

PART II: NORTHWEST ATLANTIC

A PRELIMINARY MODEL FOR THE LANCASTER SOUND REGION IN THE 1980s

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ABSTRACT

A preliminary model structure is presented for the Lancaster Sound region, northeastern Canada. The model is composed of 31 groups including 9 groups of mammals. Model inputs were derived mainly from data in Welch *et al.* (1992; Arctic 45: 343-357) and other Ecopath models constructed for other regions of similar latitude. The model balancing procedure is described and major data limitations are identified. Results are preliminary and remain to be verified and refined by scientists working on the ecology and biology of Arctic Sea species. Possible applications of the model are also identified.

INTRODUCTION

A preliminary Ecopath model was constructed for the Lancaster Sound Region (LSR), located between 80-100°W and 72-76°N, a total area of 97,698 km² (Figure 1). A brief description of the area, including depth ranges, circulation patterns and seasonal changes in ice cover is given in Welch *et al.* (1992). The region is important as a habitat and feeding area for populations of marine mammals and seabirds. It also supports four Inuit communities totaling about 2000 individuals and is the site of major industrial activity associated with mining. Further, it represents an important transportation route for aircrafts and ships across the Northwest Passage and there is a high potential for extraction of hydrocarbons. Given the concerns over exploitation of marine mammals (including polar bears) and the accumulation of pollutants in arctic carnivores, quantifying the energy flows throughout this ecosystem will be useful in ascertaining the degree of trophic interaction and dependence among various functional groups. Further, with refinement of the model and application of Ecosim, the path of marine pollutants in the ecosystem can be traced. This

exercise focuses on the first step, i. e., quantifying energy flows among functional groups.

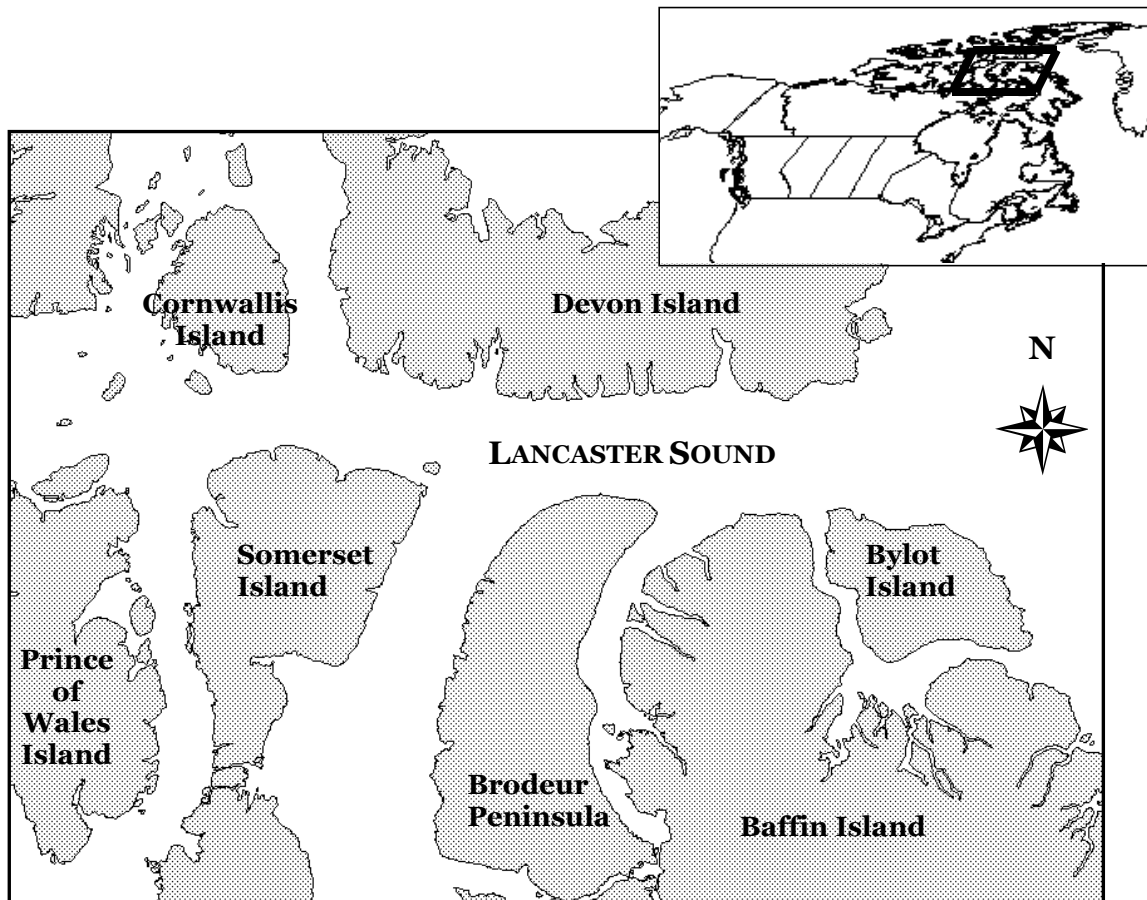
METHODOLOGY AND DATA INPUTS

The model assumes mass balance in that production of any given prey is equal to the biomass consumed by predators plus the biomass caught, (e. g., in fisheries) plus any exports from the system:

