Table 18. Population statistics of marine mammals in PWS (excl. sea otter)

Species	Mean Body weight(kg) Females	Males	Pop. (N)	Biomass (t·km⁻²)	Days in PWS	Ration (kg·day⁻¹) Males	Females	Q/B (year⁻¹)
Transients								
Fin whale	59819[a]	51361[a]	50[c]	0.078	90[b]	2055.0[a]	2393.0[a]	3.6
Humpbacks	32493[a]	28323[a]	96[b]	0.191	210[b]	365.0[a]	407.0[a]	2.7
Minke	7011[a]	6121[a]	10[i]	0.004	180[b]	107.0[a]	119.0[a]	3.1
Belugas	590[b]	860[b]	200[b]	0.003	60[b]	47.3[b]	32.5[b]	3.3
Trans. Orca	2761[a]	3068[a]	45[f]	0.005[g]	12[j]	61.6[a]	56.6[a]	2.4
Residents								
Res. Orca	1974[a]	2587[a]	176[f]	0.040[a]	365	53.7[a]	43.3[a]	7.8
Dall's porpoise	61[a]	63[a]	7,328[c]	0.052	365[b]	2.8[a]	2.7[a]	16.2
Harbor porpoise	30[a]	33[a]	768[d]	0.003	365[b]	1.6[a]	1.5[a]	18.0
Pinnipeds								
Harbor seal	77[b]	85[b]	1,300[c]	0.012	365[b]	6.4[b]	5.8[b]	27.5
Steller sea lion	263[b]	566[b]	6537[b]	0.285	365[b]	45.3[b]	21.0[b]	29.2

a) Trites and Heise (1996, Appendix Table A, B);
b) Calkins (1986);
c) Anon. (1980);
d) Estimated populations of 590 porpoises in Winter and 946 in summer (1979)[b] give an annual mean of 768 porpoises;
e) Leatherwood et al. (1990);
f) Derived from Leatherwood et al. (1990, Table 2), assuming that immature/other killer whales weigh the same as a female, and the calves weigh on average 180 kg (Calkins 1986);
g) Calkins and Pitcher (1982);
h) Based on record of 37 minke whales in the Gulf of Alaska (including PWS) during a survey conducted in 1980 (Rice and Wolman 1981);
i) Indirect estimate, obtained by first assuming a higher residence time, and evaluating its impact on the preys.

Table 19. Basic statistics for transient marine mammals in PWS.

Species	Biomass (t·km⁻²)	P/B[a] (year⁻¹)	Q/B (year⁻¹)
Fin whale	0.078	0.005	3.6
Humpback whale	0.191	0.012	2.7
Minke whale	0.004	0.001	3.1
Beluga whale	0.003	0.003	3.3
Killer whale, trans.	0.001	0.007	2.4
Total (weighted average)	0.281	0.020	3.0

a) Trites and Heise (1996).

Table 20. Basic statistics for resident marine mammals in PWS

Species	Biomass (t·km⁻²)	P/B[a] (year⁻¹)	Q/B (year⁻¹)
Killer whale, resid.	0.040	0.02	7.8
Dall's porpoise	0.052	0.02	16.2
Harbor porpoise	0.003	0.02	18.0
Total (weighted average)	0.095	0.02	12.7

Trites and Heise (1996).

Table 19-21 summarize the statistics of each of the three groups. For transient mammals, all values have been adjusted using the number of days that the species are thought to occur in the Sound in proportion to the number of days in a year. Table 22, finally, presents the diet matrix for the three groups covered here.

BALANCING THE MODEL

There are two ways that Ecopath models can be balanced, given a set of inputs such as presented here: (1) by modifying those inputs subjectively felt to be most questionable until mass-

Table 21. Basic statistics for pinnipeds in PWS.

