents Sea, and 0.81 yr^{-1} (FishBase; Froese and Pauly 2002 with a maximal length of 17.0 cm according to Nozères et al. 2010 along with a water temperature of 3°C). When the biomass and catch values for capelin were used, we obtained a production range of 0.452 to 3.451 t km^{-2} yr^{-1}. Finally, we estimated a mean P/B ratio of 0.32 yr^{-1} from previous ecosystem models in the northern Gulf (production range of 0.240 to 1.368 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.240 to 3.451 t km^{-2} yr^{-1} (mean production: 1.386 ± 1.064 t km^{-2} yr^{-1}). The production value estimated by the inverse solution for capelin was 1.449 t km^{-2} yr^{-1} (P/B = 0.61 yr^{-1}).

Consumption

Consumption estimates of capelin were derived from different sources (Table 27).

Table 27. Q/B ratios (yr^{-1}) for capelin.

Species	Q/B	Reference
Capelin	5.90	FishBase: 8.53 g and 13.7 cm[a]
	13.69	Vesin et al. (1981)[b]
	6.33	Ajiad and Pushaeva (1991)[c]
	27.56	Panasenko (1981)
	4.70	Blanchard et al. (2002)
	6.63	Mendy and Buchary (2001)
	6.57	Wilson et al. (2006)
	6.88	Bundy (2004)
	1.47	Previous northern Gulf ecosystems
	8.86	Mean

[a]: When the Q/B ratio was estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO surveys (Nozères et al. 2010) and a temperature of 3°C were used.
[b]: Vesin et al. (1981) estimated that the daily ration was 5.00% body mass in summer and 2.50% body mass in winter in the Estuary and western Gulf of St. Lawrence, giving a mean of 3.75% of body mass per day or a mean annual Q/B ratio of 13.69 yr^{-1}.
[c]: Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.33 yr^{-1} from a summer study on Barents Sea capelin.

When the biomass values and the previous Q/B ratios were used, we obtained a consumption range of 1.092 to 117.215 t km^{-2} yr^{-1} for capelin. Based on the mean production (1.386 t km^{-2} yr^{-1}) for capelin and the minimum and maximum GE limits (10–30%), we obtained

consumption values of 4.621 and 13.863 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B $\geq$ 1 or Q $\geq$ B x 1), we used 2.395 t km^{-2} yr^{-1} instead of the lowest value (1.092 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 2.395 and 117.215 t km^{-2} yr^{-1}, corresponding to a mean annual consumption of 59.805 $\pm$ 81.190 t km^{-2} yr^{-1}. The consumption value estimated by the inverse solution was 10.303 $\pm$ 5.979 t km^{-2} yr^{-1} (Q/B = 4.30 yr^{-1}) for capelin.

Diet composition

Stomach content data for capelin from the lower Estuary were available but few in number in 2003 (n = 114; D. Chabot, unpublished data). Consequently, we also used data from 2003 for the northern Gulf (n = 1033) to construct the upper and lower limit constraints in inverse modelling (D. Chabot, unpublished data). The most important prey items were large and small euphausiids, mesozooplankton, large hyperiid amphipods, and other macrozooplankton (85.1% of the diet; Table 28).

Table 28. Diet composition (%) of capelin used in modelling. Est: diet estimates from 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.

| Prey | Capelin | | | | |
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals					
Small demersals					
Capelin	**0.0**	0.0	0.0	0.0	0.0
Large pelagics					
Herring					
Small pelagics	**0.0**	0.0	0.0	0.0	0.0
Squid					
Shrimp	**0.0**	0.0	0.0	0.0	0.0
Small crabs					
Echinoderms					
Molluscs					
Polychaetes	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.					
Large euphausiids	21.8	25.8	**10.1**	**46.7**	36.7
Small euphausiids	23.0	29.8	**11.1**	**53.3**	44.8
Large hyperiid amp.	8.1	7.7	**0.0**	**10.9**	5.6
Other macrozoop.	6.8	5.6	**0.0**	**7.9**	6.0
Surface mesozoop.	7.1	8.9	**0.0**	**12.6**	3.6
Deep mesozoop.	33.2	42.0	**0.0**	**59.4**	3.3
Phytoplankton					
Detritus					
Total	100.0		21.3	190.9	100.0
TRN	10				

<u>Herring</u>

Background

Atlantic herring (*Clupea harengus*) is a pelagic fish that frequents cold Atlantic waters. Its distribution in Canada extends from the coasts of Nova Scotia to the coasts of Labrador. It travels in tight schools in order to feed, to spawn near the coast, and to overwinter in deeper waters (DFO 2010d). The same herring return to the same spawning, feeding, and wintering sites year after year. This homing phenomenon is attributed to a learned behaviour with the recruitment of young year-classes in a population. At spawning, eggs attach themselves to the sea floor, forming a carpet a few centimetres thick. The egg incubation time and larval growth are linked to ambient environmental characteristics such as water temperature. Most herring reach sexual maturity at four years of age, at a length of about 25 cm (DFO 2010d).

There are two distinct herring populations in the Gulf of St. Lawrence, the west coast of Newfoundland population and the southern Gulf of St. Lawrence population. The two Gulf herring populations are characterized by two spawning stocks. Spring herring generally spawn in April and May, and fall herring in August and September/October. The spring-spawning stock of the west coast of Newfoundland 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). In the southern Gulf of St. Lawrence, the largest spring spawning areas are in Northumberland Strait and the largest fall spawning areas are in coastal waters off Miscou and Escuminac (N.B.), North Cape and Cape Bear (P.E.I.), and Pictou (N.S.) (DFO 2010e).

Biomass

Annual biomass estimates of herring were obtained from the scientific surveys for the 2008–2010 period using the *PACES* software. This resulted in a mean annual biomass estimate of 295 t or 0.046 ± 0.028 t km^{-2} (range: 0.018 to 0.074 t km^{-2}). However, note that the herring biomass, as for the other pelagic species, was only a gross approximation. In fact, 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 herring (0.094 ± 0.107 t km^{-2}; range: 0.018–0.169 t km^{-2}).

Catch

According to the ZIFF databases, the mean landing for Atlantic herring was 15.4 t or 2.35×10^{-3} t km^{-2} yr^{-1} (SD = 1.57×10^{-3} t km^{-2} yr^{-1}) during the 2008–2010 period. These landings included by-catch values from the shrimp and Greenland halibut fisheries of 3.2 t or 4.90×10^{-4} t

km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 2.36 x 10^{-3} ± 8.57 x 10^{-4} t km^{-2} yr^{-1}.

Production

For herring, production was first estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to range between 0.20 yr^{-1} (Grégoire et al. 2004) and 0.32 yr^{-1} (FishBase; Froese and Pauly 2002, with a maximal length of 35.5 cm according to Nozères et al. 2010, along with a water temperature of 3°C). When the biomass and catch values for herring were used, we obtained a production range of 0.006 to 0.027 t km^{-2} yr^{-1}. Finally, we estimated a mean P/B ratio of 0.34 yr^{-1} from previous ecosystem models in the northern Gulf (production range of 0.006 to 0.025 t km^{-2} yr^{-1}). Combining the two methods resulted in a production range of 0.006 to 0.027 t km^{-2} yr^{-1} (mean production: 0.015 ± 0.008 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 0.055 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit (mean production: 0.030 ± 0.034 t km^{-2} yr^{-1}). The maximum production value was related to a biomass value of 0.169 t km^{-2} (see the previous biomass section). The inverse solution estimated a production of 0.054 ± 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.58 yr^{-1}.

Consumption

Consumption estimates of herring were derived from different sources (Table 29).

Table 29. Q/B ratios (yr^{-1}) for herring.

Species	Q/B	Reference
Atlantic herring	4.59	Pauly (1989)
	2.80	Fetter and Davidjuka (1996)[a]
	13.69	Rudstam et al. (1992)[b]
	5.20	Varpe et al. (2005)
	4.84	Blanchard et al. (2002)
	4.72	Mendy and Buchary (2001)
	1.55	Previous northern Gulf ecosystems
	5.34	Mean

[a]: 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 2.80 yr^{-1}.
[b]: 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. During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.69 yr^{-1}.

When the minimum and maximum biomass and the Q/B values were used, total consumption ranged from 0.027 to 2.319 t km^{-2} yr^{-1}. Based on the mean production (0.030 t km^{-2} yr^{-1}) for herring and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.101 and 0.302 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B $\geq$ 1 or Q $\geq$ B x 1), we used 0.094 t km^{-2} yr^{-1} instead of the lowest value (0.027 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 0.094 and 2.319 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.206 $\pm$ 1.574 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.216 $\pm$ 0.104 t km^{-2} yr^{-1} for herring, representing a Q/B ratio of 2.31 yr^{-1}.

Diet composition

We used the diet composition estimated by Darbyson et al. (2003) in the southern Gulf, by Savenkoff et al. (2004c) for the southern Gulf (mid-1990s; n = 718), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997) to construct the upper and lower limits used as diet constraints in inverse modelling for this group. Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of the resulting diet of herring were deep and surface mesozooplankton, other macrozooplankton, and large and small euphausiids (94.2% of the diet; Table 30).

Table 30. Diet composition (%) of herring used in modelling. Est: diet estimates from 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.

Prey	Herring				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	**0.0**	0.1	0.0	0.1	0.0
Large Green. halibut					
Small Green. halibut					
American plaice	**0.0**	0.1	0.0	0.1	0.0
Flounders	**0.0**	0.1	0.0	0.1	0.0
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals	**0.0**	0.1	0.0	0.1	0.0
Small demersals	**0.0**	0.1	0.0	0.1	0.0
Capelin	1.1	1.9	**0.0**	**3.3**	2.2
Large pelagics	**0.0**	0.1	0.0	0.1	0.0
Herring	**0.1**	0.2	0.0	0.4	0.1
Small pelagics	**0.2**	0.3	0.0	0.6	0.2
Squid					
Shrimp	**0.2**	0.4	0.0	13.7	0.2
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.	3.3	5.8	**0.0**	**10.0**	7.4
Large euphausiids	9.4	8.4	**0.0**	**32.5**	21.9
Small euphausiids	10.7	9.5	**0.0**	**37.1**	25.8
Large hyperiid amp.	**0.2**	0.1	0.0	0.7	0.2
Other macrozoop.	7.5	4.9	**0.0**	**23.3**	12.0
Surface mesozoop.	11.7	4.5	**0.0**	**17.5**	15.1
Deep mesozoop.	54.9	21.0	**0.0**	**82.5**	14.2
Phytoplankton					
Detritus	**0.3**	0.6	0.0	1.0	0.3
Total	100.0		0.0	223.4	100.0
TRN	18				

Small pelagic feeders

Background

The small pelagic feeders include white barracudina (*Arctozenus risso*; 58.8% of total biomass), Arctic cod (*Boreogadus saida*; 38.7%), and sand lance (*Ammodytes* spp.; 2.5%). Based on the summer scientific surveys, other species (e.g., Atlantic argentine *Argentina silus*, Atlantic mackerel *Scomber scombrus*) were also present in the studied area, but at other time periods.

Biomass

For the small pelagic feeders, biomass was calculated from scientific research survey data using the *PACES* software from the study area during the 2008–2010 period. The annual biomasses of each species were summed to obtain an estimate for the group. The mean biomass for the small pelagic feeders was estimated to be 17 t or 0.003 t km^{-2} (SD = 0.003 t km^{-2}; range: 0.001–0.006 t km^{-2}). However, note that the small pelagic biomass, as for the other pelagic species, was only a gross approximation. In fact, 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 pelagics (0.038 ± 0.053 t km^{-2}; range: 0.001–0.075 t km^{-2}).

Catch

There is no direct fishery for species in the small pelagic group (ZIFF databases). By-catch values from the shrimp fishery were estimated at 4.0 t or 6.13 x 10^{-4} ± 6.11 x 10^{-4} t km^{-2} yr^{-1} (J. Gauthier and L. Savard, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of 6.55 x 10^{-4} ± 3.63 x 10^{-4} t km^{-2} yr^{-1}.

Production

Information on production and total mortality (Z) of small pelagic feeders 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 range between 0.37 and 0.85 yr^{-1} (Table 31). When the biomass and catch values for the small pelagic group were used, we obtained a production range of 0.001 to 0.006 t km^{-2} yr^{-1} (mean production: 0.002 ± 0.002 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 0.062 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit (mean production: 0.031 ± 0.044 t km^{-2} yr^{-1}). The maximum production value was related to a biomass value of 0.075 t km^{-2} (see the previous biomass section). The inverse solution estimated a production of 0.062 ± 0.000 t km^{-2} yr^{-1}, representing a P/B of 1.63 yr^{-1} for small pelagic feeders.

Table 31. Natural mortality (M; yr^{-1}) for different small pelagic feeders estimated using FishBase (Froese and Pauly 2002). Maximum length (cm) observed during the DFO survey (Nozères et al. 2010) and a temperature of 3°C were used.

Species	M		Maximum length	
White barracudina	0.37		28.0	
Arctic cod	0.79		18.8	
Sand lances	0.85[a]		15.7[a]	
Northern sand lance		(1.13)		(15.7)
American sand lance		(0.56)		(15.7)

[a]: Mean values of sand lance species.

Consumption

For the small pelagic feeders, consumption estimates were derived from different sources (Table 32).

Table 32. Q/B ratios (yr^{-1}) for small pelagic feeders. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (Nozères et al. 2010) and a temperature of 3°C were used.

Species	Q/B		Reference
White barracudina	5.60		FishBase: 19.10 g and 24.1 cm
Arctic cod		(5.60)	FishBase: 18.10 g and 12.7 cm
		(3.94)	Hop et al. (1997)[a]
		(2.96)	Previous 1985-1987 northern Gulf ecosystem
	4.17[b]		Mean
Sand lances		(4.80)	FishBase: 22.73 g and 9.1 cm
		(8.16)	Gilman (1994)[c]
		(5.69)	Previous 1985-1987 northern Gulf ecosystem
	6.22[d]		Mean

[a]: Mean daily rations (% body mass per day) of Arctic cod juveniles and adults were estimated from Canadian arctic waters during 1988–1990.
[b]: Mean of Arctic cod's values.
[c]: Daily rations (% body mass) of adults on Georges Bank from 1977 to 1986 throughout the year were averaged, resulting in a mean Q/B ratio of 8.16 yr^{-1}.
[d]: Mean of sand lance's values.

Using the minimum and maximum biomass values for each small pelagic species and summing individual consumption values, total consumption varied from 0.004 to 0.468 t km^{-2} yr^{-1}. Based on the mean production (0.031 t km^{-2} yr^{-1}) for the small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.105 and 0.315 t km^{-2} yr^{-1}. Assuming that this species would eat at least as much food as its biomass (Q/B $\geq$ 1 or Q $\geq$ B x 1), we used 0.038 t km^{-2} yr^{-1} instead of the lowest value (0.004 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were 0.038 and 0.468 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.253 $\pm$ 0.304 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.259 $\pm$ 0.091t km^{-2} yr^{-1} for the small pelagic feeders, representing a Q/B ratio of 6.81 yr^{-1}.

