BASS/MODEL WORKSHOP ON HIGHER TROPHIC LEVEL MODELING
(Co-convenors: Gordon A. McFarlane, Andrei S. Krovnin, Bernard A. Megrey and Akihiko Yatsu)

The PICES BASS/MODEL Workshop to examine the feasibility of using ECOPATH/ECOSIM as a tool to model higher trophic level components of the Subarctic gyre systems, was held March 5-6, 2001, in Honolulu, U.S.A. The participants are listed in BASS Endnote 1. Objectives of the workshop were to:

1. Synthesize all trophic level data in a common format;
2. Examine trophic relationships in both the Eastern Subarctic Gyre (ESA) and Western Subarctic Gyre (WSA) using ECOPATH/ECOSIM; and
3. Examine methods of incorporating the PICES NEMURO lower trophic level model into the analysis.

Overview of ECOPATH/ECOSIM

Kerim Aydin gave a brief overview of ECOPATH/ECOSIM. An ECOPATH model creates a quantitative food web using the principle of mass-balance. Each "box" in an ECOPATH model may represent a single species or a species guild. The units may vary from model to model. The following quantities were used as input for the initial ESA and WSA models:

- Biomass (t/km^2)
- Production per unit biomass (year^{-1})
- Consumption per unit biomass (year^{-1})
- Fisheries catch (t/km^2/year)
- Diet matrix for each predator (% of diet by weight, shown here as trophic level)

From this information, ECOPATH calculates an "Ecotrophic Efficiency" for each box, which represents the ratio between the production of each box and the amount of biomass "demanded" by the predators and fisheries on a box. An Ecotrophic Efficiency greater than 1 indicates that, according to the model, more is being demanded of a box than is being produced. This quantity is a useful diagnostic tool for examining the quality of data between boxes.

The inputs used for each box in the ESA and WSA models are shown in Tables 1 and 2. No fishing was included in the model as befits the subarctic North Pacific in the early 1990s. These values represent the model as it existed at the end of the workshop and incorporate adjustments made over the course of the workshop. This model was "mass-balanced" in that all Ecotrophic Efficiency values were less than 1.

Data quality was categorized as follows (Tables 1 and 2):

- Acceptable: generally considered to be "reasonable" estimates for model use
- General: consistent with known patterns for the species in question, but may be improved through re-examination of existing data, or further consultation with other researchers
- Poor: little information for these species, or the information available to the workshop was known to be potentially inaccurate (collected outside the model domain)
- N/A: no data available: estimates were derived from ECOPATH model

There is considerable room for improving the estimates, and every attempt should be made to upgrade most of the estimates from "General" to "Acceptable" before the model is considered "functional". It was felt that much improvement in data quality could be accomplished by re-reviewing existing data using this preliminary model as a framework. Final data quality is a combination of two properties: the quality of each datum, and the sensitivity of the model to that input.

Overview of NEMURO

Bernard Megrey gave a brief review of the NEMURO lower trophic level model focusing on recent improvement to NEMURO. Topics included the addition of diagnostic calculations, validation to Station P data, addition of

Table 1 ECOPATH biomass estimates used in eastern/western subarctic gyre models.