Species	Biomass ($t \cdot km^{-2}$)	P/B[a] ($year^{-1}$)	Q/B ($year^{-1}$)
Harbor seal	0.012	0.06	27.5
Steller sea lion	0.285	0.06	29.2
Total (weighted average)	0.297	0.06	29.1

Trites and Heise (1996).

balance is achieved, or (2), more rigorously, by entering uniform, triangular or normal distributions about each of the inputs (B, P/B, Q/B, EE, DC), and using the 'Ecoranger' routine of Ecopath to identify, through a Monte-Carlo approach, a set of models fulfilling realistic mass-balance and other thermodynamic constraints. This allows not only selection, from among this set, of a 'best model' in the least-square sense, but also the output of the distributions of input values associated with the accepted models. These can then be interpreted in a Bayesian context, as 'posterior distributions', providing added knowledge on likely values for the biomass, mortalities, etc., of key elements of the ecosystem under study (Walters 1996).

We have used here the less rigorous approach in (1), pending availability of the parameter estimates with confidence intervals, or other measures of uncertainty that will be used for updating the model presented here.

Table 22. Diet matrix for the marine mammals of PWS

Predator \ prey	Euphausiids	Copepods	Small pelagics	Herring	Salmon	Pinnipeds	Porpoise	Whales (transient)	Demersal fish	Birds	Invertebrates
Marine mammals (transient)											
Fin whale[a]	0.4	0.4	0.2								
Humpback whale[a]	0.5		0.3	0.1					0.1		
Minke whale[a]	0.5		0.1	0.1	0.1				0.2		
Beluga whale[a]			0.6	0.2					0.2		
Killer whale, trans.[b]						0.56	0.21	0.21		0.02	
Marine mammals (resident)											
Killer whale[a]				0.5	0.5						
Dall's porpoise[a]			0.8						0.2		
Harbor porpoise[a]			0.5	0.25					0.25		
Pinnipeds[c]			0.2	0.05	0.05				0.65		0.05

a) Based on Calkins (1986);
b) Modified from Wada (1996, Table M), and pertaining to the Strait of Georgia;
c) Based on Hobson et al. (1997).

Few parameters, besides the diet matrix (see below) had to be modified to get the model to balance:

- The P/B ratios for resident and transient marine mammals, and for pinnipeds, were found to be incompatible with a sustained presence of

Table 23. Basic estimates and trophic levels of the various groups in the balanced model of PWS (1980-1989). Values **in bold characters** were calculated by the program.

Group	Biomass (t ww·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Annual catch (t·km^{-2})	Trophic level
1 Phytoplankton	**41.513**	190.00	0.00	0.90	0.000	**1.0**
2 Macroalgae	400.000	4.40	0.00	**~0.00**	0.000	**1.0**
3 Mesozooplankton	276.000	**9.30**	**30.99**	0.95	0.000	**2.0**
4 Inf. zoobenthos	225.000	0.60	23.00	**0.59**	0.003	**2.3**
5 Intertidal inv.	6.240	2.00	10.00	**0.79**	0.000	**2.5**
6 Macrozooplankton	92.000	**1.35**	10.50	0.95	0.000	**2.8**
7 Epi. zoobenthos	1.300	2.00	10.00	**0.92**	0.143	**2.9**
8 Wild salmon fry	0.014	**18.25**	40.00	0.78	0.000	**3.2**
9 Hatch. salmon fry	0.009	**35.15**	60.00	0.63	0.000	**3.2**
10 Herring	8.107	0.67	18.00	**0.95**	1.136	**3.3**
11 Small pelagics	**8.909**	2.00	18.00	0.95	0.000	**3.3**
12 Sea otters	0.017	**0.71**	92.00	0.10	0.000	**3.5**
13 Demersal fish	9.400	1.00	4.24	**0.96**	0.037	**3.9**
14 Birds	0.021	0.10	103.00	**0.00**	0.000	**4.1**
15 Salmon	**2.125**	0.80	1.00	0.95	1.400	**4.1**
16 Trans. mammals	0.280	0.02	3.00	**0.00**	0.000	**4.2**
17 Res. mammals	0.095	0.02	12.70	**0.44**	0.000	**4.4**
18 Pinnipeds	0.300	0.06	29.10	**0.19**	0.000	**4.5**
19 Detritus	7.000	-	-	**0.50**	0.000	**1.0**

transient killer whales in PWS. Indeed, this presence had to be reduced, from high initial guesses, to less that two weeks per year for other marine mammals to be able to accommodate the predation pressure of killer whales. The implications of this constraint will have to be followed up in future models;