Diet composition

For small pelagic feeders, we used the diet composition estimated by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; sand lance, Arctic cod, small pelagics, and small mesopelagics) and by Bundy (2004) for the eastern Scotian Shelf (1999–2000; sand lance and small mesopelagics). Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed according to the biomass proportion of each zooplankton species in the present study. We also used stomach content data for white barracudina (n = 179) from the northern Gulf in 2001 (D. Chabot, unpublished data) to construct the upper and lower limit constraints in inverse modelling for this group. The most important prey items of the resulting diet of small pelagics were large and small euphausiids and deep mesozooplankton (77.1% of the diet; Table 33).

Table 33. Diet composition (%) of small pelagic feeders used in modelling. Est: diet estimates from 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.

Prey	Small pelagic feeders				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish	**0.0**	0.0	0.0	0.2	0.0
Black dogfish					
White hake					
Large demersals					
Small demersals					
Capelin	0.7	1.2	**0.0**	**3.8**	2.0
Large pelagics					
Herring					
Small pelagics	5.7	3.1	**0.0**	**9.1**	0.0
Squid	2.1	1.9	**0.0**	**4.0**	0.0
Shrimp	1.1	1.4	**0.0**	**13.4**	7.4
Small crabs					
Echinoderms	**0.0**	0.0	0.0	0.5	0.0
Molluscs					
Polychaetes					
Other bent. inver.					
Large euphausiids	31.8	20.4	**12.1**	**46.1**	25.2
Small euphausiids	25.8	8.6	**13.9**	**31.8**	25.5
Large hyperiid amp.	1.3	1.3	**0.3**	**2.2**	1.8
Other macrozoop.	7.1	7.4	**1.9**	**18.7**	11.8
Surface mesozoop.	4.9	3.6	**1.7**	**11.4**	5.6
Deep mesozoop.	19.5	21.6	**4.1**	**53.6**	20.6
Phytoplankton					
Detritus	**0.1**	0.1	0.0	4.0	0.1
Total	100.0		34.0	198.7	100.0
TRN	13				

Squid

Background

The squid are a composite group of all squid found in the study area. The most important in terms of biomass (100% for the study period) is the northern shortfin (also called short-finned) squid (*Illex illecebrosus*). This species is highly migratory and spends only part of the year within the study area. Distributed across a broad geographic area, *I. illecebrosus* is found in the northwest Atlantic Ocean between the Sea of Labrador and the Florida Straits (Roper et al. 1998). Throughout its range of commercial exploitation, from Newfoundland to Cape Hatteras, North Carolina, the population is considered to constitute a single stock (Dawe and Hendrickson 1998; Hendrickson and Holmes 2004).

Biomass

Annual biomass estimates for squid were obtained using *PACES* to analyze research survey data from the study area during the 2008–2010 period. The mean biomass was estimated at 0.4 t or 5.36×10^{-5} t km^{-2} (SD = 9.29×10^{-5} t km^{-2}) for squid. However, based on catch information and initial inverse modelling runs (see the following production section), the previous values seemed too low to meet predator demands. Hence these values were increased for squid (0.0012 ± 0.0015 t km^{-2}; range: 0.0001–0.0022 t km^{-2}).

Catch

There is no direct fishery for squid (ZIFF databases). A by-catch value from the shrimp fishery was estimated at 0.7 t or $1.07 \times 10^{-4} \pm 1.05 \times 10^{-5}$ t km^{-2} yr^{-1} (J. Gauthier and L. Savard, Maurice Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $1.07 \times 10^{-4} \pm 4.64 \times 10^{-6}$ t km^{-2} yr^{-1} for squid.

Production

There was no information available on production or total mortality (Z) of squid within the study area. Production was estimated by multiplying biomass by natural mortality (M) plus catch. Like many squid species, *I. illecebrosus* lives for less than one year and has a high natural mortality rate (Hendrickson and Holmes 2004). A value of 1.0 yr^{-1} was thus used for natural mortality. When the biomass and catch values were used, we obtained a production range of 0.0002 to 0.0004 t km^{-2} yr^{-1} for squid (production: 0.0003 ± 0.0001 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 0.0037 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit (mean production: 0.0020 ± 0.0025 t km^{-2} yr^{-1}). The maximum production value was related to a biomass value of 0.0022 t km^{-2} (see the previous biomass section). The

production value estimated by the inverse solution was 0.0036 ± 0.0001 t km^{-2} yr^{-1} (P/B = 3.11 yr^{-1}).

Consumption

We estimated a Q/B of 2.94 yr^{-1} from the study of Maurer and Bowman (1985) for the Gulf of Maine to Cape Hatteras for 1979 and 1980 (seasonal range: 0.6 to 6.6 yr^{-1} excluding the value of 19.4 yr^{-1} related to very low squid biomass). When the biomass values were used, we obtained a consumption range of 0.0003 to 0.0066 t km^{-2} yr^{-1} for squid. Based on the previous mean production (0.0020 t km^{-2} yr^{-1}) for squid and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.0066 and 0.0197 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.0003 and 0.0197 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.0100 ± 0.0137 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.0122 ± 0.0018 t km^{-2} yr^{-1} for squid, representing a Q/B of 10.36 yr^{-1}.

Diet composition

Diet data from the studied area during the 2008–2010 period were unavailable for squid, so studies from other areas and time periods were used instead. We used the diet compositions estimated by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; short-finned squid) and by Bundy (2004) for the eastern Scotian Shelf (1999–2000; short-finned squid) to construct the upper and lower limit constraints in inverse modelling for this group. Due to the lack of information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of squid were capelin, small pelagics, squid, small cod, euphausiids, and other macrozooplankton (82.5% of the diet; Table 34).

Table 34. Diet composition (%) of squid used in modelling. Est: diet estimates from 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.

Prey	Squid				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	11.4	14.2	**0.0**	**21.5**	6.7
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake	**0.2**	0.3	0.0	0.5	0.2
Large demersals	2.4	3.4	**0.0**	**4.9**	2.2
Small demersals	1.8	2.4	**0.1**	**3.5**	2.0
Capelin	18.0	25.4	**0.0**	**35.9**	31.1
Large pelagics	5.5	7.8	**0.0**	**11.0**	2.4
Herring	2.9	4.1	**0.0**	**5.8**	1.9
Small pelagics	14.9	1.3	**14.0**	**15.8**	14.8
Squid	14.0	15.7	**2.9**	**25.1**	3.0
Shrimp					
Small crabs	1.1	1.6	**0.0**	**2.3**	1.8
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large euphausiids	8.5	3.1	**6.2**	**10.7**	9.4
Small euphausiids	9.7	3.6	**7.1**	**12.2**	11.6
Large hyperiid amp.	**0.2**	0.1	0.1	0.2	0.2
Other macrozoop.	6.1	2.3	**4.5**	**7.7**	6.7
Surface mesozoop.	0.6	0.8	**0.0**	**1.2**	1.0
Deep mesozoop.	2.8	3.9	**0.0**	**5.5**	5.0
Phytoplankton					
Detritus					
Total	100.0		34.9	163.6	100.0
TRN	16				

Shrimp (Claude Savenkoff and Louise Savard; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

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 (55.1% of total shrimp biomass) and is fished commercially. The other species are pink glass shrimp (*Pasiphaea multidentata*; 27.5%), striped shrimp (*Pandalus montagui*; 15.4%), Arctic argid (*Argis dentate*; 1.3%), Greenland shrimp (*Eualus macilentus*; 0.8%), and several other shrimp species also found but less abundant in the study area. 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 2002).

Biomass

Annual biomass estimates for shrimp were obtained using PACES to analyze research survey data from the whole area during the 2008–2010 period. The annual biomasses of each species were summed to obtain an estimate for the group. The biomass was 14,930 t or 2.326 ± 0.295 t km^{-2} (range: 2.122–2.664 t km^{-2}).

Catch

The annual total landings of shrimp were 1,016 t or 1.56×10^{-1} t km^{-2} yr^{-1} (SD = 5.33×10^{-3} t km^{-2} yr^{-1}) from 2008 to 2010 (ZIFF databases). These landings included by-catch values from the shrimp fishery of 2.6 t or 3.94×10^{-4} t km^{-2} yr^{-1} (J. Gauthier and L. Savard, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated a catch value of $1.57 \times 10^{-1} \pm 2.53 \times 10^{-3}$ t km^{-2} yr^{-1} for shrimp.

Production

Production was assumed to be equivalent to biomass multiplied by natural mortality (M) plus the catch. Natural mortality of shrimp was estimated at 0.64 yr^{-1} (Fréchette and Labonté 1981). When the biomass and catch values for shrimp were used, we obtained a production range of 1.510 to 1.865 t km^{-2} yr^{-1}. Finally, we estimated a mean P/B ratio of 1.40 yr^{-1} from previous ecosystem models in the northern Gulf (production range of 2.968 to 3.725 t km^{-2} yr^{-1}). The two methods resulted in a production range of 1.510 to 3.725 t km^{-2} yr^{-1} (mean: 2.448 ± 0.926 t km^{-2} yr^{-1}). The inverse solution estimated a production of 2.639 ± 0.221 t km^{-2} yr^{-1} (P/B = 1.13 yr^{-1}) for the shrimp group.

Consumption

A mean Q/B ratio of 6.52 yr^{-1} was estimated from previous ecosystem models in the northern Gulf (consumption range of 13.848 to 17.381 t km^{-2} yr^{-1}). Also, based on the mean production (2.448 t km^{-2} yr^{-1}) and the minimum and maximum GE limits (10–30%), we obtained a consumption range of 8.161 to 24.484 t km^{-2} yr^{-1} for shrimp. The resulting lower and upper consumption limits were 8.161 and 24.484 t km^{-2} yr^{-1}, corresponding to a mean consumption of 15.969 ± 6.830 t km^{-2} yr^{-1}.The inverse solution estimated a consumption of 10.868 ± 3.003 t km^{-2} yr^{-1} (Q/B = 4.67 yr^{-1}).

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. Stomach content data for shrimp from the lower Estuary were also available but few in number from 2000 to 2007 (n = 21) and for the studied period (n = 38) (D. Chabot, unpublished data). Small euphausiids, mesozooplankton, and detritus were the main prey items. We used all these diets to construct the upper and lower limit constraints in inverse modelling for this group. Overall, the most important prey items of shrimp were detritus, mesozooplankton, small euphausiids, and other macrozooplankton (e.g., mysids, chaetognaths) (83.2% of the diet; Table 35).

Table 35. Diet composition (%) of shrimp used in modelling. Est: diet estimates from 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.

Prey	Shrimp				
	Mean	± SD[a]	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Atlantic halibut					
Redfish					
Black dogfish					
White hake					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Herring					
Small pelagics					
Squid					
Shrimp	**0.0**	0.0	0.0	0.0	0.0
Small crabs					
Echinoderms					
Molluscs					
Polychaetes	2.3	1.2	**0.0**	**8.9**	2.4
Other bent. inver.	0.8	1.1	**0.0**	**1.5**	0.1
Large euphausiids	3.7	0.7	**1.7**	**6.0**	4.7
Small euphausiids	19.0	20.1	**4.8**	**46.3**	26.5
Large hyperiid amp.					
Other macrozoop.	9.5	9.1	**3.0**	**24.4**	23.9
Surface mesozoop.	5.8	2.2	**4.2**	**8.4**	6.8
Deep mesozoop.	24.4	6.5	**19.8**	**34.3**	22.8
Phytoplankton	4.3	6.0	**0.0**	**8.5**	3.2
Detritus	30.4	31.3	**8.0**	**52.5**	9.5
Total	100.0		41.4	190.8	100.0
TRN	10				

Crabs (Claude Savenkoff, Jean Lambert, and Bernard Sainte-Marie; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

The snow crab (*Chionoecetes opilio*) represents the key species of the crab group, which also includes other species such as toad crabs (*Hyas* spp.) and rock crab (*Cancer irroratus*). In Canada, snow crab can be found from the southern tip of Nova Scotia to midway up Labrador as well as in the Estuary and Gulf of St. Lawrence. In the Gulf of St. Lawrence, males of commercial size live at depths of around 60–220 m, except during their moulting and reproductive period when they migrate to shallower waters (DFO 2010f). Snow crab recruitment is periodic or episodic and varies considerably over a cycle of 8 to 12 years (DFO 2010f).

Snow crabs were separated into small ($\leq$ 45 mm carapace width CW) and large (> 45 mm CW) categories based on large size-related differences in diet and vulnerability to predation (in particular cannibalism; crab prey ranged between 3.9 and 48.8 mm CW; Lovrich and Sainte-Marie 1997) and the ususal minimum carapace width of adult snow crabs (40 mm CW). Only large snow crabs are fished and landings consist almost exclusively of males $\geq$ 95 mm CW.

Biomass

Current snow crab assessments do not estimate the total biomass in the Estuary (high diversity and heterogeneity of habitats that are often hard to sample). Biomass for the crab groups was estimated using the abundance of snow crabs derived from a complete bottom trawl survey conducted on the north shore of the Estuary in 2007 and 2009 (DFO 2010f). 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, Maurice Lamontagne Institute, unpublished data). We used these two years of sampling data to estimate lower and upper limit values representing potential ranges of the biomass for the crab groups. We obtained a mean biomass estimate of 2.46 ± 0.08 t km^{-2} (range: 2.41–2.52 t km^{-2}) and 0.30 ± 0.38 t km^{-2} (range: 0.04–0.57 t km^{-2}) for large and small crabs, respectively.

Catch

For large crabs, the annual total landings in the study area were 1,330 t or 2.04×10^{-1} t km^{-2} yr^{-1} (SD = 7.70×10^{-4} t km^{-2} yr^{-1}) from 2008 to 2010 (ZIFF databases). These landings included by-catch values from the shrimp and Greenland halibut fisheries of 6.5 t or 1.00×10^{-3} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice Lamontagne Institute, unpublished data). No catch values have been recorded for small crabs. The inverse solution estimated a catch value of $2.04 \times 10^{-1} \pm 7.49 \times 10^{-4}$ t km^{-2} yr^{-1} for large crabs.

Production

Production was assumed to be equivalent to biomass multiplied by natural mortality (M) plus the catch. 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 0.69 to 0.71 t km^{-2} yr^{-1} for large crabs and 0.01 to 0.20 t km^{-2} yr^{-1} for small crabs. From previous ecosystem models in the northern Gulf, we estimated mean P/B ratios of 0.24 yr^{-1} and 0.59 yr^{-1}, respectively, for large and small crabs. Accordingly, we obtained two other production ranges of 0.58 to 0.61 t km^{-2} yr^{-1} and 0.02 to 0.33 t km^{-2} yr^{-1}, respectively, for large and small crabs. The two methods resulted in a production range of 0.58 to 0.71 t km^{-2} yr^{-1} for large crabs (mean: 0.65 ± 0.02 t km^{-2} yr^{-1}) and 0.01 to 0.33 t km^{-2} yr^{-1} for small crabs (mean: 0.14 ± 0.18 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.64 ± 0.02 t km^{-2} yr^{-1} (P/B = 0.26 yr^{-1}) for large crabs and 0.15 ± 0.08 t km^{-2} yr^{-1} (P/B = 0.49 yr^{-1}) for small crabs.