$$B_i * (P/B)_i * EE_i = Y_i + \sum B_j * (Q/B)_j * DC_{ij} + E_{xi} \quad \dots 1)$$

where B_i and B_j are biomass for the prey and its consumers respectively, $(P/B)_i$ is the production/biomass ratio, EE_i is the ecotrophic efficiency or fraction of production available for consumption within the system, Y_i is the harvest, $(Q/B)_j$ is the food consumption per unit biomass of the predator 'j', and DC_{ij} is the proportion of prey 'i' in the diet of predator 'j'. All weights are given in tonnes, area in km² and the time unit is a year. The model requires that the diet composition of all groups is known and at least two of the following three parameters: EE , P/B or Q/B are known for each functional group and calculates the missing value by balancing a series of linear equations of the form above for each functional group in the system. P/B , Q/B , fishing mortality (F) and natural mortality (M) are expressed per year.

Initially, apart from primary producers (phytoplankton, algae and kelp), 33 functional groups were identified, based on diet and relative abundance (for lower trophic levels). However, for reasons discussed in the balancing procedure these were reduced to the following 28: polar bear, killer whale, narwhal, beluga whale, bowhead, harp seal, bearded seal, ringed seal, walrus, glaucous gull, murre, black guillemot, northern fulmar, kittiwake, Arctic cod, Greenland halibut, finfish, copepods, other herbivorous zooplankton, ice amphipods, chaetognaths, *Parathemisto* sp., other omnivorous zooplankton, *Mertensia ovum*, other carnivorous zooplankton, *Mya truncata*, other bivalves and other benthos. Input data were acquired from Welch *et al.* (1992) and other sources. These pertained mainly to the late 1980s and given on an annual basis rather than seasonal, (i. e., summer or winter period). When appropriate estimates could not be found, various assumptions were made based on previous studies in other regions of similar latitude.



Primary production

Biomass estimates of 560 t·km⁻², 50 t·km⁻² and 11 t·km⁻² were calculated from data in Welch *et al.* (1992) for phytoplankton, algae and kelp respectively. P/B ratios for phytoplankton (150 year⁻¹) and algae (50 year⁻¹) were obtained from a model of Prince William Sound, Alaska (Okey and Pauly 1998). A P/B of 50 year⁻¹ was assumed for kelp.

Mammals

Polar bear

Estimates of biomass (0.00364 t·km⁻²) and Q/B (3.325 year⁻¹) were derived using data on abundance, mean body weight and distribution area found in Welch *et al.* (1992) and computed as biomass = (mean body weight * abundance)/distribution area. A P/B of 0.02 was assumed. Harvest was estimated at 0.00008 t·km⁻² year⁻¹, given a quota of 38 bears at a mean size of 200 kg and distribution area equivalent to the entire LSR. Polar bear diet was assumed to consist of 95% ringed seal, 1.5% bearded seal, 1.5% harp seal and 1.5% walrus based on Welch *et al.* (1992).

Marine mammals

Marine mammals were divided into eight groups: killer whales, narwhals, beluga whales, bowheads, harp seals, bearded seals, ringed seals and walrus.

Biomass estimates for all groups except bowheads and bearded seals were calculated using estimates of abundance, mean body size and distribution area provided in Welch *et al.* (1992) (Table 1). Killer whale distribution was assumed to be the same as for narwhals, their main prey. Abundance estimates for bowheads and bearded seals were obtained from the Vancouver Aquarium Lancaster Sound 1998 exhibit, while mean size of bowheads was taken from Trites and Pauly (1998). Mean size of bearded seals was estimated using yield in numbers and corresponding weight in Welch *et al.* (1992) (mean size = yield/number caught). The corresponding distribution area was assumed to be the entire LSR. Distribution of bowheads was assumed to be the same as for killer whales.

Table 1. Biomass estimates for marine mammals

Species	Abundance	Mean weight (t)	Area (km ²)	Biomass (t·km ⁻²)
Killer whale	20 ^a	2.3	85,778	0.0005
Narwhal	20 000	0.854	85,778	0.199
Beluga	12 000	0.880	79,968	0.132
Bowhead	200	31.075	85,778	0.072
Harp seal	25 000 ^a	0.106	88,525	0.030
Bearded seal	200	0.250	97,697	0.0005
Ringed seal	161 200	0.50	97,697	0.825
Walrus	1 000 ^a	0.512	30,000 ^a	0.017

^a Crude estimates after Welch *et al.*, 1992

Table 2. Consumption biomass ratios for marine mammals.