	Eastern Gyre		Western Gyre		Data
Group	**t**	**t/km²**	**t**	**t/km²**	**Quality**
Sperm whales	3,364	0.000929	2,014	0.000929	Acceptable
Toothed whales (orca)	100	0.000028	2,168	0.001000	General
Fin	100,992	0.027883	60,450	0.027883	Poor
Sei	21,379	0.005902	12,796	0.005902	Not. Avail.
Minke	-	-	2,168	0.001000	
Northern fur seals	890	0.000246	533	0.000246	
Elephant seals	1,558	0.000430	-	-	
Dall's porpoise	21,683	0.005986	12,978	0.005986	
Pacific white sided dolphin	14,352	0.003962	8,591	0.003962	
Northern right whale dolphin	14,116	0.003897	8,449	0.003897	
Common dolphin	-	-	2,168	0.001000	
Albatross	143	0.000040	3,361	0.001550	
Shearwaters	1,449	0.000400	2,681	0.001237	
Storm Petrels	203	0.000056	340	0.000157	
Kittiwakes	189	0.000052	249	0.000115	
Fulmars	269	0.000074	328	0.000151	
Puffins	209	0.000058	698	0.000322	
Skuas	195	0.000054	174	0.000080	
Jaegers	137	0.000038	132	0.000061	
Sharks (Blue & Salmon)	181,100	0.050000	53,550	0.024700	
Dogfish	181,100	0.050000	53,550	0.024700	
Daggertooth	18,110	0.005000	2,003	0.000924	
Large gonatid squid	108,660	0.030000	102,330	0.047200	
Clubhook squid	43,464	0.012000	160,432	0.074000	
Flying squid	1,629,900	0.450000	47,696	0.022000	
Sockeye	324,733	0.089656	6,721	0.003100	
Chum	196,080	0.054136	32,954	0.015200	
Pink	84,272	0.023267	427,746	0.197300	
Coho	16,131	0.004453	12,574	0.005800	
Chinook	33,696	0.009303	8,455	0.003900	
Steelhead	33,696	0.009303	8,455	0.003900	
Pomfret	760,620	0.210000	115,121	0.053100	
Saury	1,629,900	0.450000	102,546	0.047300	
Japanese anchovy	-	-	381,250	0.175853	
Pacific sardine	-	-	37,207	0.017162	
Misc. Forage (Stickleback)	3,763,258	1.039000	897,552	0.414000	
Micronektonic squid	3,462,632	0.956000	1,903,504	0.878000	
Mesopelagic fish	16,299,000	4.500000	14,092,000	6.500000	
Lg. Jellyfish	14,488,000	4.000000	1,017,264	0.469217	
Ctenophores	32,960,200	9.100000	21,680,000	10.000000	
Salps	28,976,000	8.000000	21,680,000	10.000000	
Chaetognaths	23,905,200	6.600000	115,737,135	53.384287	
Sergestid shrimp	18,110,000	5.000000	17,634,512	8.134000	
Oth. Lg. Zoop. (Larv., Poly)	18,359,194	5.068800	17,634,512	8.134000	
Amphipods (most. Hyp)	36,718,387	10.137600	18,449,680	8.510000	
Pteropods	36,718,387	10.137600	35,269,024	16.268000	
Euphausiids	91,795,968	25.344000	88,172,560	40.670000	
Copepods	126,219,456	34.848000	101,267,280	46.710000	
Microzooplankton	126,219,456	34.848000	49,232,701	22.708810	
Bacteria	75,880,000	35.000000	355,601,864	164.023000	
Large phytoplankton	252,453,400	69.700000	148,386,592	68.444000	
Small phytoplankton	275,272,000	76.000000	187,694,600	86.575000	
DNH3	-	-	-	-	
DNO3	-	-	-	-	
PON	-	-	-	-	

Table 2 Life history and diet parameters of eastern and western subarctic gyre ECOPATH Models.