Consumption

For large and small crabs, 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 1.46 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 1.30 yr^{-1}. From previous ecosystem models in the northern Gulf, we estimated another Q/B of 2.29 yr^{-1} for large crabs and 5.09 yr^{-1} for small crabs. When the minimum and maximum biomass values for each crab group and the previous Q/B ratios were used, we obtained a consumption range of 3.14 to 5.77 t km^{-2} yr^{-1} for large crabs and 0.05 to 2.89 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%; Christensen and Pauly 1992), we obtained consumption ranges of 2.15 to 6.45 t km^{-2} yr^{-1} for large crabs and 0.47 to 1.82 t km^{-2} yr^{-1} for small crabs. The resulting consumption ranges were 2.15 to 6.45 t km^{-2} yr^{-1} (mean: 4.38 ± 2.06 t km^{-2} yr^{-1}) for large crabs and 0.05 to 2.89 t km^{-2} yr^{-1} (mean: 1.21 ± 1.26 t km^{-2} yr^{-1}) for small crabs. The inverse solution estimated a consumption of 2.20 ± 0.62 t km^{-2} yr^{-1} (Q/B = 0.89 yr^{-1}) for large crabs and 0.86 ± 0.61 t km^{-2} yr^{-1} (Q/B = 2.85 yr^{-1}) for small crabs.

Diet composition

For large crabs, diet data were available from baie Sainte-Marguerite (Lovrich and Sainte-Marie 1997); the main prey items were benthic invertebrates (molluscs, polychaetes, and others), shrimp, and small crabs. We also used the diet composition estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; large crabs > 95 mm CW) to construct the upper and lower limits used as constraints in inverse modelling for this group. Due to the lack of

information on zooplankton species identification, the diet proportions for large and small zooplankton from these studies were redistributed in the resulting diet according to the biomass proportion of each zooplankton species. The most important prey items of the resulting diet of large crabs were polychaetes, detritus, echinoderms, and molluscs (72.7% of the diet; Table 36).

For small crabs, we used the diet composition estimated by Lovrich and Sainte-Marie (1997) for baie Sainte-Marguerite. The main prey items were other benthic invertebrates, echinoderms, molluscs, detritus, and polychaetes (97.0% of the diet) (Table 36).

Table 36. Diet compositions (%) of large and small crabs used in modelling. Est: diet estimates from 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										
Atlantic halibut										
Redfish										
Black dogfish										
White hake										
Large demersals										
Small demersals	3.0	5.2	**0.0**	**18.2**	0.3	1.2	1.2	**0.0**	**2.5**	0.0
Capelin										
Large pelagics										
Herring										
Small pelagics										
Squid										
Shrimp	7.9	8.7	**2.0**	**33.3**	19.5	**0.0**	0.0	0.0	0.0	0.0
Small crabs	9.0	8.3	**0.1**	**44.5**	2.6	1.8	2.1	**0.0**	**5.1**	0.6
Echinoderms	17.6	11.6	**0.0**	**30.3**	16.2	23.6	11.0	**8.8**	**38.5**	21.8
Molluscs	17.2	4.6	**5.8**	**39.0**	14.2	16.8	12.2	**1.8**	**31.7**	22.3
Polychaetes	19.8	9.3	**5.6**	**30.3**	10.6	8.3	5.2	**2.5**	**15.4**	6.7
Other bent. inver.	5.7	5.7	**0.0**	**12.0**	10.5	36.6	24.2	**15.3**	**71.9**	33.4
Large euphausiids	**0.4**	0.4	0.0	0.7	0.4	**0.0**	0.0	0.0	0.0	0.0
Small euphausiids	**0.5**	0.4	0.0	0.8	0.5	**0.0**	0.0	0.0	0.0	0.0
Large hyperiid amp.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Other macrozoop.	**0.3**	0.3	0.0	0.5	0.3	**0.0**	0.0	0.0	0.0	0.0
Surface mesozoop.	**0.1**	0.1	0.0	0.2	0.1	**0.0**	0.0	0.0	0.0	0.0
Deep mesozoop.	**0.3**	0.5	0.0	0.8	0.3	**0.0**	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus	18.1	11.3	**0.0**	**31.1**	24.5	11.8	3.9	**7.7**	**17.1**	15.1
Total	100.0		13.4	241.7	100.0	100.0		36.0	182.2	100.0
TRN	14					14				

Benthic invertebrates

Background

The benthic invertebrates other than shrimp and crabs were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. The main echinoderm species are the heart urchin *Brisaster fragilis*, the brittle star *Ophiura robusta*, the sea urchin *Strongylocentrotus pallidus*, and the sea stars. The Stimpson clam *Spisula polynyma*, the sea scallop *Placopecten magellanicus*, other Pectinidae, the whelks *Buccinum* spp., the wedgeclam *Mesodesma deauratum*, and the propeller clam *Cyrtodaria siliqua* are the most abundant mollusc species. The polychaete group are mainly represented by the worm *Exogene hebes*. The last benthic invertebrate group consisted mainly of miscellaneous crustaceans (mainly gammarid amphipods), sea anemones, nematodes, and other meiofauna. Information was very limited for most of these species in the studied area.

Biomass

Biomass data were lacking for benthic invertebrates from the study area. Consequently, it was assumed that the mean biomasses ranged 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 63.70 (ESS) to 112.30 t km^{-2} (NFLD) for echinoderms (mean: 88.00 ± 34.37 t km^{-2}), 42.10 (NFLD) to 57.40 t km^{-2} (ESS) for molluscs (mean: 49.75 ± 10.82 t km^{-2}), 10.50 (NFLD) to 11.90 t km^{-2} (ESS) for polychaetes (mean: 11.20 ± 0.99 t km^{-2}), and 4.90 (ESS) to 7.80 t km^{-2} (NFLD) for other benthic invertebrates (mean: 6.35 ± 2.05 t km^{-2}).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 2008–2010 period. Only echinoderms (sea urchins *Strongylocentrotus* spp.) and molluscs were commercially harvested; however, echinoderm catches were too coastal and shallow to be included in the models. Commercial molluscs are Stimpson clam (*Spisula polynyma*), sea scallop (*Placopecten magellanicus*), other Pectinidae, and whelks (*Buccinum* spp.), species caught at depths > 15 m. The average annual landing from the ZIFF databases was 503 t or 7.72 x 10^{-2} t km^{-2} yr^{-1} (SD = 3.51 x 10^{-2} t km^{-2} yr^{-1}). These landings included by-catch values from the shrimp and Greenland halibut fisheries of 1.3 t or 1.91 x 10^{-4} t km^{-2} yr^{-1} (J. Gauthier, L. Savard, and B. Bernier, Maurice-Lamontagne Institute, unpublished data). Only part of the mollusc biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shell 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 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). Using the previous ratio (0.166) 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 $1.28 \times 10^{-2} \pm 5.82 \times 10^{-3}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch value of $1.28 \times 10^{-2} \pm 3.30 \times 10^{-3}$ t km^{-2} yr^{-1} for molluscs.

Production

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

Echinoderms

Warwick et al. (1978) estimated an annual production of 0.23 t km^{-2} yr^{-1} (P/B = 0.34 yr^{-1}) for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) obtained an estimate of 0.11 t km^{-2} yr^{-1} (P/B = 0.30 yr^{-1}). However, higher echinoderm productions have been reported in the New York Bight (70.11 t km^{-2} yr^{-1} or P/B = 1.20; Steimle 1985) and on Georges Bank (64.22 t km^{-2} yr^{-1} or P/B = 1.00; Steimle 1987). Also, Robertson (1979) estimated an annual P/B of 0.65 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.60 yr^{-1} on the southern shelf of British Columbia. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 0.26 yr^{-1}. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 16.53 to 134.76 t km^{-2} yr^{-1}, corresponding to an annual production of 54.71 $\pm$ 31.96 t km^{-2} yr^{-1}. The inverse solution estimated a production of 36.98 $\pm$ 27.34 t km^{-2} yr^{-1}, representing a P/B of 0.42 yr^{-1}.

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of 3.82 t km^{-2} yr^{-1} (P/B = 0.85 yr^{-1}) in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated 4.67 t km^{-2} yr^{-1} (P/B = 2.14 yr^{-1}) in Long Island Sound (northeaster USA). Higher production estimates were reported by Steimle (1985) (82.12 t km^{-2} yr^{-1} or P/B = 1.00 yr^{-1}) and by Borkowski (1974) (23.53 t km^{-2} yr^{-1} or P/B = 3.83 yr^{-1}). On the other hand, Buchanan and Warwick (1974) reported a lower estimate (0.60 t km^{-2} yr^{-1}; P/B = 1.11 yr^{-1}). Also, Robertson (1979) estimated an annual P/B of 0.76 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.70 yr^{-1} on the southern shelf of British Columbia. Finally, we estimated a mean P/B ratio of 0.97 yr^{-1} based on previous ecosystem models for the northern Gulf. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 29.47 to 219.84 t km^{-2} yr^{-1}, corresponding to an annual production of 70.62 $\pm$ 53.43 t km^{-2} yr^{-1}. The inverse solution estimated a production of 61.08 $\pm$ 29.62 t km^{-2} yr^{-1}, representing a P/B of 1.23 yr^{-1}.

Polychaetes

Estimates of the annual polychaete P/B ratio ranged between 1.09 and 4.32 yr^{-1} in the literature (P/B = 1.30 yr^{-1} in Buchanan and Warwick 1974, P/B = 2.26 yr^{-1} in Warwick et al. 1978, P/B = 2.05 yr^{-1} in Sanders 1956, P/B = 2.53 yr^{-1} in Collie 1987, P/B = 4.30 yr^{-1} in Peer 1970, P/B = 4.32 yr^{-1} in Nichols 1975, P/B = 1.09 yr^{-1} in Curtis 1977, and P/B = 3.00 yr^{-1} in Steimle 1985). Finally, we estimated a mean P/B ratio of 1.90 yr^{-1} based on previous ecosystem models for the northern Gulf. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 11.45 to 51.41 t km^{-2} yr^{-1}, corresponding to an annual production of 28.31 ± 13.04 t km^{-2} yr^{-1}. The inverse solution estimated a production of 28.12 ± 8.83 t km^{-2} yr^{-1}, representing a P/B of 2.51 yr^{-1}.

Other benthic invertebrates

Estimates of P/B ratio for other benthic invertebrates ranged between 1.65 and 4.00 yr^{-1} (P/B = 3.40 yr^{-1} in Sheader 1977, P/B = 4.00 yr^{-1} in Klein et al. 1975, P/B = 1.65 yr^{-1} in Cederwall 1977, and P/B = 2.80 yr^{-1} in Collie 1985). Also, Mills and Fournier (1979) estimated an annual P/B of 0.25 yr^{-1} on the Scotian Shelf and Jarre-Teichmann and Guénette (1996) used an estimate of 0.25 yr^{-1} on the southern shelf of British Columbia. Based on previous ecosystem models for the northern Gulf, we estimated a mean P/B ratio of 1.26 yr^{-1}. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 6.18 to 31.20 t km^{-2} yr^{-1}, corresponding to an annual production of 16.43 ± 6.00 t km^{-2} yr^{-1}. The inverse solution estimated a production of 12.67 ± 6.39 t km^{-2} yr^{-1}, representing a P/B of 2.00 yr^{-1}.

Consumption

In the absence of information on food consumption, consumption values were first estimated using a gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992) and mean production values. For echinoderms, this produced a consumption range between 182.37 and 607.89 t km^{-2} yr^{-1}. We estimated a Q/B ratio of 1.06 yr^{-1} based on previous ecosystem models for the northern Gulf (consumption range: 67.55 to 119.08 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were thus 67.55 and 607.89 t km^{-2} yr^{-1}, corresponding to a mean consumption of 244.22 ± 246.95 t km^{-2} yr^{-1} (Q/B = 2.78 yr^{-1}). The inverse solution estimated a consumption of 190.21 ± 155.09 t km^{-2} yr^{-1}, representing a Q/B ratio of 2.16 yr^{-1}.

For molluscs, this produced a consumption range between 235.40 and 784.66 t km^{-2} yr^{-1}. We estimated a Q/B ratio of 3.70 yr^{-1} based on previous ecosystem models for the northern Gulf (consumption range: 155.58 to 212.13 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were thus 155.58 and 784.66 t km^{-2} yr^{-1}, corresponding to a mean consumption of 346.94 ± 293.73 t km^{-2} yr^{-1} (Q/B = 6.97 yr^{-1}). The inverse solution estimated a consumption of 300.20 ± 249.53 t km^{-2} yr^{-1}, representing a Q/B ratio of 6.03 yr^{-1}.

For polychaetes, this produced a consumption range between 94.36 and 314.55 t km^{-2} yr^{-1}. We estimated a Q/B ratio of 9.39 yr^{-1} based on previous ecosystem models for the northern Gulf (consumption range: 98.61 to 111.76 t km^{-2} yr^{-1}). The resulting lower and upper consumption

limits were thus 94.36 and 314.55 t km^{-2} yr^{-1}, corresponding to a mean consumption of 154.82 $\pm$ 106.74 t km^{-2} yr^{-1} (Q/B = 13.82 yr^{-1}). The inverse solution estimated a consumption of 120.92 $\pm$ 45.02 t km^{-2} yr^{-1}, representing a Q/B ratio of 10.80 yr^{-1}.

For other benthic invertebrates, this produced a consumption range between 54.76 and 182.55 t km^{-2} yr^{-1}. We estimated a Q/B ratio of 5.43 yr^{-1} based on previous ecosystem models for the northern Gulf (consumption range: 26.58 to 42.32 t km^{-2} yr^{-1}). The resulting lower and upper consumption limits were thus 26.58 and 182.55 t km^{-2} yr^{-1}, corresponding to a mean consumption of 76.55 $\pm$ 71.60 t km^{-2} yr^{-1} (Q/B = 12.06 yr^{-1}). The inverse solution estimated a consumption of 67.11 $\pm$ 54.22 t km^{-2} yr^{-1}, representing a Q/B ratio of 10.57 yr^{-1}.

Diet composition

Due to a lack of data in the study area, diet information for echinoderms was taken from literature for the most abundant species in the present study: heart urchins, brittle stars, sea urchins, and sea stars. The diet of ophiuroids or brittle stars ranges from bottom detritus to suspended particles and plankton, depending on the species (Reese 1966). Some brittle stars can also prey on small crustaceans, molluscs, and worms (Palaeos 1999). Most sea star species are generalist predators, eating molluscs such as mussels, clams, oysters, some snails, or any other animal too slow to evade the attack (e.g., other echinoderms or dying fish) (Dale 2000). Some sea stars are detritivores, eating decomposed animal and plant material or organic films attached to substrate. Sea urchins eat plant and animal matter. The preferred food is kelps of the genus *Laminaria*. In areas where macroalgae do not grow, urchins will eat benthic diatoms, decaying matter, and small invertebrates such as ascidians, polychaetes, young mussels, sponges, brittle stars, and crinoids (Chenoweth 1994). All these potential food items were accounted for in the final diet composition of echinoderms (Table 37).