- The ill-founded initial standing stock estimate of 10 t·km^{-2} for phytoplankton was abandoned and the EE value fixed at 0.9 instead. The biomass was then estimated by Ecopath, based on the estimated primary production in PWS;

- The initial Q/B value of 10.5 year^{-1} for mesoplankton, which generated an excessively high gross conversion efficiency (GE = (P/B) / (Q/B)), had to be abandoned, and GE fixed at 0.3. Normally, GE values can only exceed 0.5 for groups such as fast-growing fish larvae, nauplii, or bacteria. For most groups, GE values range between 0.1-0.3. (Christensen and Pauly 1992b).

- The original density estimate of 1.17 t·km^{-2} for salmon was abandoned and the EE fixed at 0.95 instead, leaving the density as a free parameter to be estimated by Ecopath. The resulting estimate was higher than the initial value, which is appropriate, since the initial value was known to be an underestimate (see above).

Table 24. Diet matrix, expressing the trophic interactions of the various groups of the balanced model of PWS (1980-1989). Values **in bold characters** were changed from initial estimates, i.e., modified as required to achieve mass-balance.

Prey \ pred.	Mammals (res.)	Herring	Sm. pel.	Sea otters	Dem. fish	Intertid. inv.	Macrob. -epi.	Macrob. -inf.	Zoopl. -macro.	Zoopl, -meso.	Birds	Mammals (trans.)	Salmon	Pinnipeds	Wild salm. fry	Hatch. salm. fry
Mammals (res.)												0.001				
Herring	0.296				**0.080**							**0.067**		**0.051**		
Small pelagics	0.487				**0.260**						0.459	**0.138**	0.850	**0.362**		
Sea otters	0.001															
Demersal fish	0.150				0.100						0.136	**0.193**		**0.500**		
Intertid. inv.				1.000	**0.025**	0.100					0.216			**0.070**		
Epi. zoobenthos					**0.030**		**0.080**	**0.000**								
Inf. zoobenthos			0.101		**0.130**		**0.500**	**0.010**								
Macrozooplankton	0.010	0.400	**0.299**		**0.265**						0.187	**0.459**	0.150		0.250	0.250
Mesozooplankton		0.600	**0.600**		**0.100**	0.360	0.100	**0.290**	0.750			**0.137**			0.750	0.750
Phytopl.						0.230			0.250	**0.800**						
Macroalgae							**0.199**				0.002					
Birds																
Mammals (trans.)												**0.000**				
Salmon	0.056											**0.001**		**0.017**		
Pinnipeds												**0.004**				
Wild salm. fry					**0.005**											
Hatch. salm. fry					**0.005**											
Detritus						0.310	**0.121**	**0.700**		**0.200**						

RESULTS AND DISCUSSION

Table 23 shows the basic parameters and estimated trophic levels, by functional group of the balanced model of PWS; Table 24 shows the corresponding diet matrix.

A graphic version of the model is presented in Fig 2.

It must be stressed that this model is tentative and intended as an exercise to identify knowledge gaps. Many estimates have been adopted from other models and/or other locations, or periods other than the 1980s. Moreover, some groups, such as nearshore fishes, herring fry and other fish larvae are not considered, while other groups, e.g., such as demersal, and pelagic fishes, are very over-aggregated. Also, seasonal changes were not explicitly considered, though rigorous procedures exist for doing so (Walters 1996).

However, useful inferences can be drawn even from a simple model, and this is illustrated in Fig. 3 and 4. Figure 3 represent a trophic impact matrix, expressing the effects the various groups of the systems have on each other. This type of matrix, often reflecting the cascade-like effects of changes in the biomass of top predators on the lower trophic levels of ecosystems, was transferred from economics (Leontief 1951) into ecology by Hannon (1979). However, their interpretation in the PWS context will be discussed when more detailed models become available.