Group	Prod./Bio. ($year^{-1}$)	Cons./Bio. ($year^{-1}$)	Trophic Level East	Trophic Level West	Data Quality
Sperm whales	0.060	6.608	5.4	5.4	Acceptable
Toothed whales (orca)	0.025	11.157	5.3	5.3	General
Fin	0.020	4.562	4.1	4.3	Poor
Sei	0.020	6.152	4.1	4.3	Not. Avail.
Minke	0.020	7.782	-	4.4	
Northern fur seals	0.235	39.030	5.2	5.2	
Elephant seals	0.368	11.078	5.2	-	
Dall's porpoise	0.100	27.471	5.3	5.2	
Pacific white sided dolphin	0.140	25.828	5.2	5.2	
Northern right whale dolphin	0.160	24.138	5.3	5.2	
Common dolphin	0.100	24.983	-	5.2	
Albatross	0.050	81.586	5.9	5.5	
Shearwaters	0.100	100.127	4.7	4.8	
Storm Petrels	0.100	152.083	4.6	4.7	
Kittiwakes	0.100	123.000	4.6	4.7	
Fulmars	0.100	100.256	4.9	5.1	
Puffins	0.100	104.333	4.7	4.8	
Skuas	0.075	96.600	4.8	4.9	
Jaegers	0.075	96.600	4.8	4.9	
Sharks (Blue & Salmon)	0.200	10.950	5.4	5.3	
Dogfish	0.200	10.950	4.9	5.0	
Daggertooth	1.000	10.000	5.0	5.0	
Large gonatid squid	2.555	7.300	4.2	4.4	
Clubhook squid	2.555	7.300	4.9	5.1	
Flying squid	2.555	6.205	5.3	5.1	
Sockeye	1.265	10.132	4.3	4.4	
Chum	1.932	14.507	3.7	3.9	
Pink	3.373	18.494	4.2	4.1	
Coho	2.472	16.548	4.9	4.8	
Chinook	0.800	5.333	4.9	4.9	
Steelhead	0.800	5.333	4.9	4.8	
Pomfret	0.750	3.750	4.8	5.0	
Saury	1.600	7.900	3.8	3.5	
Japanese anchovy	1.500	5.000	-	3.8	
Pacific sardine	0.400	3.000	-	3.2	
Misc. Forage (Stickleback)	1.500	5.000	3.9	4.1	
Micronektonic squid	3.000	15.000	3.9	4.1	
Mesopelagic fish	0.900	3.000	3.9	3.9	
Lg. Jellyfish	3.000	10.000	3.6	3.7	
Ctenophores	4.000	110.000	2.7	2.7	
Salps	9.000	30.000	2.7	2.7	
Chaetognaths	2.555	12.045	3.5	3.5	
Sergestid shrimp	2.555	12.045	3.5	3.5	
Oth. Lg. Zoop. (Larv., Poly)	2.555	12.045	3.5	3.5	
Amphipods (most. Hyp)	2.555	12.045	3.1	3.1	
Pteropods	2.555	12.045	3.1	3.1	
Euphausiids	2.555	12.045	3.1	3.1	
Copepods	23.725	112.420	2.4	2.4	
Microzooplankton	48.910	233.235	2.3	2.3	
Bacteria	18.450	25.000	2.0	2.0	
Large phytoplankton	42.340	-	1.0	1.0	
Small phytoplankton	129.575	-	1.0	1.0	
DNH3	-	-	1.0	1.0	
DNO3	-	-	1.0	1.0	
PON	-	-	1.0	1.0	

zooplankton vertical migration, examining the effects of including a microbial loop approximation, and performing a sensitivity analysis and data assimilation

Diagnostic calculations

In order to perform regional comparisons of model performance, several diagnostic calculations were added to NEMURO. These included Production/ Biomass (P/B) ratios for phytoplankton and zooplankton, Food Consumption/Biomass (C/B) ratios for small, large and predatory zooplankton, and Ecotrophic Efficiency (a measure of how much primary production transfers up the food web to the zooplankton species and ultimately to higher trophic level species) calculations.

Comparison of model output and field measurements

NEMURO was parameterized for Ocean Station P and output was compared to data collected from that site. Results were favourable. The C/B and P/C ratios are both reasonable. Annual primary production from the model (149 $gC/m^2/yr$) is only 6% higher than the best current estimate (140 $gC/m^2/yr$). An f-ratio (assuming that the production of the large phytoplankton is primarily fuelled by "new" nitrogen was 0.23.