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. However, sea scallops can consume phytoplankton and mesozooplankton (e.g., ciliated protozoa) (Hart and Chute 2004). The gut contents generally reflected the available organisms in the surrounding habitat, indicating that sea scallops are opportunistic filter feeders that take advantage of both benthic and pelagic food (Shumway et al. 1987). All these potential food items were accounted for in the final diet composition (Table 37).

Polychaetes are considered to have a diet of 100% detritus (Nesis 1965, Fauchald and Jumars 1979). However, more 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 38.

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). Sea anemones are mainly carnivores that can eat fish, mussels, zooplankton (e.g., copepods, other small crustacean larvae), small crustaceans (e.g., isopods, amphipods), and worms. However, organic detritus has

also been reported as main source of food for some sea anemone species (Chintiroglou and Koukouras 1992). All these potential food were accounted for in the final diet composition of other benthic invertebrates (Table 38).

Table 37. Diet compositions (%) of echinoderms and molluscs used in modelling. Est: diet estimates from 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.

Prey	Echinoderms					Molluscs				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Atlantic halibut										
Redfish										
Black dogfish										
White hake										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Herring										
Small pelagics										
Squid										
Shrimp										
Small crabs										
Echinoderms	9.2	35.4	**0.0**	**50.0**	17.7					
Molluscs	9.4	35.4	**0.0**	**50.0**	18.5					
Polychaetes	1.1	3.5	**0.0**	**5.0**	1.8					
Other bent. inver.	9.4	35.4	**0.0**	**50.0**	2.6					
Large euphausiids										
Small euphausiids										
Large hyperiid amp.										
Other macrozoop.										
Surface mesozoop.										
Deep mesozoop.	0.7	3.5	**0.0**	**5.0**	2.9	4.8	7.1	0.0	10.0	0.9
Phytoplankton	2.3	7.1	**0.0**	**10.0**	9.1	9.5	14.1	0.0	20.0	16.8
Detritus	67.9	70.7	**0.0**	**100.0**	47.5	85.7	14.1	80.0	100.0	82.3
Total	100.0		0.0	270.0	100.0	100.0		80.0	130.0	100.0
TRN	7					3				

Table 38. Diet compositions (%) of polychaetes and other benthic invertebrates used in modelling. Est: diet estimates from 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.

Prey	Polychaetes					Other benthic invertebrates				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Atlantic halibut										
Redfish										
Black dogfish										
White hake										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Herring										
Small pelagics										
Squid										
Shrimp										
Small crabs										
Echinoderms										
Molluscs						11.6	35.4	**0.0**	**50.0**	32.6
Polychaetes	13.4	16.5	**1.8**	**25.1**	11.6	2.3	7.1	**0.0**	**10.0**	5.2
Other bent. inver.						23.3	70.7	**0.0**	**80.0**	8.7
Large euphausiids										
Small euphausiids										
Large hyperiid amp.										
Other macrozoop.										
Surface mesozoop.										
Deep mesozoop.						1.2	3.5	**0.0**	**5.0**	3.5
Phytoplankton	43.3	8.2	**37.5**	**49.1**	47.8					
Detritus	43.3	8.2	**37.5**	**49.1**	40.6	61.6	70.7	**0.0**	**100.0**	50.0
Total	100.0		76.7	123.3	100.0	100.0		0.0	245.0	100.0
TRN	3					5				

Macrozooplankton (Claude Savenkoff, Michel Harvey, and Ian McQuinn; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

Organisms and species representing this group are greater than 5 mm in length. To identify competitors with rorquals for the euphausiid resource, we distinguish four groups: (1) large euphausiids (*Meganyctiphanes norvegica*), (2) small euphausiids (*Thysanoessa raschii* and *T. inermis*), (3) large hyperiid amphipods (*Themisto libellula*), and (4) other macrozooplankton such as chaetognaths (mainly *Sagitta elegans*, *Pseudosagitta maxima*, and *Eukrohnia hamata*), small hyperiid amphipods (*Themisto abyssorum*, *T. gaudichaudi*, and *T. compressa*), jellyfish (cnidarians [mainly *Aglantha digitalis*, *Dimophyes arctica*, and *Obelia* spp.] and ctenophores [mainly *Beroe* spp.]), mysids (mainly *Boreomysis arctica*, *Mysis mixta*, and *Erythrops erythrophthalma*), tunicates, and ichthyoplankton. Macrozooplankton contains omnivorous (most euphausiids, hyperiid amphipods, mysids, and large tunicates) and carnivorous (chaetognaths and jellyfish) species.

Euphausiids (krill) are the most important prey items of blue whales. The lower St. Lawrence Estuary (LSLE) and the Gulf of St. Lawrence (GSL) are inhabited by four euphausiid species *M. norvegica*, *T. raschii*, *T. inermis* and *T. longicaudata* (Brunel et al. 1998). The two more abundant euphausiid species were *M. norvegica* and *T. raschii* (Descroix et al. 2005, Harvey and Devine 2009). In our study, we distinguished large from small euphausiids.

Hyperiid amphipods are also important components of macrozooplankton communities throughout the LSLE and the GSL. The LSLE and the GSL are inhabited by eight hyperiid amphipod species (Brunel et al. 1998), but largely dominated by only three species, *T. libellula*, *T. abyssorum*, and *T. compressa*. As typical carnivores, large hyperiid amphipods (*T. libellula*) prey on various other zooplankton species (largely copepods and small euphausiids) and so, we decided to distinguish them from other macrozooplanton species (Ikeda and Shiga 1999).

Among the other macrozooplankton species, mysids are the most important components in the deep waters of the LSLE and the northwest GSL (Descroix et al. 2005, Harvey et al. 2009). According to Brunel et al. (1998), the LSLE and the GSL are inhabited by more than twenty mysid species, but largely dominated by only two species, *Boreomysis arctica* and *Mysis mixta*. Chaetognaths are also an important component of the macrozooplankton communities in the St. Lawrence marine system. They are present in variable proportions depending on the region. The LSLE and the GSL are inhabited by five chaetognath species (see Brunel et al. 1998) but largely dominated by only two species, *Sagitta elegans* and *Eukrohnia hamata*. Finally, cnidarians and ctenophores are present throughout the St. Lawrence marine system in different proportions depending on the region.

Biomass

The biomass for each macrozooplankton group was calculated from zooplankton data gathered during the 2008–2009 period (area: 11,000 km^2; Harvey and Devine 2009). The sampling design consists of 44 stations along eight sections from Les Escoumins in the lower

Estuary to Sept-Îles in the northwestern Gulf conducted in October–November (Harvey and Devine 2009). The survey was done using the BIONESS, which is a multiple opening–closing 333 μm mesh net system and the protocol includes the use of a stroboscope (Novatech, ST400A Xenon Flasher; 55 LUX) fixed in the mouth of the BIONESS since 2007 (Harvey and Devine 2009). This gives overall biomass estimates of 11.95 ± 17.57 t km^{-2} for large euphausiids, 12.53 ± 14.48 t km^{-2} for small euphausiids, 0.38 ± 0.38 t km^{-2} for large hyperiid amphipods, and 12.30 ± 6.26 t km^{-2} for other macrozooplankton.

For euphausiids, we also used biomass estimates from an acoustique survey conducted in the Estuary and northern Gulf of St. Lawrence in 2009 (Ian McQuinn, Maurice-Lamontagne Institute, unpublished data). This gave a biomass value of 21.86 ± 1.63 t km^{-2} for large euphausiids and 44.43 ± 4.34 t km^{-2} for small euphausiids. Accordingly, we recalculated biomass values at 17.15 ± 6.36 t km^{-2} for large euphausiids (range: 8.30–21.86 t km^{-2}) and 19.59 ± 17.12 t km^{-2} for small euphausiids (range: 6.73–44.43 t km^{-2}).

Catch

There was no commercial fishery for species in this group during the 2008–2010 period in the study area.

Production

For large euphausiids, we estimated a P/B ratio range from 1.60 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985) to 3.80 yr^{-1} (range: 1.300–6.300 yr^{-1}; Lindley 1982) for the North Sea. When the biomass values were applied to the overall mean P/B ratio (2.70 yr^{-1}), we obtained a production range of 22.406 to 59.025 t km^{-2} yr^{-1}, corresponding to a mean production of 46.309 ± 17.163 t km^{-2} yr^{-1} for large euphausiids. The inverse solution estimated a production of 38.044 ± 14.932 t km^{-2} yr^{-1} (P/B of 2.22 yr^{-1}) for large euphausiids.

For small euphausiids, two P/B ratios were obtained: 2.75 yr^{-1} (range: 1.30–4.20 yr^{-1}; Lindley 1980) for the North Sea and American coastal waters and 4.00 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977). When the biomass values were applied to the overall mean P/B ratio (3.38 yr^{-1}), we obtained a production range of 22.711 to 149.941 t km^{-2} yr^{-1}, corresponding to a mean production of 66.106 ± 57.794 t km^{-2} yr^{-1} for small euphausiids. The inverse solution estimated a production of 57.701 ± 45.001 t km^{-2} yr^{-1} (P/B of 2.95 yr^{-1}) for small euphausiids.

For large hyperiid amphipods, Ikeda and Shiga (1999) estimated a mean P/B ratio of 0.016 d^{-1} (or 5.84 yr^{-1}) in Toyama Bay, southern Japan Sea (range: 0.011–0.028 d^{-1}). We then applied the biomass values to this P/B ratio to obtain a production range of 0 to 4.449 t km^{-2} yr^{-1}, corresponding to a mean production of 2.225 ± 2.229 t km^{-2} yr^{-1} for hyperiid amphipods. The inverse solution estimated a production of 1.718 ± 1.363 t km^{-2} yr^{-1} (P/B of 4.51 yr^{-1}) for hyperiid amphipods.

For other macrozooplankton, the production estimates were obtained from Pauly and Christensen (1996) in mass-balance models of northeastern Pacific ecosystems. These authors reported P/B ranges of 2.00 to 4.00 yr^{-1} (mean: 3.00 yr^{-1}) for carnivorous jellies and 1.00 to 3.00 yr^{-1} (mean: 2.00 yr^{-1}) for chaetognaths. When the biomass values were applied to the overall mean

P/B ratio (2.50 yr^{-1}), we obtained a production range of 26.519 to 34.978 t km^{-2} yr^{-1}, corresponding to a mean production of 30.748 ± 15.642 t km^{-2} yr^{-1} for other macrozooplankton. The inverse solution estimated a production of 29.164 ± 2.343 t km^{-2} yr^{-1} (P/B of 2.37 yr^{-1}) for other macrozooplankton.

Consumption

Consumption was estimated from data on large euphausiids in the Gulf of St. Lawrence (mean Q/B = 5.01 yr^{-1}, range: 4.81–5.22 yr^{-1}; Sameoto 1976). When the biomass values were applied to the mean Q/B ratio, we obtained a consumption range of 41.57 to 109.50 t km^{-2} yr^{-1}. Based on the mean production (46.31 t km^{-2} yr^{-1}) for large euphausiids and the minimum and maximum GE limits (10–30%; Christensen and Pauly 1992), we obtained two other consumption values of 154.36 and 436.09 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 41.57 and 436.09 t km^{-2} yr^{-1}, corresponding to a mean consumption of 192.13 ± 186.50 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 223.17 ± 150.46 t km^{-2} yr^{-1} for large euphausiids, representing a Q/B ratio of 13.01 yr^{-1}.

For small euphausiids, consumption was also estimated from Sameoto (1976) in the Gulf of St. Lawrence (overall mean Q/B = 14.38 yr^{-1}, range: 7.95–21.56 yr^{-1}). When the biomass values were applied to the mean Q/B ratio, we obtained a consumption range of 96.75 to 638.73 t km^{-2} yr^{-1}. Based on the mean production (66.11 t km^{-2} yr^{-1}) for small euphausiids and the minimum and maximum GE limits (10–30%; Christensen and Pauly 1992), we obtained two other consumption values of 220.35 and 661.06 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 96.75 and 661.06 t km^{-2} yr^{-1}, corresponding to a mean consumption of 404.22 ± 288.28 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 311.17 ± 273.11 t km^{-2} yr^{-1} for small euphausiids, representing a Q/B ratio of 15.89 yr^{-1}.

To estimate the Q/B ratio of large hyperiid amphipods, two studies were used. Auel and Werner (2003) estimated an ingestion of 1.9 ± 0.6% of body carbon per day (or Q/B = 6.94 yr^{-1}) for the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. Marion et al. (2008) estimated that the daily ingestion rates of *T. libellula* ranged from 6.32 to 16.82% of body dry mass per day in the LSLE and northwestern GSL (i.e., Q/B range: 23.07 to 61.39 yr^{-1}). When the biomass values were applied to the mean overall Q/B ratio (30.47 yr^{-1}), we obtained a consumption range of 0 to 23.21 t km^{-2} yr^{-1}. Based on the mean production (2.22 t km^{-2} yr^{-1}) for large hyperiid amphipods and the minimum and maximum GE limits (10–30%; Christensen and Pauly 1992), we obtained two other consumption values of 7.42 and 22.25 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0 and 23.21 t km^{-2} yr^{-1}, corresponding to a mean consumption of 13.22 ± 11.40 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 10.73 ± 4.95 t km^{-2} yr^{-1} for large hyperiid amphipods, representing a Q/B ratio of 28.17 yr^{-1}.

For other macrozooplankton, Pauly and Christensen (1996) reported a Q/B value of 10.00 yr^{-1} for carnivorous jellies and a Q/B range of 10.00 to 40.00 yr^{-1} for chaetognaths in mass-balance models of northeastern Pacific ecosystems. For chaetognaths, three other values were estimated. First, Kotori (1976) estimated that the carbon requirement of a chaetognath community from the Bering Sea and the north Pacific 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. Secondly, Feigenbaum (1979) found specific daily rations between 0.08 and 0.12 dry weight basis for chaetognaths in the Gulf Stream, near Miami, corresponding to a mean Q/B ratio of 36.50 yr^{-1}. Finally, Falkenhaug (1991) estimated a mean daily specific ingestion (dry weight basis) of 0.022 d^{-1} in the Barents Sea, 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 small hyperiid amphipods, two studies were used. 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 (or 23.00 yr^{-1}). Froneman et al. (2000) estimated two other daily rations, 11.5% and 19.8%, for the hyperiid amphipod *T. gaudichaudi* in the Prince Edward Archipelago (Southern Ocean) ecosystem. The resulting mean Q/B ratio for small hyperiid amphipods was 0.125 d^{-1} or 45.75 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 biomass values were applied to the overall mean Q/B ratio (22.09 yr^{-1}), we obtained a consumption range of 234.31 to 309.05 t km^{-2} yr^{-1}. Based on the mean production (30.75 t km^{-2} yr^{-1}) for other macrozooplankton and the minimum and maximum GE limits (10–30%; Christensen and Pauly 1992), we obtained two other consumption values of 102.49 and 307.48 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 102.49 and 309.05 t km^{-2} yr^{-1}, corresponding to a mean consumption of 238.34 ± 97.04 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 164.89 ± 49.53 t km^{-2} yr^{-1} for other macrozooplankton, representing a Q/B ratio of 13.41 yr^{-1}.