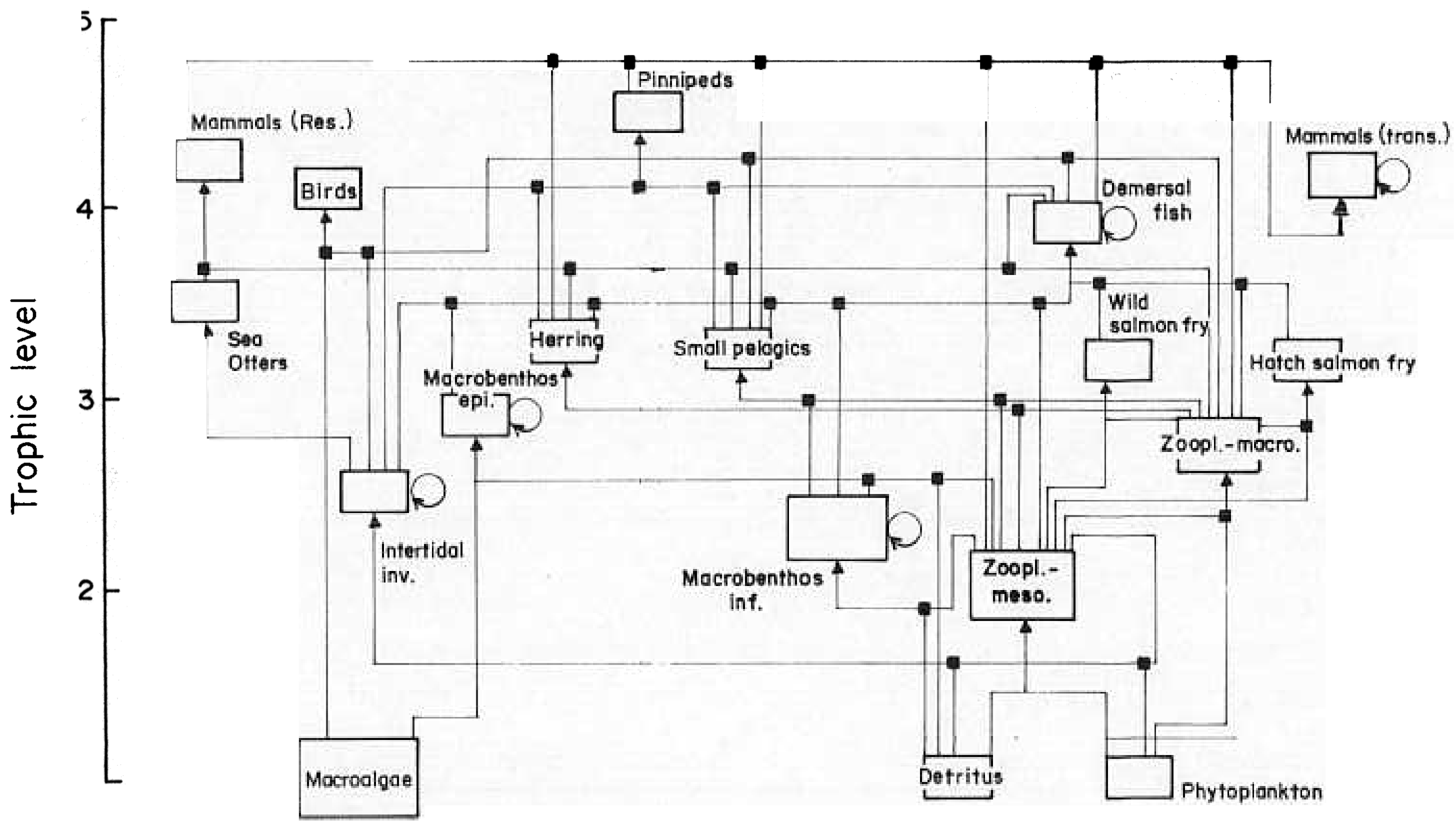

Fig. 1. Simplified flowchart of Ecopath model of PWS. Box sizes are proportional to log(density) of the group represented; flows exiting from a box do so from its upper half; flows exiting from a box cannot divide, but can merge with flows from other boxes. The adult salmon box and the backflows to the detritus are omitted for clarity.