Vertical migration

At Station P, during spring, the large zooplankton component (ZP) should be dominated by *Calanus/Neocalanus* spp. which undergo a strong ontogenetic vertical migration. Thus, the model population should increase in biomass in the early spring independently of food availability/grazing. Later in the year, the population should decrease by some amount to simulate the descent of the large zooplankton to deeper depths. NEMURO was modified to reflect this situation.

Results without migration of predatory zooplankton (ZP) show a large diatom bloom around day 73. The prevailing view is that there is no spring bloom at Station P. Thus the bloom is an artifact of the "box" nature of the model. With ZP migration, values of PL drop by a factor of 2 and generate more reasonable diagnostics. The estimates of Ecotropic Efficiency are not significantly affected.

Microbial loop approximation

Climate change patterns that produce warmer water and greater rainfall enhance stratification of the water column. This lowers primary production by reducing or eliminating the mixing that is needed to propel nutrients into the surface photic zone. Data from Ocean Station P show decreased nitrogen and reduced primary production with warmer temperatures over a period of about 25 years. These conditions change the quantity of phytoplankton as well as the phytoplankton assemblage. With high nutrient concentrations, large phytoplankton that are eaten by copepods dominate the phytoplankton assemblage (i.e. the pelagic food chain). This energy is transferred to larval and adult planktivorous fishes. With low nutrient concentrations, the phytoplankton assemblage is altered, with the microbial loop food chain being favoured over the pelagic food chain. Small nanoplankton are favoured, which are eaten by protozoans like rotifers, with secondary production generally becoming unavailable to fish.

A pragmatic approach to including the microbial food web is through the variable BetaZS (growth efficiency of Small Zooplankton, ZS)

BetaZS = 0.3 (1+ PhySn/(PhySn+PhyLn))

This means that the gross growth efficiency of the small zooplankton can vary between 0.3 and 0.09, and will probably average about 0.16 over the year at Station P. For the base model run, a constant BetaZS=0.3 was used.

Including a microbial loop had only a small impact on the standing stocks of small and large zooplankton. Predatory zooplankton were reduced by about one half reducing potentially available biomass for fish production. These differences are due to the decreased net trophic efficiency of the system, which results when a large portion of the primary production passes through a microbial community before entering the zooplankton community.

Sensitivity analysis

A Monte Carlo analysis of the WSA with 600 replications randomly varied the input parameters and initial values by ±10% using a uniform error distribution. Principal component analysis (PCA) reduced the 600 sets of output of biological parameters and initial values. The PCA indicated that four factors explained 22% of variance in the data. The first principal component, was clearly related to photosynthesis of PL. It accounted for 10% of variance and was correlated with the variables VmaxS, VmaxL, and PL, $N0_3$, NH_4. The second principal component was related to the zooplankton state variables, ZL and ZS.

Based on the sensitivity analysis, the parameters selected to estimate from the observed data were V_{maxS}, V_{maxL}, λ_P, MorZP0 and VD2N0. Data from the A-line (off Hokkaido, Japan - outside the Oyashio region) was used with a conjugate gradient method to calculate the local minimum of the cost function, which is defined as the squared differences between observed and simulated data. After estimating these parameters, the time-dependent features of each compartment of the NEMURO/FORTRAN Box model were calculated.

The boundary areas selected for the two ECOPATH models coincide with PICES' definitions of the Western Subarctic (WSA) and the Eastern Subarctic (ESA), namely the regions above 45°N, bounded by the shelf breaks and divided by 165°W. The total areas for the WSA and the ESA are 2 168 000 km^2 and 3 622 000 km^2 respectively.

BASS Endnote 1

Participation List

Canada
- Richard J. Beamish
- Jacqueline R. King
- Gordon A. McFarlane
- Daniel M. Ware

China
- Qi-Sheng Tang

Japan
- Makoto Kashiwai
- Michio J. Kishi
- Hiroyuki Sakano
- Lan Smith
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U.S.A.
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