Diet composition

No diet information was available for euphausiids in the Estuary for the study period. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and copepods (Mauchline 1980). Pauly and Christensen (1996) reported that the relative proportions of prey in the diet composition of euphausiids in the northeastern Pacific ecosystems were 5% zooplankton, 85% phytoplankton, and 10% detritus. In coastal waters of the northeast Atlantic, Båmstedt and Karlson (1998) found that 23% of *Meganyctiphanes norvegica* (range: 10–44%) and 15% of *Thysanoessa inermis* (range: 0.1–20%) fed carnivorously based on the average values for the highest stomach fullness (1.00) of the krill species. *Calanus finmarchicus* copepodids (stages 2 and 3) were by far the most dominant prey, making up 85% to 95% of the copepod prey mass (Båmstedt and Karlson 1998). Based on these results, a diet composition for small (*Thysanoessa inermis* and *T. raschii*) and large (*Meganyctiphanes norvegica*) euphausiids may be assumed. Overall proportions of each prey item for the diet compositions of the large and small euphausiids were weighted according to their biomass in the present study. The most important prey items of the resulting diets of large and small euphausiids were phytoplankton, detritus, and deep mesozooplankton (96.4% and 98.0%, respectively, of the diet; Table 39).

Hyperiid amphipods of the genus *Themisto* are principally carnivorous (Kane 1967, Sheader and Evans 1975, Falk-Petersen et al. 1987, Marion et al. 2008) and mainly feed on a large variety of zooplankton such as calanoid copepods, euphausiids, and chaetognaths (Hopkins 1985, Pakhomov and Perissinotto 1996, Froneman et al. 2000, Auel et al. 2002). In the lower St.

Lawrence Estuary, Marion et al. (2008) found that the diet of *T. libellula* was mostly composed of copepods and euphausiids, which made up on average 61.6% and 31.7% of prey biomass, respectively. Amphipods, chaetognaths, and detritus accounted for the remainder of the prey, and they contributed 6.7% of the food biomass. Overall proportions of each prey item for the diet composition of the large hyperiid amphipods were weighted according to their biomass in the present study to obtain the resulting diet (Table 40).

For the diet of other macrozooplankton, we used different studies. The mysid species *Boreomysis arctica* is probably a filter-feeder, consuming phytodetritus, although it also feeds on crustacean carcasses (Cartes and Sorbe 1998) and thus consumes mainly organic detritus (100% detritus). However, the pelagic mysid *Mysis mixta* is a common planktivore, feeding on phytoplankton, detritus, and small mesozooplankton (Viherluoto and Viitasalo 2001).

For chaetognaths, included in the other macrozooplankton group, Pauly and Christensen (1996) reported that mesozooplankton accounted for 100% of the diet composition in northeastern Pacific ecosystems. Small prey such as tintinnids and rotifers may be important in the diet of young chaetognaths (Pearre 1981), but the main diet consists of copepod nauplii and copepodid stages (Sameoto 1987, Tonnesson and Tiselius 2005). Barnacle nauplii, appendicularians, chaetognaths, cladocerans, and fish larvae also contribute to the diet periodically (Tonnesson and Tiselius 2005). Based on the diet composition of *Sagitta enflata* in the western Indian Ocean reported by Øresland (2000 and reference therein; see their Table 1), we estimated that (1) cannibalism accounted for 1% to 3% of the diet, (2) large copepods (including appendicularians [Larvacea]) ranged between 7% and 10% of the diet, and (3) small copepods represented between 54% and 79% of the diet.

For other amphipods, included in the other macrozooplankton group, we used first the diet composition reported by Pauly and Christensen (1996) on mass-balance models of northeastern Pacific ecosystems. These authors estimated that the relative proportions of each prey were 5% large zooplankton (i.e., our macrozooplankton groups), 90% small zooplankton (i.e., our mesozooplankton groups), and 5% detritus. Sheader and Evans (1975) found that *Parathemisto gaudichaudi* consumed 11% copepods, 24% decapods, 37% chaetognaths, and 34% euphausiids. From the Strait of Georgia, Haro-Garay (2003) found that the stomach contents of *Parathemisto pacifica* included 52% copepods, 19% amphipods, 8% cladocera (included in our mesozooplankton groups), 7% ostracods (included in our mesozooplankton groups), 4% crustacean larvae, 8% diatoms, and 2% euphausiids, while the diet composition of *Cyphocaris challengeri* was 41% amphipods, 33% copepods, 12% cladocera, 4% ostracods, 7% crustacean larvae, and 3% diatoms. Finally, Pakhomov and Perissinotto (1996) found in South Georgia that *Themisto gaudichaudi* fed 12% on euphausiids, 3% on chaetognaths, and 84% on small zooplankton. The most important prey items of the resulting diet of other amphipods were deep mesozooplankton (24.9%–74.2%), other macrozooplankton (1.7%–40.6%), and surface mesozooplankton (5.3%–15.8%).

For jellies, included in the other macrozooplankton group, Pauly and Christensen (1996) reported that the relative proportions of prey were 0% to 33% large zooplankton, 62% to 100% small zooplankton, and 0% to 5% detritus in northeastern Pacific ecosystems. Overall proportions of each prey item for the diet compositions of other macrozooplankton species were weighted according to their biomas. Finally, the different diet proportions were weighted by the biomass proportion of each macrozooplankton species in the study area to estimate the overall diet of the other macrozooplankton group. The most important prey items of the resulting diet of other

macrozooplankton were mesozooplankton groups, detritus, and phytoplankton (92.8% of the diet; Table 40).

Table 39. Diet compositions (%) of large and small euphausiids used in modelling. Est: diet estimates from 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.

Prey	Large euphausiids					Small euphausiids				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large euphausiids	**0.4**	0.3	0.2	0.6	0.4	**0.0**	0.0	0.0	0.0	0.0
Small euphausiids	**0.5**	0.3	0.2	0.7	0.5	**0.4**	0.5	0.0	0.8	0.4
Large hyperiid amp.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Other macrozoop.	**0.3**	0.2	0.1	0.4	0.3	**0.3**	0.3	0.0	0.5	0.3
Surface mesozoop.	2.6	2.9	**0.6**	**7.6**	0.7	1.2	0.8	**0.2**	**3.5**	0.8
Deep mesozoop.	12.2	13.5	**2.7**	**35.6**	3.8	5.8	3.9	**0.8**	**16.3**	1.5
Phytoplankton	60.8	34.3	**28.0**	**85.0**	82.5	64.9	28.5	**40.0**	**85.0**	83.5
Detritus	23.3	18.7	**10.0**	**45.0**	11.8	27.4	24.6	**10.0**	**49.5**	13.6
Total	100.0		41.8	175.0	100.0	100.0		51.0	155.5	100.0
TRN	8					8				

Table 40. Diet compositions (%) of large amphipods and other macrozooplankton used in modelling. Est: diet estimates from 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 amphipods					Other macrozooplankton				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large euphausiids	14.8	12.2	**0.0**	**29.6**	24.5	2.3	2.0	**0.0**	**3.8**	3.3
Small euphausiids	16.9	14.0	**0.0**	**33.8**	18.2	2.6	2.3	**0.0**	**4.4**	3.7
Large hyperiid amp.	**0.1**	0.1	0.0	0.3	0.1	**0.1**	0.1	0.0	0.1	0.1
Other macrozoop.	3.5	5.6	**0.0**	**14.6**	11.3	2.3	2.1	**0.0**	**4.0**	3.5%
Surface mesozoop.	10.8	5.0	**5.1**	**20.0**	15.9	8.4	3.9	**4.9**	**11.2**	6.7
Deep mesozoop.	50.8	23.4	**23.9**	**94.1**	27.3	39.3	18.1	**22.9**	**52.8**	24.0
Phytoplankton	**0.0**	0.0	0.0	0.0	0.0	9.0	12.7	**0.0**	**18.0**	16.3
Detritus	3.1	5.4	**0.0**	**16.8**	2.7	36.2	26.1	**17.8**	**55.1**	42.4
Total	100.0		29.0	209.2	100.0	100.0		45.6	149.5	100.0
TRN	8					8				

Mesozooplankton (Claude Savenkoff and Stéphane Plourde; Fisheries and Oceans Canada, Mont-Joli, Qc)

Background

The mesozooplankton includes small zooplankton ≤ 5 mm in length. The copepod species dominate the planktonic community in the LSLE and large calanoid copepods (i.e., *Calanus finmarchicus* and *C. hyperboreus*) are clearly major components (Plourde et al. 2002). Smaller organisms were mainly *Oithona* spp., *Microcalanus* spp., and a high proportion of nauplii stages while *Pseudocalanus* spp. and *Temora longicornis* are present but few in number (Runge and Simard 1990, Plourde et al. 2002, Harvey and Devine 2009). The mesozooplankton also included other organisms such as molluscs (gastropoda, mainly *Limacina helicina*), heterotrophic protozoa (flagellates, dinoflagellates, and ciliates), meroplankton, and tunicates < 5 mm, which are generally underestimated by sampling gear (Strong 1981).

The copepod species composition shows a marked seasonal pattern. *Calanus finmarchicus* and *C. hyperboreus* dominated the population from May to September, whereas *Oithona* spp. was predominant from September to March (Plourde et al. 2002). The summer composition of the copepod population in the LSLE is biased towards a dominance of late-development stages of *Calanus* spp. in comparison to adjacent waters of the GSL and northwest Atlantic (Runge and Simard 1990, de Lafontaine et al. 1991). Runge and Simard (1990) hypothesized that this unusual copepod species composition results from the combined effect of the export in the residual surface outflow of early life stages of *Calanus* spp. and small surface-dwelling species and the upstream advection of late-development stages of *Calanus* spp. in the inflowing deep water of the

Laurentian Channel.

In the Estuary, the mean seasonal pattern of *C. finmarchicus* shows a maximum abundance of females in May, but peak population egg production rate and naupliar (N3–N6) abundance occur in early July, just after onset of the late spring–early summer phytoplankton bloom. The population stage structure is characterized by low summer abundance of early copepodite stages C1–C3 and high stage C5 abundance in autumn (Plourde et al. 2001). These authors suggested that the main features of *C. finmarchicus* population dynamics in the lower St. Lawrence Estuary are (1) late reproduction resulting from food limitation prior to the onset of the summer phytoplankton bloom, (2) probable export of early developmental stages in the surface layer during summer, and (3) advection into the central lower St. Lawrence Estuary of overwintering stage C5 in autumn from downstream regions in the deeper waters. Finally, Plourde et al. (2001) proposed that the overwintering stock in the LSLE originates from two distinct sources: (1) an "early" component mainly exported in spring and renewed by the advection of animals from the northwestern GSL through the deep residual upstream currents, and (2) a "late" component synchronized with the summer environmental conditions (phytoplankton bloom, high temperature) favouring its local development and maintenance.

A three–year life cycle for *C. hyperboreus* adult females (stage C6f) was suggested by Plourde et al. (2003) in the LSLE, with the main reproductive event occurring during the second year of life as C6f. *C. hyperboreus* females initiate gonad maturation in early December and reproduce until late March, three to six months prior to the onset of the phytoplankton bloom. The development of the early stages of *C. hyperboreus* appeared independent of the phytoplankton bloom in the LSLE. There is a decrease in total abundance of *C. hyperboreus* from April to early June likely resulting from the interplay between the timing of reproduction and the ontogenetic ascent to the surface in copepodid stages C4, C5, and C6f in April–May after their overwintering period and the timing of the period of maximum freshwater runoff (surface outflow) from April to June (Plourde et al. 2003). In late June – early July, there is an increase in total abundance of the *C. hyperboreus* population in the LSLE. Plourde et al. (2003) explained this increase by a deep advection of the overwintering population from the adjacent northwest GSL in summer. Assuming that the late development stages of *C. hyperboreus* migrated to deep water for overwintering in late May in the northwest GSL, the advection time of the deep upstream component of the estuarine two–layer circulation would explain the presence of the overwintering late-development stages issued from the northwest GSL in the LSLE in early summer (Plourde et al. 2003). The interaction between the life cycle strategy of *C. hyperboreus* and the seasonal circulation pattern in the LSLE favours massive export of the locally produced cohort by strong surface outflow in late spring and deep advection of the overwintering population from the adjacent northwest GSL in summer.

When *C. finmarchicus* and *C. hyperboreus* enter diapause, they do not feed and they have reduced metabolic rates. In order to reproduce the diapause behaviour and population dynamics of calanoid copepods, we separated mesozooplankton into two groups: surface (0–100 m depth; active component) and deep (100–320 m depth; inactive component, i.e., in diapause).

Biomass

The biomass was calculated from zooplankton data gathered at a station located 16 km north of Rimouski in the deep (330 m) Laurentian Channel. The station was visited at various time intervals from April to November in 2008 and 2009 (total of 39 visits; S. Plourde, Institut Maurice-Lamontagne, unpublished data). Data from 2010 were not yet available when we began our analyses. Zooplankton were sampled with a 0.75 m diameter, 200 μm mesh ring net equipped with a closing device in two discrete depth, i.e. 0–100 m and 100–320 m. This gives overall biomass estimates of 15.99 ± 18.49 t km^{-2} and 75.14 ± 44.81 t km^{-2}, respectively, for surface and deep mesozooplankton for the study area.

Catch

None.

Production

We used a P/B ratio of 0.10 d^{-1} for surface mesozooplankton (Diel and Tande 1992, McLaren and Leonard 1995, Hirst and Bunker 2003, Plourde et al. 2009). When the biomass values were applied to this P/B ratio expressed per year, we obtained a production range for surface mesozooplankton of 465.66 to 701.39 t km^{-2} yr^{-1}, corresponding to an annual production of 583.52 ± 674.85 t km^{-2} yr^{-1}. The inverse solution estimated a production of 666.52 ± 48.91 t km^{-2} yr^{-1}, representing a P/B of 41.69 yr^{-1} for surface mesozooplankton.

On the Scotian Shelf, McLaren et al. (2001) estimated that mortality (equal here to P/B) for the generation produced by overwintered population (our deep mesozooplankton) from egg to copepodid stage 5 in June was ~4%·d^{-1} but subsequently was nearly constant at ~1%·d^{-1}. When the biomass values were applied to these two P/B ratios expressed per year, we obtained a production range for deep mesozooplankton of 124.49 to 1,696.00 t km^{-2} yr^{-1}, corresponding to an annual production of 685.61 ± 408.89 t km^{-2} yr^{-1}. The inverse solution estimated a production of 129.10 ± 6.06 t km^{-2} yr^{-1}, representing a P/B of 1.72 yr^{-1} for deep mesozooplankton.

Consumption

Based on Vézina et al. (2000), we estimated a Q/B ratio range for the surface mesozooplankton (active component that consumes) from 0.08 d^{-1} for the summer and fall periods to 0.22 d^{-1} for the winter and spring periods (overall mean: 0.15 d^{-1} or 55.59 yr^{-1}) in the Gulf of St. Lawrence. When the biomass values were applied to the overall mean Q/B ratio, we obtained a consumption range for surface mesozooplankton (active component) of 709.23 to 1,068.27 t km^{-2} yr^{-1}. Based on the mean production (583.52 t km^{-2} yr^{-1}) for surface mesozooplankton and the minimum and maximum GE limits (25–50%; Christensen and Pauly 1992), we obtained two other consumption values of 1,167.05 and 2,334.09 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 709.23 and 2,334.09 t km^{-2} yr^{-1},

corresponding to a mean consumption of 1,319.66 ± 704.32 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1,360.29 ± 103.69 t km^{-2} yr^{-1}, representing a Q/B of 85.09 yr^{-1} for surface mesozooplankton.