Species	Ingestion (t·km ⁻² ·year ⁻¹)	Biomass (t·km ⁻²)	Q/B (year ⁻¹)
Killer whale	-	0.0004	2.4 ^c
Narwhal	0.372	0.199	1.87
Beluga	0.294	0.132	2.23
Bowhead	-	0.072	2.23 ^b
Harp seal	0.094 ^a	0.030	3.13
Bearded seal	-	0.0005	15.67 ^b
Ringed seal	1.285	0.082	15.67
Walrus	0.381 ^a	0.017	22.41

^a Crude estimates according to Welch *et al.* (1992)

^b Assumed

^c 3% body weight (2.3 t) eaten per day (Trites and Heise, 1996) equivalent to 5.13t over 75 days residence time (Welch *et al.*, 1992) gives Q/B of 2.4 year⁻¹

P/B ratios were taken from Trites and Heise (1996). P/B values of 0.06 year⁻¹ were assigned to pinnipeds and 0.02 year⁻¹ to whales. Q/B ratios (Table 2) were estimated as for polar bears using data from Welch *et al.* (1992). Diet composition was estimated based on data from the same source (Table 3). Harvest rates were estimated from data on yield (t·year⁻¹) and distribution area in Welch *et al.* (1992). Killer whales were not harvested and it was assumed that bowheads were also not caught. Estimates are given in Table 4.

Marine birds

Marine birds were organized in five different groups: glaucous gulls, guillemot (adults and juveniles), fulmar (adults and juveniles), murre (adults, juveniles and chicks) and kittiwake (adults and juveniles). Biomass of birds (Table 5) was estimated using the same method as for polar bears and data from Welch *et al.* (1992). P/B ratios were assumed the same as that for similar species in the Prince William Sound region (Okey and Pauly, 1998) (Table 5). Juveniles and chicks were assumed to have P/B of 1.5 times that of adults because of their faster growth rate. Q/Bs were estimated using the same method as for polar bears using data from Welch *et al.* (1992) (Table 5). Diet composition (Table 6) data were taken from Welch *et al.* (1992) and were slightly modified based on further details given for northern fulmars and black-legged kittiwakes. In addition to Arctic cod, these species also consume copepods and amphipods, which were assumed to be of similar proportions in the diet.

Table 3. Diet composition of marine mammals.

Species	NA	BE	BS	RS	AC	GH	OB	PA	MA	OBV
Killer whale	0.512	0.092	0.092	0.092	0.12					
Narwhal					0.75	0.25				
Beluga					1.0					
Bowhead					0.8		0.2			
Harp seal					0.95		0.05			
Bearded seal					0.95 ^a		0.05 ^a			
Ringed seal					0.6		0.15	0.25		
Walrus									0.85	0.15

NA - Narwhals, BE - Beluga, BS - Bearded Seal, RS - Ringed Seal, AC - Arctic Cod, GH - Greenland Halibut, OB - Other Benthos, PA - *Parathemisto* sp., MA - *Mya truncata*, OBV - Other Bivalves.

^aDiet composition assumed same as for harp seal.

Table 4. Harvest estimates of marine mammals.

Species	Yield (t·year ⁻¹)	Distribution area (km ²)	Harvest (t·km ⁻² ·year ⁻¹)
Narwhal	306	85,778	0.004
Beluga	37	79,968	0.00046
Harp seal	35	88,525	0.00039
Bearded seal	45	97,697	0.00046
Ringed seal	375	97,697	0.0038
Walrus	10	30,000	0.00034

Fishes

The main species of importance in the region are Arctic cod, Greenland halibut and other finfish, mainly capelin. The latter is a major food source of the Greenland halibut. Arctic cod biomass was estimated at 0.062 t·km⁻² (Welch *et al.* 1992). Biomass estimates for Greenland halibut and finfish were not available and therefore these were left for estimation by Ecopath using ecotrophic efficiencies (EE) of 0.98 and 0.94 respectively. This implies almost full utilization by predators in the system.

P/B estimates for Pacific cod (1.2 year⁻¹) and Pacific halibut (0.32 year⁻¹) were taken from Okey and Pauly (1998), assuming the parameters are similar for the Arctic cod and Greenland halibut respectively. In the case of Pacific halibut however, P/B was equal to total mortality estimated in the Prince William Sound region. The applicability of the same estimate for Greenland halibut in the Arctic is highly questionable. Further, differences in growth rate of the two species should also be considered in relation to their respective habitats. This is also applicable to capelin, for which a P/B of 3.5 year⁻¹ was also taken from Okey and Pauly (1998).

Again, Q/B estimates were taken from Okey and Pauly (1998) with the same assumptions as for P/B. The estimate used for Arctic cod was 4 year⁻¹. For Greenland halibut (with an asymptotic total length of 138 cm, after Bowering and Lilly, 1992) the Q/B for Pacific halibut over 80 cm TL (1.095 year⁻¹) was used. A Q/B value of 18 year⁻¹ for capelin was taken from the same source.