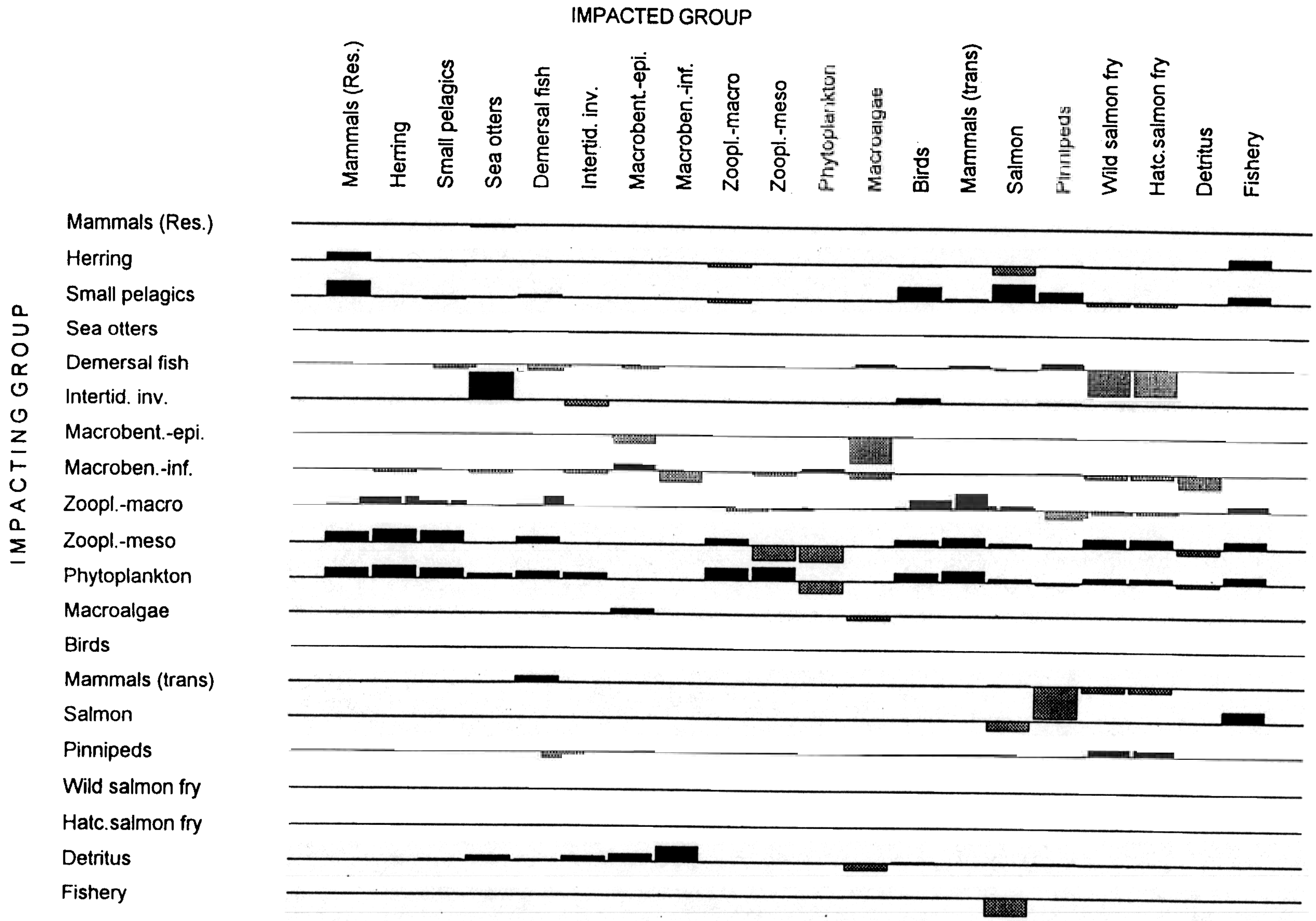

Fig. 2. Mixed trophic impacts of groups in the PWS ecosystem model, representing the impact an infinitesimal increase in any of the (horizontal) groups would have on all the other groups in the system. The impacts (black positive, shaded negative) are relative but comparable within rows.