The deep mesozooplankton represent the component in diapause and they do not feed.

Diet composition

Mesozooplankton feed on both autotrophic and heterotrophic microplankton, and there is ample empirical evidence that mesozooplankton are omnivorous (Stoecker and Capuzzo 1990, Ohman and Runge 1994, Vézina et al. 2000). Mesozooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to surface mesozooplankton, the only active component (Table 41). We used the trophic fluxes estimated by Vézina et al. (2000) for the summer–fall and winter–spring periods as lower and upper diet constraints.

Table 41. Diet composition (%) of surface mesozooplankton used in modelling. Est: diet estimates from 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.

	Surface mesozooplankton				
Prey	Mean	± SD	Min	Max	Est
Large euphausiids					
Small euphausiids					
Large hyperiid amp.					
Other macrozoop.					
Surface mesozoop.	50.2	32.3	**27.4**	**73.1**	27.6
Deep mesozoop.					
Phytoplankton	47.2	35.4	**22.2**	**72.2**	71.4
Detritus	2.6	3.1	**0.4**	**4.8**	0.9
Total	100.0		50.0	150.0	100.0
TRN	3				

Phytoplankton (Claude Savenkoff, Michel Starr, and Liliane St-Amand; Fisheries and Oceans Canada, Mont-Joli, Qc)

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 *Thalassiosira nordenskioeldii* during winter and by *Thalassiosira* spp. (*T. punctigera*, *T. nordenskioeldii*, *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 at a station located 16 km north of Rimouski in the deep (330 m) Laurentian Channel. The station was visited at various time intervals from April to November in 2008 and 2010 (total of 69 visits) (M. Starr and L. St.-Amand, 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 1 g C (Christensen and Pauly 1992). The mean biomass for the entire area was 46.76 ± 55.80 t km^{-2}.

Primary Production

Production was calculated from data gathered at a station located 16 km north of Rimouski in the deep (330 m) Laurentian Channel from 2000 to 2005 (no data in recent years). The station was visited at various time intervals from April to October (total of 104 visits) (M. Starr and L. St.-Amand, Institut Maurice-Lamontagne, unpublished data). A value of $1,682.32 \pm 1,570.40$ mg C m^{-2} d^{-1} was estimated over the euphotic zone, giving production rates of 614.05 ± 573.20 g C m^{-2} yr^{-1} or $6,140.47 \pm 5,731.97$ t km^{-2} yr^{-1}. The minimum–maximum range was 2,689.60 to 9,899.00 t km^{-2} yr^{-1}. The inverse solution estimated a production of $3,276.83 \pm 907.65$ t km^{-2} yr^{-1}, and thus, a net production of $2,924.11 \pm 939.49$ t km^{-2} yr^{-1}, representing a P/B of 62.53 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 production 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 (in g C m^{-2}), PP is primary production (in g C m^{-2} yr^{-1}), and E is the euphotic depth (in m).

The overall annual primary production was 614.0 ± 573.2 g C m^{-2} yr^{-1} for the 2000–2005 period (range: 269.0–989.9 g C m^{-2} yr^{-1}). The euphotic depth is estimated at 12.9 ± 1.4 m (M. Starr and L. St.-Amand, Institut Maurice-Lamontagne, unpublished data). The primary production limits and euphotic depth were substituted into equation 6 above, giving a range of detritus biomass estimates from 7.3 to 25.4 g C m^{-2}, or 73.39 to 254.38 t wet mass km^{-2}, using a conversion factor of 10 g wet mass = 1 g C (Christensen and Pauly 1992). This resulted in a mean detritus biomass of 161.30 ± 150.57 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.

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 previous studies in the Gulf of St. Lawrence, Savenkoff et al. (2009) estimated a total detrital (or bacterial) respiration over the entire water column close to 88.3 ± 42.4 g C m^{-2} yr^{-1} or 882.96 ± 423.75 t wet mass km^{-2} yr^{-1} (range: 459.21–1,306.71 t km^{-2} yr^{-1}). They also estimated a primary production of 245.9 ± 109.9 g C m^{-2} yr^{-1} or $2,459.00 \pm 1,098.82$ t km^{-2} yr^{-1} (range: 1,360.18–3,557.82 t km^{-2} yr^{-1}). The percentage of total detrital respiration of primary production ranges thus between 34% and 37%. When the primary production values for the present study and the previous ratios were used, a total detrital respiration range could be estimated as 908.04 to 3,635.69 t km^{-2} yr^{-1} (mean: $2,404.88 \pm 985.27$ t km^{-2} yr^{-1}). The inverse solution estimated a detrital respiration of $1,576.09 \pm 882.51$ 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. Based on Silverberg et al. (1987) and Savenkoff et al. (2001), we estimated a burial flux of particulate organic carbon close to 0.74 mol C m^{-2} yr^{-1} at a station located in the Laurentian Trough of the lower St. Lawrence while

Silverberg et al. (2000) measured a burial flux of 0.46 mol C m^{-2} yr^{-1} at the Anticosti Gyre. This represents a detrital export range of 5.5 C m^{-2} yr^{-1} to 8.9 C m^{-2} yr^{-1} or 55.2 to 89.3 t wet mass km^{-2} yr^{-1} (mean: 72.2 ± 24.1 t km^{-2} yr^{-1}). The inverse solution estimated a detrital export of 59.07 ± 8.76 t km^{-2} yr^{-1}.

Data synthesis

Data on biomass, export (e.g., commercial catch), production, and consumption are summarized in Tables 42 and 43. The estimated values from the final solution are presented in Appendix 4.

Table 42. Observed biomass and export for each group used as input data for modelling for the 2008–2010 period in the lower St. Lawrence Estuary. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimated by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Group	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Blue whales	0.249	0.119	0.149	0.381					
Other mysticetes	0.070	0.031	0.006	0.298	**3.52 x 10^{-3}**	1.54 x 10^{-3}			3.52 x 10^{-3}
Belugas	0.044	0.013	0.017	0.080	**1.49 x 10^{-4}**	4.36 x 10^{-5}			1.57 x 10^{-4}
Other odontocetes	0.001	0.001	0.000	0.007	**4.83 x 10^{-5}**	4.73 x 10^{-5}			3.85 x 10^{-5}
Harp seals	0.001	0.001	0.000	0.002	2.67 x 10^{-4}	3.21 x 10^{-4}	**7.22 x 10^{-5}**	**6.38 x 10^{-4}**	7.44 x 10^{-5}
Grey seals	0.022	0.010	0.010	0.039	**1.81 x 10^{-5}**	2.06 x 10^{-5}	2.16 x 10^{-6}	4.14 x 10^{-5}	2.28 x 10^{-5}
Harbour seals	0.011	0.003	0.008	0.018	**8.84 x 10^{-6}**	1.53 x 10^{-5}	0	2.65x 10^{-5}	1.12 x 10^{-5}
Seabirds	0.003	0.001	0.002	0.004	2.55 x 10^{-4}	1.13 x 10^{-4}	**1.75 x 10^{-4}**	**3.35 x 10^{-4}**	1.92 x 10^{-4}
Large cod	0.09	0.06	0.03	0.14	**7.65 x 10^{-6}**	1.08 x 10^{-5}	0	1.53 x 10^{-5}	9.05 x 10^{-6}
Small cod	0.05	0.03	0.02	0.08	**1.55 x 10^{-3}**	1.21 x 10^{-3}	6.91 x 10^{-4}	2.41 x 10^{-3}	1.58 x 10^{-3}
Large Green. halibut	1.00	0.12	0.87	1.11	**4.82 x 10^{-2}**	1.14 x 10^{-3}	4.74 x 10^{-2}	4.90 x 10^{-2}	4.84 x 10^{-2}
Small Green. halibut	1.69	0.14	1.57	1.84	**1.29 x 10^{-3}**	2.93 x 10^{-4}	1.08 x 10^{-3}	1.50 x 10^{-3}	1.27 x 10^{-3}
Amer. plaice	0.18	0.02	0.17	0.21	**2.33 x 10^{-3}**	3.15 x 10^{-4}	2.11 x 10^{-3}	2.55 x 10^{-3}	2.30 x 10^{-3}
Flounders	0.21	0.05	0.15	0.25	**2.29 x 10^{-4}**	3.37 x 10^{-5}	2.05 x 10^{-4}	2.53 x 10^{-4}	2.27 x 10^{-4}
Skates	0.55	0.08	0.47	0.61	**3.01 x 10^{-3}**	8.68 x 10^{-4}	2.40 x 10^{-3}	3.63 x 10^{-3}	3.11 x 10^{-3}
Atlantic halibut	0.07	0.04	0.05	0.12	**7.11 x 10^{-4}**	1.65 x 10^{-4}	5.94 x 10^{-4}	8.28 x 10^{-4}	7.15 x 10^{-4}
Redfish	0.04	0.02	0.02	0.06	**1.59 x 10^{-4}**	4.41 x 10^{-5}	1.27 x 10^{-4}	1.90 x 10^{-4}	1.65 x 10^{-4}
Black dogfish	0.14	0.14	0.02	0.29	**9.29 x 10^{-5}**	1.32 x 10^{-5}	8.36 x 10^{-5}	1.02 x 10^{-4}	9.25 x 10^{-5}
White hake	0.012	0.006	0.006	0.018	**2.49 x 10^{-4}**	5.47 x 10^{-5}	2.10 x 10^{-4}	2.87 x 10^{-4}	2.56 x 10^{-4}
Large demersals	0.34	0.41	0.05	0.63	**1.36 x 10^{-3}**	1.13 x 10^{-4}	1.28 x 10^{-3}	1.44 x 10^{-3}	1.35 x 10^{-3}
Small demersals	0.58	0.60	0.16	1.00	**2.12 x 10^{-3}**	6.86 x 10^{-4}	1.64 x 10^{-3}	2.61 x 10^{-3}	2.20 x 10^{-3}
Large pelagics	0.001	0.001	0.000	0.002	**2.23 x 10^{-4}**	4.10 x 10^{-5}	1.94 x 10^{-4}	2.52 x 10^{-4}	2.28 x 10^{-4}
Capelin	2.39	1.76	0.75	4.25	**5.87 x 10^{-3}**	8.85 x 10^{-4}	5.25 x 10^{-3}	6.50 x 10^{-3}	5.82 x 10^{-3}

Table 42. Cont.

Group	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Herring	0.094	0.107	0.018	0.169	**2.35 x 10^{-3}**	1.57 x 10^{-3}	1.59 x 10^{-3}	3.55 x 10^{-3}	2.36 x 10^{-3}
Small pel. feeders	0.038	0.053	0.001	0.075	**6.13 x 10^{-4}**	6.11 x 10^{-4}	1.81 x 10^{-4}	1.04 x 10^{-3}	6.55 x 10^{-4}
Squid	0.0012	0.0015	0.0001	0.0022	**1.07 x 10^{-4}**	1.05 x 10^{-5}	9.94 x 10^{-5}	1.14 x 10^{-4}	1.07 x 10^{-4}
Shrimp	2.326	0.295	2.122	2.664	**1.56 x 10^{-1}**	5.33 x 10^{-3}	1.52 x 10^{-1}	1.60 x 10^{-1}	1.57 x 10^{-1}
Large crabs	2.465	0.079	2.409	2.521	**2.04 x 10^{-1}**	7.70 x 10^{-4}	2.04 x 10^{-1}	2.05 x 10^{-1}	2.04 x 10^{-1}
Small crabs	0.302	0.376	0.037	0.568					
Echinoderms	88.000	34.365	63.700	112.300					
Molluscs	49.750	10.819	42.100	57.400	**1.28 x 10^{-2}**	5.82 x 10^{-3}	8.70 x 10^{-3}	1.69 x 10^{-2}	1.28 x 10^{-2}
Polychaetes	11.200	0.990	10.500	11.900					
Other benthic invertebrates	6.350	2.051	4.900	7.800					
Large euphausiids	17.152	6.357	8.299	21.861					
Small euphausiids	19.587	17.124	6.729	44.427					
Large hyperiid amphipods	0.381	0.382	0	0.762					
Other macrozooplankton	12.299	6.257	10.608	13.991					
Surface mesozooplankton	15.987	18.489	12.758	19.216					
Deep mesozooplankton	75.136	44.810	34.107	116.165					
Phytoplankton	46.762	55.804	18.782	65.075					
Detritus	161.302	150.571	73.387	254.383	7.22 x 10^{1}	2.41 x 10^{1}	**5.52 x 10^{1}**	**8.93 x 10^{1}**	5.91 x 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.

Table 43. Observed production and consumption used as input data for modelling for the 2008–2010 period in lower St. Lawrence Estuary. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimated by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Group	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Blue whales	0.016	0.008	**0.009**	**0.024**	0.011	0.922	0.924	**0.268**	**1.575**	1.170
Other mysticetes	0.008	0.003	**0.004**	**0.022**	0.006	0.407	0.551	**0.018**	**0.796**	0.589
Belugas	0.007	0.002	**0.003**	**0.012**	0.003	0.494	0.454	**0.174**	**0.815**	0.282
Other odontocetes	0.0002	0.0002	**0.0001**	**0.0010**	0.0001	0.028	0.038	**0.001**	**0.055**	0.010
Harp seals	0.0001	0.0001	**0.0000**	**0.0002**	0.0001	0.005	0.006	**0.000**	**0.009**	0.008
Grey seals	0.0029	0.0023	**0.0010**	**0.0061**	0.0016	0.163	0.177	**0.038**	**0.288**	0.160
Harbour seals	0.0013	0.0010	**0.0005**	**0.0029**	0.0006	0.082	0.072	**0.030**	**0.133**	0.060
Seabirds	0.0009	0.0003	**0.0006**	**0.0012**	0.0009	0.399	0.381	**0.089**	**0.892**	0.111
Large cod	0.045	0.027	**0.013**	**0.093**	0.052	0.270	0.249	**0.094**	**0.446**	0.180
Small cod	0.034	0.018	**0.015**	**0.060**	0.059	0.280	0.252	**0.061**	**0.612**	0.260
Large Green. Halibut	0.285	0.107	**0.165**	**0.415**	0.262	1.844	1.059	**0.910**	**2.847**	0.899
Small Green. Halibut	0.745	0.216	**0.506**	**1.103**	0.521	6.060	4.827	**1.687**	**11.034**	1.735
Amer. plaice	0.055	0.018	**0.038**	**0.087**	0.052	0.479	0.374	**0.184**	**0.978**	0.227
Flounders	0.066	0.029	**0.031**	**0.102**	0.064	0.522	0.328	**0.219**	**0.922**	0.263
Skates	0.179	0.082	**0.103**	**0.338**	0.138	1.917	1.928	**0.595**	**4.684**	0.611
Atlantic halibut	0.013	0.006	**0.009**	**0.021**	0.014	0.226	0.216	**0.073**	**0.378**	0.074
Redfish	0.007	0.005	**0.003**	**0.016**	0.015	0.181	0.205	**0.036**	**0.326**	0.082
Black dogfish	0.028	0.028	**0.004**	**0.059**	0.033	0.394	0.360	**0.139**	**0.648**	0.142
White hake	0.007	0.003	**0.003**	**0.011**	0.007	0.058	0.049	**0.017**	**0.123**	0.029
Large demersals	0.102	0.128	**0.011**	**0.192**	0.188	1.552	2.093	**0.072**	**3.032**	0.725
Small demersals	0.283	0.345	**0.039**	**0.527**	0.526	3.747	4.687	**0.433**	**7.061**	2.061
Large pelagics	0.001	0.001	**0.0001**	**0.002**	0.001	0.018	0.023	**0.001**	**0.034**	0.005
Capelin	1.386	1.064	**0.240**	**3.451**	1.449	59.805	81.190	**2.395**	**117.215**	10.303

Table 43. Cont.