Table 5. Biomass, P/B and Q/B estimates for marine birds.

Group number, Species	Abundance	Mean body weight (kg)	Area (km ²)	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Ingestion (t·km ⁻² ·year ⁻¹)	Q/B (year ⁻¹)
10, Glaucous Gulls	-	-	-	-	15	NA	130
11, Murre (adults)	452,000	0.9	43,643	0.009	11	0.2749	30.54
11, Murre (juv.)	218,000	0.9	43,643	0.004	16.5 ^a	0.0573	14.34
11, Murre (chicks)	169,500	0.2	43,643	0.00078	16.5 ^a	0.0043	5.51
	-	-	-	0.01378^c	-	-	16.79^d
12, Black guillemot (adults)	34,000	0.4	97,697	0.00014	11 ^a	0.0039	27.86
12, Black guillemot (juv.)	17,000	0.4	97,697	0.00007	16.5 ^a	0.0011	15.71
	-	-	-	0.00021^c	-	-	21.79^d
13, Northern fulmar (adults)	320,000	0.65	78,925	0.003	6	0.1022	34.07
13, Northern fulmar (juv.)	160,000	0.65	78,925	0.001	9 ^a	0.0204 ^b	20.4
	-	-	-	0.004^c	-	-	27.26^d
14, Kittiwake (adults)	200,000	0.365	43,643	0.0017	7 ^a	0.0618	36.35
14, Kittiwake (juv.)	100,000	0.365	43,643	0.0008	10.5 ^a	0.0124 ^a	15.5
	-	-	-	0.0025^c	-	-	25.93^d

^aAssumed value (see text);

^bAssuming ratio of adult to juvenile ingestion rate is 5, i. e., the average observed for other species. Source: Okey and Pauly (1998);

^cSum;

^dMean.

Table 6. Estimates of diet composition for marine birds.

Species	AC	PA	SA	CO	MJ	MC	FF
Gulls	0.29 ^a				0.15 ^a	0.15 ^a	0.41 ^a
Murre (adults)	0.85	0.10	0.05				
Murre (juv.)	0.85	0.10	0.05				
Murre (chicks)	1.0						
Black guillemot (adults)	0.80	0.20					
Black guillemot (juv.)	0.80	0.20					
Northern fulmar (adults)	0.7	0.10 ^a	0.10 ^a	0.10 ^a			
Northern fulmar (juv.)	1.0						
Kittiwake (adults)	0.7	0.10 ^a	0.10 ^a	0.10 ^a			
Kittiwake (juv.)	1.0						

AC- Arctic cod; PA - *Parathemisto* sp; SA- sympagic amphipods; CO – copepods; MJ – Murres juveniles; MC - Murres chicks; FF – Finfish (mainly capelins).

^a Assumed value (see text).

Information on diet composition (Table 7) from FishBase (1998) was modified according to groups present in the system. The diet of Arctic cod was 83% zooplankton and 17% zoobenthos (Craig *et al.*, 1982). The proportion of the diet attributed to zooplankton was divided equally among all such groups and the proportion attributed to zoobenthos divided equally between *M. truncata*, other bivalves and other benthos. The diet of Greenland Halibut comprised 96.9% nekton, 3% zoobenthos and 0.1% zooplankton

(Bowering and Lilly, 1992). The nekton was assumed to comprise of finfish solely while the zooplankton proportion was divided equally among all associated groups. The zoobenthos component was attributed to the ‘other benthos’ group. Planktonic invertebrates are the main food source of capelins. As a result diet was attributed equally to all planktonic groups in the system and 0.5% of the diet divided equally among algae and kelp assuming that these are digested incidentally.

Table 7. Diet composition of fishes.

Species	CO	OHZ	CA	PA	OZ	MO	OB+	CG	KE+	FF
Arctic cod	0.1185	0.1185	0.1185	0.1185	0.1185	0.1185	0.170	0.1185		
Greenland halibut	0.0003				0.0003		0.030	0.0003		0.969
Finfish (capelin)	0.142	0.142	0.142	0.142	0.142	0.142		0.142	0.005	

CO – copepods, OHZ – other herbivorous zooplankton; CA – chaetognaths; PA – *Parathemisto* sp.; OZ – other omnivorous zooplankton; MO – *Mertensia ovum*; OB+ – includes *Mya truncata*, other bivalves and other benthos; CG – other carnivorous zooplankton; KE+ – kelp and algae; FF – finfish (mainly capelin).

Zooplankton

Zooplankton were divided into three groups: herbivorous, omnivorous and carnivorous zooplankton.