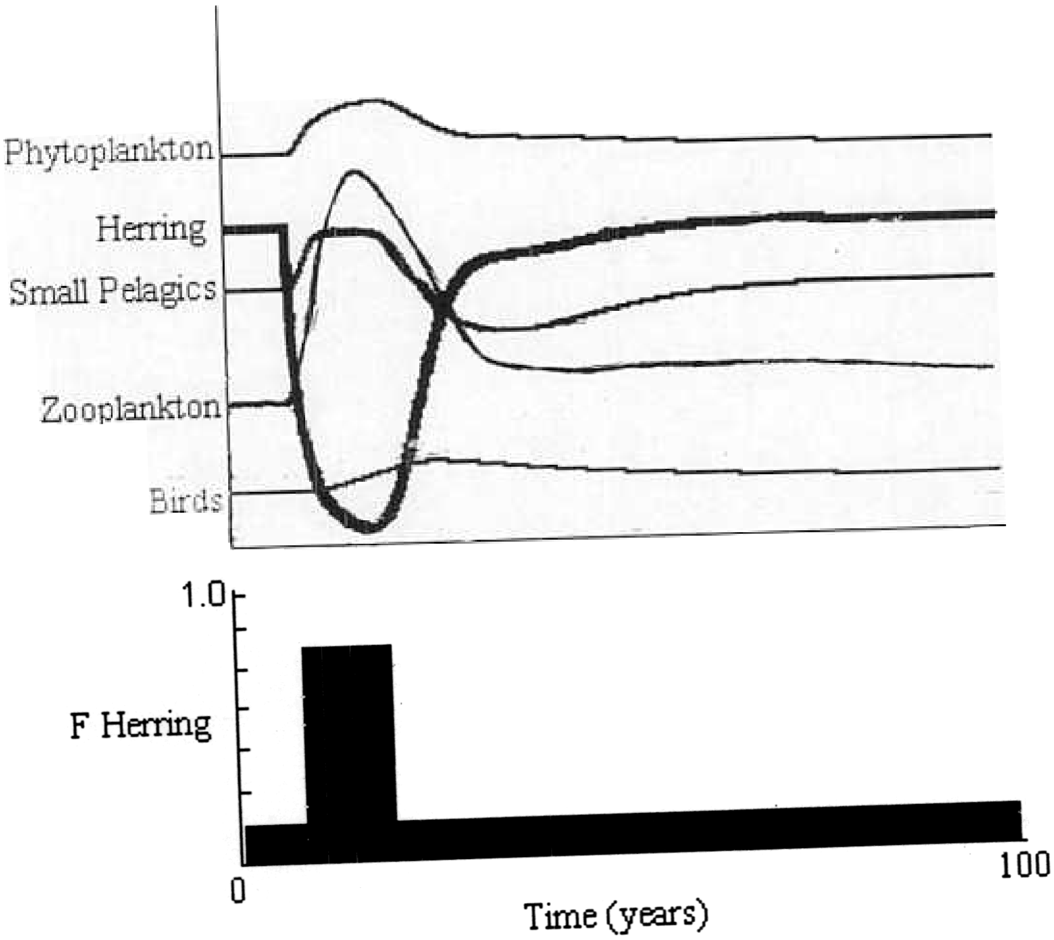

Fig. 4. Results of an Ecosim run of the PWS file generated by Ecopath, showing the system impact of increasing fishing pressure (or generally: mortality) for ten years on an important groups in the system (here: herring). Note the increase of their preys and competitors, and the long time it takes for the system to return to its initial state (model was run with all boxes in the system, but the graph was simplified to show changes for selected groups only).