Group	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Herring	0.030	0.034	**0.006**	**0.055**	0.054	1.206	1.574	**0.094**	**2.319**	0.216
Small pel. feeders	0.031	0.044	**0.001**	**0.062**	0.062	0.253	0.304	**0.038**	**0.468**	0.259
Squid	0.0020	0.0025	**0.0002**	**0.0037**	0.0036	0.0100	0.0137	**0.0003**	**0.0197**	0.0122
Shrimp	2.448	0.926	**1.510**	**3.725**	2.639	15.969	6.830	**8.161**	**24.484**	10.868
Large crabs	0.645	0.021	**0.580**	**0.709**	0.644	4.379	2.062	**2.151**	**6.454**	2.204
Small crabs	0.142	0.176	**0.013**	**0.334**	0.148	1.207	1.260	**0.048**	**2.891**	0.862
Echinoderms	54.710	31.962	**16.527**	**134.760**	36.977	244.223	246.951	**67.549**	**607.891**	190.208
Molluscs	70.619	53.427	**29.470**	**219.842**	61.076	346.941	293.729	**155.585**	**784.657**	300.196
Polychaetes	28.309	13.042	**11.445**	**51.408**	28.123	154.819	106.743	**94.364**	**314.548**	120.919
Other benthic invertebrates	16.429	5.999	**6.178**	**31.200**	12.670	76.552	71.597	**26.583**	**182.545**	67.110
Large euphausiids	46.309	17.163	**22.406**	**59.025**	38.044	192.129	186.498	**41.566**	**436.092**	223.173
Small euphausiids	66.106	57.794	**22.711**	**149.941**	57.701	404.224	288.278	**96.746**	**661.065**	311.169
Large hyperiid amphipods	2.225	2.229	**0**	**4.449**	1.718	13.218	11.398	**0**	**23.209**	10.731
Other macrozooplankton	30.748	15.642	**26.519**	**34.978**	29.164	238.335	97.042	**102.494**	**309.052**	164.892
Surface mesozooplankton	583.523	674.848	**465.656**	**701.390**	666.521	1319.660	704.315	**709.231**	**2334.091**	1360.290
Deep mesozooplankton	685.614	408.893	**124.490**	**1696.003**	129.095					
Phytoplankton	6140.469	5731.965	**2689.602**	**9899.002**	3276.832					

DISCUSSION

Uncertainty in the input data

The present data set was used to construct ecosystem models of the lower St. Lawrence Estuary for the 2008–2010 period. The time period was chosen based on the availability of reliable information for the different species. Data on the abundance and distribution of fishes and macroinvertebrates have been collected each summer in the Estuary and the northern Gulf of St. Lawrence from 1990 to 2010. Since 2008, the coverage of the lower Estuary has been increased by adding four shallower strata in order to index the depths between 37 and 183 m (20 and 100 fathoms). This process improved our knowledge on the distribution and abundance of the species in shallow water (e.g., cod, shrimp), but comparisons with data previously gathered (1990–2007) became more complicated.

Ecosystem modelling requires the collection of a considerable amount of information. This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the lower Estuary during the 2008–2010 period. All parameter estimations were made within a collaborative framework in which experts for the various functional groups were consulted. The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence that we have in them). Even though most of the data are good estimates for the LSLE ecosystem, some input values are rough estimates only (e.g., benthic invertebrates, pelagic fishes), meaning that these values are assembled from different literature sources and not from independently measured parameters. Hence, the quality of the input data was variable. Catch estimates of commercial species are considered quite reliable although there is indirect evidence for non-negligible fishing mortality that was not accounted for (Fréchet et al. 2006). Biomass estimates for most fishes and shrimp were based on catches in bottom-trawl surveys conducted each summer in the Estuary and the northern Gulf of St. Lawrence using a Campelen trawl. Abundance and biomass estimates obtained from these surveys are considered as minimal values given that the nearshore region (depths < 37 m) is not covered and that some species may not be properly sampled (low catchability, e.g., pelagic species). Biomass estimates for several other model compartments were based on data from other surveys (cetaceans, seals, zooplankton, and phytoplankton) and population models (seabirds, crabs). In other cases, biomass was based on densities reported from other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates) or was estimated by initial models to meet predator demands (large and small demersal feeders, capelin, herring, large and small pelagic feeders, squid). Adults of many fishes or marine mammals in the LSLE ecosystem undertake seasonal migrations between feeding grounds within our study area and overwintering grounds elsewhere. When information was available, biomass was adjusted for residence time (e.g., cetaceans, seals). For fishes, little feeding occurs on the overwintering grounds, so seasonal migrations out of the study area are of little consequence for our mass-balance models in terms of consumption by these migratory fishes.

Very little is known about fish and invertebrate production and consumption in the Estuary and Gulf of St. Lawrence. For most groups, total mortality or production 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 information reported in the literature or estimated using FishBase (Froese and Pauly 2002) for consumption estimates.

Diet compositions were constructed using field data from the study area whenever possible. However, these data do not exist for some species. 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.

These different sources of data (local and literature) explain the high coefficients of variations for diet, production, and consumption data (173%, 70%, and 96%, respectively) compared with that of export (46%). 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 provides an overall view of the ecosystem based on the integration of information available (data, expertises, etc.).

Strengths and weaknesses of inverse models

Trophic relationships in ecosystems are often studied by describing only one steady-state model, without including parameter uncertainty and the ensuing uncertainty in the interpretation of the results (e.g., Ecopath literature). Thus, we decided to randomly perturb each term by up to its standard deviation in order to represent the uncertainties of the input data. This procedure allowed us to appraise the uncertainty in the estimated flows given the uncertainties in the input data. In this study, the final solution is always the mean of one solution without perturbation (the "initial solution") plus 30 iterations with random perturbations of the input data to provide an overall view of the ecosystem and to identify robust patterns. 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). Our current model, even with 41 compartments, still represents simplifications of the trophic interactions in the LSLE.

The use of upper and lower limits to constrain the majority of input values (production, consumption, export, 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. This is done by finding the solution that minimizes (minimum norm inversion) both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors (minimizes the imbalances between inputs and outputs) consistent with the constraints. In the present study, the low sums of squared residuals for all mass-balance and data equations show a good fit between input data and modelling estimates (all: 2.1×10^{-15}; mass-balance eqs.: 3.2×10^{-19}; export eqs.: 4.5×10^{-25}; predation eqs.: 2.1×10^{-15}). The final solution is thus consistent with a steady-state representation of the flows in each compartment.

The minimum norm (MN) inversion is thought to be a parsimonious solution to the ecosystem flow inverse problem. Vézina et al. (2004) examined different goal functions to solve inverse problems. Although they proposed a new minimization (smoothed norm, SN), which simultaneously minimizes the squared flows and the squared differences between flows, as

probably the most attractive option, their simulated experiments also indicated that the MN inversion is a reasonable choice for comparative inverse analyses. One problem with the MN inversion is that it can lead to a number of zeros in the flow network (Vézina et al. 2004). This occurs when there are alternative pathways out of a compartment with no a priori constraints on the relative size of these pathways. The associated effect is that many flows are bound to either their upper or lower limits (active constraints). A large number of active constraints suggests that the optimum may not have been found and that the solution was determined by a priori bounds rather than by patterns in the data. In this study, by randomly perturbing data inputs, we constructed a set of 31 balanced iterations and the final solution was the mean of these iterations. This process reduced significantly the number of active constraints (flows estimated at their pre-set limits) compared to the initial solution before perturbation (Appendix 5). Although individual iterations had a large number of active constraints (like the initial solution), these varied from iteration to iteration. One realization of the data was thus not sufficient to constrain the model. However, many realizations of the data (mean of different iterations) allowed us to construct a solution that was nearly insensitive to the constraints. Most model estimates fell between the upper and lower limits. Overall, 10% of the constraints were active (Appendix 5). Ecotrophic efficiency (20%) had the largest proportion of active constraints. Working with averages of many modelling iterations (and their variation) is thus a much stronger approach than to only consider one iteration and gives more confidence in the results and their interpretation.

CONCLUSION

A steady-state model of the lower Estuary food web was constructed based on a comprehensive set of data that were collected in the years 2008–2010. Energy flows were estimated by means of an inverse methodology of constrained optimization based on the Minimum Norm criterion, i.e., on the minimization of both the sum of squares of the residuals and of the sum of squares of energy flows. The solution was constrained by a set of inequalities that were derived from general eco-physiological knowledge and site–specific data on energy flows. The trophic network was represented by 41 groups, including single-species compartments for the species of high economical or ecological relevance.

The models enabled us to bring together wide-ranging data concerning the LSLE ecosystem and produced values that were logically consistent with our model structure and constraints. These values are meaningful in the sense that they meet some clearly imposed constraints that reflect how we think the system is working. However, even though the model was useful in constraining observations into a coherent picture, it remains that the results are sensitive to choices made regarding the modelling structure and that other equivalent solutions are possible. Such a model provides a useful starting point to frame hypotheses about the ecosystem, to identify data gaps, to show where the uncertainties in the food web occur, and to improve the input parameters in order to enhance the quality of future modelling efforts.

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Appendix 1. Flows (in t km^{-2} yr^{-1}; 646 flows) estimated by inverse modelling and weighting applied during the estimation. Var: variance, CV: coefficient of variation, B: biomass, Q: consumption, DC: proportion in diet (by mass), Obs: locally observed.

Flows	Description

Respiration (41 flows)

Weight: Var(B_y^{obs})

Notation: R_y

Respiration of group y. As bacteria were considered part of the detritus, detritus is assumed to respire.

Egestion (38 flows)

Weight: Var(B_y^{obs})

Notation: D_y

Flow of group y to detritus (detrital flow or non-assimilated food). No egestion term for deep mesozooplankton, phytoplankton (included in mortality term), or detritus.

Other mortality causes (40 flows)

Weight: Var(B_y^{obs})

Notation: MO_y

Natural mortality other than predation of group y including diseases and other natural causes of death (flow to detritus). No mortality term for detritus.

Predation (487 flows)

Weight: Var($Pr_{x \to y}$) = (Q_y^{obs})^2*(CV($DC_{x \to y}^{obs}$)^2+CV(Q_y^{obs})^2)

Notation: $Pr_{x \to y}$

Predation of group x by group y based on the diet composition of each group.

Export (29 flows)

Weight: Var(EX_y^{obs})

Notation: EX_y

Export (including catches) of group y out of the system. No export term for several groups (blue whales, small crabs, echinoderms, polychaetes, other benthic invertebrates, zooplankton groups, and phytoplankton).

Appendix 1. Cont.

Flows	Description

Advection (8 flows)

        Weight: $\mathrm{Var}(B_x^{obs})$

        Notation: ADV_x

        For zooplankton, phytoplankton, and detritus groups, we introduced an "advection" term, which is a residual inflow or outflow that may be required to balance the models in order to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990).

Flow from surface to deep mesozooplankton (1 flow)

        Weight: $\mathrm{Var}(B_x^{obs})$

        Notation: $F_{x \rightarrow y}$

        Inflow from surface mesozooplankton (x) to deep mesozooplankton (y) to reproduce the overwintering of surface population in the deep layer.

Metabolic loss of deep mesozooplankton (1 flow)

        Weight: $\mathrm{Var}(B_x^{obs})$

        Notation: ML_x

        Metabolic loss related to the decrease in the mean body dry weight during winter (Plourde et al. 2003).

Phytoplankton production (1 flow)

        Weight: $\mathrm{Var}(P_{Phy}^{obs})$

        Notation: P_{Phy}

        Gross phytoplankton production (i.e., primary production measured).

Appendix 2. Mass balance and data equations (212 equations) and corresponding weights used in inverse modelling. Var: variance; CV: coefficient of variation; B: biomass; Q: consumption; DC: proportion in diet (by mass); Obs: locally observed; ε: residual, the difference between observations and model estimates.

Mass balance for	Description

Consumers (37 eqs.)

Weight: $\quad$ Var(B_y^{obs})

Equation: $\quad \sum_x Pr_{x \to y} - R_y - D_y - \sum_u Pr_{y \to u} - MO_y - EX_y \pm ADV_y = \Delta B_y + \varepsilon$

For a consumer y, consumption ($\sum_x Pr_{x \to y}$) representing the input must balance the sum of the outputs consisting of respiration (R_y), egestion (detrital flow, D_y), natural mortality (predation by other groups [$\sum_u Pr_{y \to u}$], and other natural causes of death [MO_y]) and fishing mortality (export, EX_y). For macrozooplankton groups, we added an "advection" term (ADV_y) to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990). We assumed that there was no change in biomass ($\Delta B_y = 0$) for these groups.

Surface mesozooplankton (1 eq.)

Weight: $\quad$ Var(B_y^{obs})

Equation: $\quad \sum_x Pr_{x \to y} - R_y - D_y - \sum_u Pr_{y \to u} - MO_y - F_{x \to y} \pm ADV_y = \Delta B_y + \varepsilon$

Consumption ($\sum_x Pr_{x \to y}$) representing the input must balance the sum of the outputs consisting of respiration (R_y), egestion (D_y), predation by other groups ($\sum_u Pr_{y \to u}$), other natural causes of death (MO_y), and outflow from surface to deep mesozooplankton ($F_{x \to y}$). We added an "advection" term (ADV_y) to reproduce the passive export of organisms by the estuarine circulation (Runge and Simard 1990).

Appendix 2. Cont.

Mass balance for	Description

Deep mesozooplankton (1 eq.)

Weight: $\text{Var}(B_y^{obs})$

Equation: $F_{x \to y} - R_y - MO_y - \sum_u Pr_{y \to u} - ML_y \pm ADV_y = \Delta B_y + \varepsilon$

The inflow from surface to deep mesozooplankton ($F_{x \to y}$) must balance the sum of the outputs (respiration [R_y], other natural causes of death [MO_y], and predation by other groups [$\sum_u Pr_{y \to u}$]). We also added a metabolic loss ML_y to represent the decrease in the mean body dry weight during winter and an "advection" term (ADV_{Phy}) to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990).

Phytoplankton (1 eq.)