Copepods were the only herbivorous zooplankton, amphipods, chaetognaths and *Parathemisto* sp. were the only omnivorous zooplankton, and *Mertensia ovum* was the only carnivorous jelly zooplankton for which detailed information were available. Biomass estimates were taken from Welch *et al.* (1992, Table 4), and converted to the appropriate units using conversion parameters in Table 8. Initially, P/B and Q/B were estimated from data in Welch *et al.* (1992) as growth/biomass and ingestion/biomass respectively; however, the results obtained were several orders of magnitude greater than what has been reported for the respective species. As a result, inputs were taken from other sources (Table 9). The categories 'other herbivorous zooplankton', 'other omnivorous zooplankton' and 'other carnivorous zooplankton' were included to incorporate species not represented in the data, but which may contribute significantly to the diet of other groups.

Several assumptions were made given the general lack of data for lower trophic levels (as was acknowledged by Welch *et al.*, 1992), and they remain to be verified. Biomass of 'other herbivorous zooplankton' was assumed to be equal to that of copepods, 'other omnivorous zooplankton' equal to *Parathemisto* sp., and 'other carnivorous gelatinous zooplankton' equal to *M. ovum*.

Table 8. Conversion parameters used to derive input estimates.

1g C	dw = 10 g ww
Phytoplankton	dw = 0.1 ww
Zooplankton	dw = 0.1 ww
Amphipods	dw : ww = 26:74
Copepods	dw = 10.86% ww
<i>Parathemisto</i> sp.	dw = 0.25 ww
Chaetognaths	dw : ww = 0.083
<i>Mertensia ovum</i>	dw = 0.25 ww
<i>Mya truncata</i>	dw = 0.25 ww

'dw' is dry weight and 'ww' is wet weight.

Diet of copepods and other herbivorous zooplankton was assumed to comprise 50% phytoplankton and 50% algae. For chaetognaths, the diet was assumed to be comprised mainly of copepods and other herbivorous zooplankton (66.7% divided equally between each group), 16.7% algae and 16.7% phytoplankton. This was based on the observation that diet consisted mainly of small herbivorous zooplankton in Arai (1996). For *Parathemisto* sp., and other omnivorous zooplankton, a diet composition of 16.7% copepods, 16.7% other herbivorous zooplankton, 33.3% phytoplankton and 33.3% zooplankton was assumed. Similarly, for ice amphipods a diet composition of 16.7% copepods, 16.7% other herbivorous zooplankton, 16.7% kelp, 16.6% phytoplankton and 33.3% algae was assumed. *Mertensia ovum* diet was assumed to comprise 67% herbivorous zooplankton, 23% omnivorous zooplankton and 10% phytoplankton. The diet of other carnivorous gelatinous zooplankton was assumed to be comprised of 20% for each of the copepod, other herbivorous zooplankton, *M. ovum* and other carnivorous gelatinous zooplankton groups, and 10% for each of *Parathemisto* spp. and other omnivorous zooplankton groups.

Table 9. Biomass, P/B and Q/B input parameters for zooplankton, benthic invertebrates and other benthos.

Group	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)
Copepods	13.26	21 ^a (mean)	70 ^d (mean)
Other herbivorous zoo.	13.26 ^d	21 ^a (mean)	70 ^a (mean)
Ice amphipods	0.019	2.4 ^b	12 ^d
Chaetognaths	12.000	3 ^c	10 ^d
<i>Parathemisto</i> sp.	2.72	6.45 ^d	21.5 ^d
Other omnivorous zoo.	2.72 ^d	6.45 ^a (mean)	21.5 ^a (mean)
<i>Mertensia ovum</i>	2.29	8.82 ^a	29.4 ^a
<i>Mya truncata</i>	580	0.034	28.6
Other bivalves	-	0.034 ^d	23 ^a
Other benthos	-	0.885 ^a	23 ^a
Other carnivorous zoopl.	2.29 ^d	8.82 ^a	29.4 ^a

^a Okey and Pauly (1998). Mean estimates are calculated from Tables 9 and 10 of the reference paper; ^b Jarre-Teichman and Guénette (1996) for southern B.C. Model; ^c Arai (1996) Alaska Gyre Model; ^d Assumed value. Unmarked inputs are taken from Welch *et al.*, (1992).

Benthic invertebrates

Benthic invertebrates were divided into two broad groups: bivalves and other benthos. As with zooplankton, data were unavailable for this trophic level group. The biomass estimate of *Mya truncata* (bivalve), 580 t·km⁻², was derived using data from Welch *et al.* (1992). No estimates were available for other bivalves such as *Hiatella arctica*, *Serripes groenlandicus* and *Macoma calcarea*, hence these were grouped under 'other bivalves' and their biomass estimated by Ecopath assuming an ecotrophic efficiency of 0.81 (after Jarre–Teichmann and Guénette, 1996) and a P/B similar to that of *Mya truncata*. A P/B value for the latter species of 0.34 year⁻¹ was estimated from data in Welch *et al.* (1992), while Q/B was set at 28.6 year⁻¹ (Okey and Pauly, 1998 for benthos) assumed. It must be cautioned that the method for deriving Q/B (i. e., ingestion/biomass) using data in Table 4 of Welch *et al.* (1992) yielded unrealistic estimates (see above). A diet composition of 100% detritus was applied to all filter-feeding bivalves (*M. truncata* and other bivalves).