Given the definitions of its various terms, the system of linear equations in Box (1) can be written

$$0 = [B_i \cdot (P/B)_i \cdot EE_i] - [(F_i \cdot B_i) + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ji}] \qquad ...1)$$

which is another way of stating that production and consumption are balanced within a system. However, we can reinterpret this as a system of ordinary differential equations, viz.

$$dB/dt_i = [B_i \cdot (P/B)_i \cdot EE_i] - [(F_i \cdot B_i) + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ji}] \qquad ...2)$$

where all terms are defined as in Box 1. We refer to Walters et al. (1997) for details on how the system of equations in (2) is implemented within Ecosim; Fig. 4 illustrates a run of Ecosim with the Ecopath file whose creation was documented here.

Other applications of the Ecopath model whose construction was documented here are presented in Appendix 1 and 2. We hope that this model - if only by eliciting constructive criticism - will be found a useful basis for the more detailed models that will explicitly account for input uncertainty during their construction in 1998.

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Appendix 1

Cross-validation of trophic level estimates from a mass-balance models of, and $^{15}N/^{14}N$ data from Prince William Sound[a]

by

Thomas C. Kline Jr.[1]

and

Daniel Pauly[c]

Abstract

Trophic mass-balance models of ecosystems constructed using the Ecopath approach and software include the diet composition of the various groups as one of the inputs; trophic level estimates for these groups is one of the outputs. Trophic level can also be determined using On the other hand, the well-documented 0.34% enrichment of $^{15}N/^{14}N$ that occurs at each feeding step in food webs.

This contribution is the first to examine the relationship between trophic levels estimated by these two independent methods. This was achieved using an Ecopath model of Prince William Sound (PWS) constructed by J. Dalsgaard and D. Pauly, who also identified the species groups included as 'boxes' in the model, then estimating $^{15}N/^{14}N$ ratios as a mean for each of these groups. Re-expression of theses ratios as absolute estimate of trophic levels (TL) was done following calibration using the herbivorous copepod *Neocalanus cristatus*, for which TL = 2.

The correlation between both sets of TL values (n= 7) was extremely high (r = 0.915), with the points evenly distributed about the 1:1 line. Moreover the variance of the TL estimates based on $^{15}N/^{14}N$ data also correlated (r = 0.495) with the variance of the Ecopath estimates, i.e., with the 'omnivory index' (OI) output by Ecopath.

Applying $^{15}N/^{14}N$ data from PWS to an Ecopath model of the Alaska gyre resulted in reduced correlations, suggesting that TL and OI estimates can be transferred between ecosystems, though at the cost of reduced precision. These encouraging results warrant further exploration.

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Appendix 2

Mass-balance food web ecosystem models as an alternative approach for combining multiple information sources in fisheries[a]

by

Daniel Pauly[b]

Johanne Dalsgaard[2]

and

Robert Powell[c]

Abstract:

Highly parameterized analytical single-species models offer a tempting framework for integrating data from different sources, e.g., survey biomass estimates, fishery catches and catch composition data. We argue, however, that forcing data that usually cover a number of species into single-species models, however sophisticated, does not optimally use such data.

Rather, emphasis should be given to models that explicitly account for multi-species interactions, especially trophic models. While mathematically not complex, trophic models can be made 'complete', i.e., they can be made to include all groups in a system, and thus consider direct and indirect trophic impact on target species. Such completeness also, in itself provides set limits on difficult-to-estimate stock sizes, production and mortality rates, i.e., on processes directly relevant to fisheries resource management. In addition, these models lend themselves to answering questions about ecosystem dynamics and the responses of ecosystems to anthropogenic changes.

As an example, we discuss the properties and behavior of a mass-balance trophic model representing the Prince William Sound ecosystem from 1980 to 1989, i.e., prior to the Exxon Valdez Oil Spill.

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