Weight: $\text{Var}(B_{Phy}^{obs})$

Equation: $P_{Phy} - R_{Phy} - MO_{Phy} - \sum_y Pr_{Phy \to y} \pm ADV_{Phy} = 0 + \varepsilon$

Production (P_{Phy}) must balance the sum of the outputs (phytoplankton respiration, phytoplankton mortality including the egestion term [MO_{Phy}] and consumption of phytoplankton by other groups [$\sum_y Pr_{Phy \to y}$]). We also added an "advection" term (ADV_{Phy}) to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990).

Detritus (1 eq.)

Weight: $\text{Var}(B_{Det}^{obs})$

Equation: $\sum_x D_x + \sum_x MO_x - \sum_y Pr_{Det \to y} - R_{Det} - EX_{Det} \pm ADV_{Det} = 0 + \varepsilon$

Inputs (egestion [$\sum_x D_x$] and other natural causes of death [$\sum_x MO_x$] for other groups) must balance the sum of the outputs (consumption of detritus by other groups [$\sum_y Pr_{Det \to y}$], bacterial remineralization of detritus [R_{Det}], and burial [EX_{Det}]). As bacteria were considered part of the detritus, detritus was assumed to respire. We also added an "advection" term (ADV_{Det}) to reproduce the passive transport of organisms by the estuarine circulation (Runge and Simard 1990).

Appendix 2. Cont.

Mass balance for	Description

Export (26 eqs.)

Weight: $\text{Var}(EX_y^{obs})$

Equation: $EX_y^{obs} = EX_y + \varepsilon$

Export estimated by inverse modelling (EX_y) is equal to observed export (EX_y^{obs}) from local field studies (except for harp seals, seabirds, and detritus).

Predation[a] (145 eqs.)

Weight: $\text{Var}(Pr_{u \to y}) = (Q_y^{obs})^2 * (\text{CV}(DC_{u \to y}^{obs})^2 + \text{CV}(Q_y^{obs})^2)$

Equation: $DC_{u \to y}^{obs} = \dfrac{Pr_{u \to y}}{\sum\limits_{x} Pr_{x \to y}} + \varepsilon$

Proportion of the prey u in the diet (by mass) of consumer y estimated by inverse modelling ($\dfrac{Pr_{u \to y}}{\sum\limits_{x} Pr_{x \to y}}$) is equal to the observed diet proportion ($DC_{u \to y}^{obs}$) from local field studies or available only as low estimates with low SD ($< 0.6\%$).

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[a] Note that the weight of the additional diet equations (predation) for groups with no information on diet proportion variability is the average of all known coefficients of variation for diet proportion ($\text{CV}(DC_{u \to y}^{obs})_{\text{mean}} = 185\%$). Q_y^{obs} is observed consumption from local field studies or the literature ($\text{CV}(Q_y^{obs})_{\text{mean}} = 96\%$).

Appendix 3. Constraints (1729 constraints) used in the inverse modelling.

Constraint for	Description

Non-negativity (638 constraints)

Inequality: $R_y \geq 0; D_y \geq 0; MO_y \geq 0; Pr_{x \to y} \geq 0; EX_y \geq 0; P_{Phy} \geq 0$

All the unknown flows are non-negative.

Growth efficiency (76 constraints)

Inequality: $GE_y^{min} < \dfrac{\sum_x Pr_{x \to y} - R_y - D_y}{\sum_x Pr_{x \to y}} < GE_y^{max}$

Growth efficiency (of food conversion; GE = production/consumption) ranges: 0.1–1% for marine mammals and seabirds; 10–30% for fish, shrimp, crabs, and macrozooplankton; 9–30% for benthic invertebrates; and 25–50% for surface mesozooplankton (Christensen and Pauly 1992).

Assimilation efficiency (76 constraints)

Inequality: $AE_y^{min} < \dfrac{\sum_x Pr_{x \to y} - D_y}{\sum_x Pr_{x \to y}} < AE_y^{max}$

Assimilation efficiency (AE) ranges between 70 and 90% for all the groups (Winberg 1956) except for macrozooplankton and surface mesozooplankton (50–90%) (Christensen and Pauly 1992).

Ecotrophic efficiency (80 constraints)

Inequality: $EE_y^{min} < \dfrac{\sum_x Pr_{x \to y} - R_y - D_y - MO_y}{\sum_x Pr_{x \to y} - R_y - D_y} < EE_y^{max}$

Ecotrophic efficiency (EE: production exported or consumed within the system) ranges between 0 and 0.95 for all groups except for detritus (no constraint[a]) (Christensen and Pauly 1992).

Consumption (76 constraints)

Inequality: $Q_y^{min} < \sum_x Pr_{x \to y} < Q_y^{max}$

Predation of group x by group y ($\sum_x Pr_{x \to y}$) ranges between the minimum and maximum observed consumption values. No term for deep mesozooplankton.

Appendix 3. Cont.

Constraint for	Description

Export (6 constraints)

Inequality: $Exp_y^{min} < EX_y < Exp_y^{max}$

Export of group y ranges between the minimum and maximum observed values (i.e., harp seals, seabirds, and detritus).

Predation (684 constraints)

Inequality: $DC_{u \to y}^{min} < \dfrac{Pr_{u \to y}}{\sum\limits_{x} Pr_{x \to y}} < DC_{u \to y}^{max}$

Proportion of the prey u in the diet (by mass) of consumer y ranges between the minimum and maximum observed values.

Production (80 constraints)

Inequality: $P_y^{min} < \sum\limits_{x} Pr_{x \to y} - R_y - D_y < P_y^{max}$

Production of group y ranges between the minimum and maximum observed values.

Appendix 3. Cont.

Constraint for	Description

Metabolic loss of deep mesozooplankton (2 constraints)

Inequality: $ML_y^{min} < ML_y < ML_y^{max}$

Metabolic loss of deep mesozooplankton (y) ranges between 30% and 50% of the inflow from surface mesozooplankton to deep mesozooplankton (Plourde et al. 2003).

Respiration of macrozooplankton groups and surface mesozooplankton (5 constraints)

Inequality: $0.20 * \sum_x Pr_{x \to y} < R_y$

Respiration (R_y) of group y is at least 20% of total consumption ($\sum_x Pr_{x \to y}$) (Vézina and Pace 1994).

Respiration of deep mesozooplankton (2 constraints)

Inequality: $0.10 * R_x < R_y < 0.20 * R_x$

Respiration of deep mesozooplankton (component in diapause; R_y) ranges between 10% and 20% of respiration of surface mesozooplankton (active component; R_x) (Ingvarsdottir et al. 1999).

Respiration of phytoplankton (2 constraints)

Inequality: $0.05 * P_{Phy} < R_{Phy} < 0.30 * P_{Phy}$

Respiration of phytoplankton ranges between 5% and 30% of gross primary production (Vézina and Savenkoff 1999).

Bacterial respiration (2 constraints)

Inequality: $R_y^{min} < R_y < R_y^{max}$

Bacterial respiration ranges between the minimum and maximum observed values.

[a]: The ecotrophic efficiency of the detritus group is defined as the ratio of what flows out of a detritus box to what flows into that same box (Christensen and Pauly 1992). Under the steady-state assumption, this ratio should be equal to 1 if the mass balance residual of detritus is "0".

Appendix 4. Estimated values (in t km^{-2} yr^{-1}) from the final solution based on 31 balanced and ecologically realistic random perturbations. P_i: production; Q_i: consumption; R_i: respiration; D_i: egestion (detrital flow); MO_i: other mortality; EX_i: fishing mortality (export); SD: standard deviation.

Group	P_i	±SD	Q_i	±SD	R_i	±SD	D_i	±SD	MO_i	±SD	EX_i	±SD
Blue whales	0.011	0.002	1.17	0.67	0.92	0.26	0.24	0.13	0.011	0.002		
Other mysticetes	0.006	0.002	0.59	0.17	0.47	0.15	0.12	0.08	0.002	0.002	3.5×10^{-3}	8.9×10^{-4}
Belugas	0.0028	0.0001	0.010	0.005	0.20	0.02	0.08	0.02	0.003	0.000	1.6×10^{-4}	2.3×10^{-5}
Other odontocetes	0.0001	0.0001	0.28	0.02	0.008	0.006	0.002	0.002	0.0001	0.0001	3.9×10^{-5}	2.5×10^{-5}
Harp seals	0.0001	0.0000	0.008	0.003	0.006	0.001	0.002	0.001	4.7×10^{-6}	1.7×10^{-6}	7.4×10^{-5}	2.4×10^{-6}
Grey seals	0.0016	0.0007	0.06	0.01	0.11	0.05	0.05	0.02	0.002	0.001	2.3×10^{-5}	9.0×10^{-6}
Harbour seals	0.0006	0.0001	0.16	0.06	0.04	0.01	0.02	0.01	0.0006	0.0001	1.1×10^{-5}	6.9×10^{-6}
Seabirds	0.0009	0.0002	0.11	0.09	0.08	0.05	0.03	0.03	0.0007	0.0002	1.9×10^{-4}	6.4×10^{-5}
Large cod	0.05	0.01	0.18	0.05	0.08	0.05	0.05	0.01	0.003	0.004	9.1×10^{-6}	5.2×10^{-6}
Small cod	0.059	0.003	0.26	0.09	0.13	0.09	0.07	0.04	0.003	0.000	1.6×10^{-3}	7.5×10^{-4}
Large Green. Halibut	0.26	0.04	0.90	0.04	0.44	0.10	0.20	0.09	0.21	0.04	4.8×10^{-2}	4.8×10^{-4}
Small Green. Halibut	0.52	0.02	1.74	0.16	0.81	0.17	0.41	0.16	0.51	0.02	1.3×10^{-3}	1.6×10^{-4}
Amer. plaice	0.05	0.01	0.23	0.12	0.13	0.10	0.05	0.03	0.04	0.02	2.3×10^{-3}	1.5×10^{-4}
Flounders	0.06	0.01	0.26	0.14	0.14	0.13	0.06	0.04	0.009	0.014	2.3×10^{-4}	1.7×10^{-5}
Skates	0.14	0.03	0.61	0.04	0.33	0.07	0.14	0.06	0.039	0.047	3.1×10^{-3}	3.4×10^{-4}
Atlantic halibut	0.014	0.005	0.07	0.00	0.04	0.01	0.01	0.01	0.008	0.007	7.1×10^{-4}	7.4×10^{-5}
Redfish	0.015	0.001	0.08	0.03	0.05	0.04	0.02	0.01	0.0008	0.0001	1.7×10^{-4}	2.2×10^{-5}
Black dogfish	0.033	0.013	0.142	0.00	0.08	0.02	0.03	0.01	0.03	0.01	9.2×10^{-5}	7.5×10^{-6}
White hake	0.007	0.003	0.029	0.01	0.01	0.02	0.01	0.01	0.001	0.001	2.6×10^{-4}	2.8×10^{-5}
Large demersals	0.19	0.01	0.73	0.24	0.34	0.21	0.20	0.09	0.009	0.001	1.4×10^{-3}	5.6×10^{-5}
Small demersals	0.526	0.002	2.06	1.03	0.99	0.70	0.55	0.12	0.026	0.000	2.2×10^{-3}	3.0×10^{-4}
Large pelagics	0.001	0.001	0.005	0.002	0.002	0.002	0.001	0.001	0.0001	0.0000	2.3×10^{-4}	2.2×10^{-5}
Capelin	1.45	0.77	10.30	5.98	6.36	6.54	2.49	2.25	0.49	0.72	5.8×10^{-3}	5.0×10^{-4}

Appendix 4. Cont.

Group	P_i	$\pm$SD	Q_i	$\pm$SD	R_i	$\pm$SD	D_i	$\pm$SD	MO_i	$\pm$SD	EX_i	$\pm$SD
Herring	0.054	0.001	0.22	0.10	0.10	0.08	0.06	0.04	0.003	0.000	2.4×10^{-3}	8.6×10^{-4}
Small pel. feeders	0.062	0.000	0.26	0.09	0.13	0.10	0.06	0.03	0.003	0.000	6.5×10^{-4}	3.6×10^{-4}
Squid	0.0036	0.0001	0.012	0.002	0.005	0.001	0.003	0.001	1.8×10^{-4}	5.4×10^{-6}	1.1×10^{-4}	4.6×10^{-6}
Shrimp	2.64	0.22	10.87	3.00	6.09	4.44	2.14	1.43	0.14	0.07	1.6×10^{-1}	2.5×10^{-3}
Large crabs	0.64	0.02	2.20	0.62	0.93	0.17	0.63	0.13	0.44	0.02	2.0×10^{-1}	7.5×10^{-4}
Small crabs	0.15	0.08	0.86	0.61	0.49	0.71	0.22	0.26	0.01	0.02		
Echinoderms	36.98	27.34	190.21	155.09	112.51	142.57	40.72	47.85	2.77	5.44		
Molluscs	61.08	29.62	300.20	249.53	177.49	222.97	61.63	55.94	3.44	2.49	1.3×10^{-2}	3.3×10^{-3}
Polychaetes	28.12	8.83	120.92	45.02	62.84	45.48	29.96	21.75	6.43	10.26		
Other benthic invertebrates	12.67	6.39	67.11	54.22	36.04	37.75	18.41	19.28	1.21	2.19		
Large euphausiids	38.04	14.93	223.17	150.46	137.38	139.15	47.75	60.26	23.82	17.45		
Small euphausiids	57.70	45.00	311.17	273.11	164.39	207.85	89.08	129.11	38.35	45.27		
Large hyperiid amphipods	1.72	1.36	10.73	4.95	6.72	5.87	2.29	3.64	0.62	1.18		
Other macrozooplankton	29.16	2.34	164.89	49.53	99.76	82.98	35.97	32.08	15.84	5.65		
Surface mesozooplankton	666.52	48.91	1360.29	103.69	364.48	132.15	329.29	146.65	35.99	9.89		
Deep mesozooplankton	129.10	6.06			36.45	13.21			59.32	31.59		
Phytoplankton	2924.11	939.49			352.72	319.07			1355.79	1065.78		
Detritus					1576.09	882.51					59.1	8.8

Appendix 5. Number of active constraints for different parameters (estimates at the limit set by the constraints) for the 2008–2010 period. Only the estimates based on the upper and lower constraint limits are used here. Initial solution: first iteration without perturbation; final solution: mean of 31 balanced iterations. P_i: production, Q_i: consumption, EX_i: export, GS_i (=1-AE_i): proportion of food not assimilated, GE_i: growth efficiency, EE_i: ecotrophic efficiency, $DC_{u \to y}$: proportion of prey u in diet (by mass) of consumer y, R_i: respiration, ML_i: metabolic loss of deep mesozooplankton.

		Flow/efficiency									
		P_i	Q_i	EX_i	GS_i	GE_i	EE_i	$DC_{u \to y}$	R_i	ML_i	Total
Initial solution	Number of active constraints	20	14	3	36	30	20	283	4	1	411
	Number of total estimates	40	38	3	38	38	40	342	8	1	548
	% of active constraints	50%	37%	100%	95%	79%	50%	83%	50%	100%	75%
Final solution	Number of active constraints	1	1	0	0	4	8	41	1	1	57
	Number of total estimates	40	38	3	38	38	40	342	8	1	548
	% of active constraints	3%	3%	0%	0%	11%	20%	12%	13%	100%	10%