'Other benthos' includes sea cucumbers, sea urchins, brittle stars, anemones, terebellid polychaetes, pycnogonids, small crustaceans and molluscs. Welch *et al.* (1992) gave estimates of density for some species in Barrow Strait. These could be converted to biomass, given mean weight of the respective species. However, because of lack of data and associated additional assumptions regarding P/B and Q/B, these taxa were aggregated into the general category 'other benthos'. P/B and Q/B for the group were taken from Okey and Pauly (1998) (Table 9). An ecotrophic efficiency of 0.81 was assumed (the mean estimated for major benthic groups in Jarre–Teichmann and Guénette, 1996) and biomass estimated by Ecopath. Diet composition was estimated to be 70% detritus, 29% other bivalves and 1% zooplankton (divided equally between other herbivorous and other omnivorous zooplankton), based on data for major benthic groups in Jarre–Teichmann and Guénette (1996).

BALANCING THE MODEL AND ASSOCIATED RESULTS

The model was balanced using a systematic approach, first adjusting the parameters of respective groups for which there was the least confidence in accuracy. The resulting parameters, diet matrix, and output summary statistics are shown in Table 10-12. Trophic interactions are represented in Figure 2. The area of each box is proportional to the logarithm of the biomass of

the respective group and all flows are in t·km⁻²·year⁻¹·ww.

Primary producers

Initially, an EE value >1 was obtained for algae. This indicates either low P/B or low biomass compared to the quantities consumed. Given the greater confidence in biomass estimate, the P/B was increased to 70 year⁻¹ until EE was no longer larger than 1. This solution also resulted in a positive estimate for the respiration.

Marine mammals

Ecotrophic efficiencies (EE) >1 were obtained for bearded and ringed seals. This implies one of four things: low biomass, low P/B, inaccurate diet composition of associated predators or some combination of the other three. Adjusting diet composition is the most difficult 'fix', given the possible consequences for other animals in the ecosystem. Hence, balancing the model focused on altering the biomasses which were often poorly known (Welch *et al.*, 1992). In the case of ringed seals, EE was set at 0.95 since their utilization by predators was considered close to maximum possible yield (Welch *et al.*, 1992) and the biomass increased to 0.22 t·km⁻². The resulting P/B estimated by Ecopath was 0.08 year⁻¹. The biomass for bearded and harp seals was gradually increased to 0.05 t·km⁻² when their EE became smaller than 1. Also, to achieve mass-balance for this group, the original narwhal biomass was increased to 0.3 t·km⁻².

Marine birds

EE >1 was derived for juveniles of all groups and murre chicks. Also, P/B ratios were greater than (Q/B)/2 for these groups. Since diet composition of adult and juvenile marine seabirds was the same in most instances, all life stages of each species were grouped into one category, the biomass summed and average Q/B used. P/B was assumed to be that for adults. Further, the diet composition of the predatory glaucous gulls was altered to include 30% murre, 29% arctic cod and 41% finfish (mainly capelin). Also, the diet composition of northern fulmars and kittiwakes was adjusted to include copepods, which comprised 10% of juvenile diet for both groups. It is to be noted, however, that most predation and cannibalism among marine birds is not represented in the model (hence the EE of zero for each group except murre). The model further

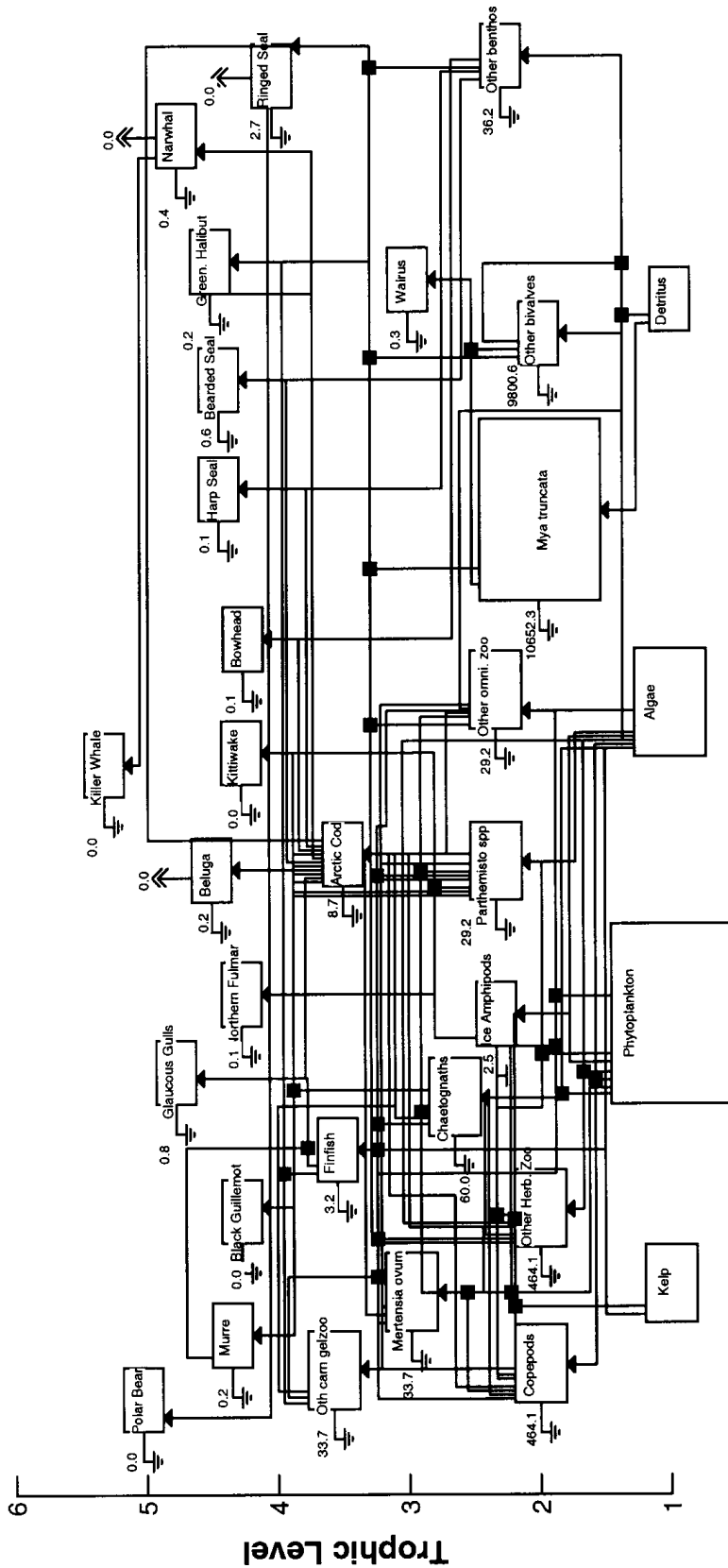


Figure 2. Flow chart of trophic interaction in the Lancaster Sound Region (preliminary model).

indicated $P/B > (Q/B)/2$ for murre and black guillemots indicative of growth in excess of what can be accommodated with the input Q/B . Thus their Q/B was increased, from 16.79 year⁻¹ to 23 year⁻¹ for murre and from 21.79 year⁻¹ to 23 year⁻¹ for black guillemot. A negative respiration was noted for murre and the P/B was increased gradually from 11 year⁻¹ until the respiration estimate became positive. This occurred at $P/B = 27$ year⁻¹. The Q/B was increased accordingly to 54 year⁻¹ to avoid $P/B > (Q/B)/2$, which is so extremely unlikely as to be impossible.

Fishes

Ecopath assigned a negative respiration to arctic cod indicative of either low biomass or low P/B

ratio. Since Welch *et al.* (1992) indicated that cod biomass may have been underestimated as acoustic surveys failed to detect schools in deep waters, this parameter was left for estimation by Ecopath. Further, since predation on the species is high, an EE of 0.95 was assumed. Ecopath estimated a biomass of 4.347 t·km⁻². Hop *et al.* (1997), working on the bio-energetics of cod at low temperatures, suggested that biomass must have been about five times the value found in Welch *et al.* (1992). This would give a biomass estimate of 0.31 t·km⁻², considerably lower than the estimate obtained here. Further refinement of the model should verify which of the two estimates is more accurate.

Table 10. Parameters of the balanced Lancaster Sound model. All biomass are expressed in wet weight. Parameters estimated by Ecopath are in bold italics.

Group number and name	Trophic level	Biomass in habitat area (t·km ⁻²)	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	P/Q
1 Polar bear	4.9	0.004	0.004	0.02	3.325	0	0.006
2 Killer whale	5.1	0.001	0.001	0.02	2.4	0	0.008
3 Narwhal	4.5	0.3	0.3	0.02	1.87	0.871	0.011
4 Beluga	4.3	0.132	0.132	0.02	2.23	0.462	0.009
5 Bowhead	4.1	0.072	0.072	0.02	2.23	0	0.009
6 Harp seal	4.3	0.05	0.05	0.06	3.13	0.197	0.019
7 Bearded seal	4.3	0.05	0.05	0.06	15.67	0.293	0.004
8 Ringed seal	3.9	0.22	0.22	0.08	15.67	0.95	0.005
9 Walrus	3.0	0.017	0.017	0.06	22.41	0.745	0.003
10 Glaucous gulls	4.5	0.009	0.009	15	130	0	0.115
11 Murre	4.2	0.014	0.014	27	54	0.929	0.5
12 Black guillemot	4.1	0.001	0.001	11	23	0	0.478
13 Northern fulmar	4.1	0.004	0.004	6	27.26	0	0.22
14 Kittiwake	4.1	0.003	0.003	7	25.93	0	0.27
15 Arctic cod	3.3	4.347	4.347	1.2	4	0.95	0.3
16 Greenland halibut	4.2	0.447	0.447	0.32	1.095	0.98	0.292
17 Copepods	2.0	13.26	13.26	21	70	0.358	0.3
18 Other herbivorous zooplankton	2.0	13.26	13.26	21	70	0.359	0.3
19 Ice amphipods	2.3	0.019	0.019	220	440	0.939	0.5
20 Chaetognaths	2.3	12	12	3	10	0.187	0.3
21 <i>Parthemisto</i> sp.	2.3	2.72	2.72	6.45	21.5	0.821	0.3
22 Other omnivorous zooplankton	2.3	2.72	2.72	6.45	21.5	0.781	0.3
23 <i>Mertensia ovum</i>	3.0	2.29	2.29	8.82	29.41	0.806	0.3
24 <i>Mya truncata</i>	2.0	580	580	0.034	23	0.066	0.001
25 Other bivalves	2.0	576.801	533.62	0.034	23	0.81	0.001
26 Other benthos	2.0	2.225	2.225	0.885	23	0.81	0.038
27 Kelp	1.0	11.05	11.05	50	-	0.003	-
28 Other carnivorous jelly zooplankton	2.3	2.29	2.29	8.82	29.41	0.806	0.3
29 Phytoplankton	1.0	560	560	150	-	0.012	-
30 Algae	1.0	50	50	70	-	0.283	-
31 Finfish	3.2	0.29	0.29	3.5	18	0.94	0.194
32 Detritus	1.0	-	-	-	-	0.289	-

Table 12. Summary statistics of the preliminary ecosystem model for the Lancaster Sound Region

Parameter	Value
Sum of all consumption ^a	28925
Sum of all exports ^a	65633
Sum of all respiratory flows ^a	22419
Sum of all flows into detritus ^a	92276
Total system throughput ^a	209253
Sum of all production ^a	88773
Mean trophic level of the catch	4.350
Calculated total net primary production ^a	88053
Total primary production/total respiration	3.928
Net system production ^a	65633
Total primary production/total biomass	48
Total biomass/total throughput	0.009
Total biomass (excluding detritus) ^b	795
Total catches ^a	0.010
Connectance index	0.143
System Omnivory Index	0.142

^a Unit: Wet weight (t·km⁻²·year⁻¹); ^b Unit: Wet weight (t·km⁻²)

DISCUSSION

The exercise can be considered at best a first pass at the application of ecosystem modeling using Ecopath for the Lancaster Sound Region. However, as recognized by Welch *et al.* (1992), upon which this exercise is based, major data gaps for intermediate trophic levels, most benthic species and most zooplankton species exist. Also, data on feeding habitats, ranges and populations are incomplete, resulting in difficulties in estimating total kill and prey consumption in whales and birds. This is a direct result of migration out of the region (Welch *et al.*, 1992).

Although assumptions regarding P/B and Q/B for individual species are possible based on studies conducted elsewhere, the same cannot be done for biomass. In some instances, therefore, assumptions regarding the ecotrophic efficiency were made, allowing for estimation of biomass by Ecopath once the other three input parameters were known. Even so, these assumptions can severely affect interpretations derived from output parameters if environmental or habitat conditions for other studies are markedly different from the LSR. Differences in P/B and Q/B associated with the temperature changes implied with increasing latitude should be accounted for. It must be cautioned that a balanced model does not imply accurate depiction of the existing situation. The predictions are only as reliable as the input

parameters used. The lack of data forced assumptions to be made, which may or may not reflect the existing situation in the LSR.

Further, clarification remains to be sought regarding the estimation of growth and ingestion parameters for zooplankton, benthic invertebrates and arctic cod in Welch *et al.* (1992). Once this is done, accurate parameters representative of these functional groups in the LSR can be substituted into the model. It would also be useful if data inputs for the summer and winter period were treated separately, as this would allow differences in bio-energetics associated with each period to be incorporated in the model. Welch *et al.* (1992) also gives estimates of respiration and gross growth efficiencies for some species, which can be compared with model outputs (or used in the 'alternative input' routine of Ecopath).

Further refinement of the Ecopath model for the LSR should be a collaborative effort among scientists with research interests on species in the area to strengthen the reliability of the input parameters to the model and facilitate a greater understanding of the trophic dynamics of the system. The usefulness of such an exercise is the ability to trace accumulation of pollutants up the food web using the routine now implemented in Ecosim and/or to examine implications of possible policy options regarding harvesting of marine mammals (including polar bears) and fish species.

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