

Cross-Validation of Trophic Level Estimates from a Mass-Balance Model of Prince William Sound Using $^{15}\text{N}/^{14}\text{N}$ Data

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Abstract

Trophic mass-balance models of ecosystems constructed using the Ecopath approach and software include the diet composition of functional groups as model inputs, and trophic level estimates for these same groups as a model outputs. The well-documented 0.34% enrichment of $^{15}\text{N}/^{14}\text{N}$ that occurs at each feeding step in food webs can be used to determine trophic level as well. This contribution is the first to ever examine the relation between trophic levels estimated by these two independent methods. This was achieved by using a published Ecopath model of Prince William Sound (PWS) as reference, i.e., estimating $^{15}\text{N}/^{14}\text{N}$ ratios for each of the model's functional groups. Re-expression of these 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 ($r = 0.986$), with the points evenly distributed about the 1:1 line. Also, the magnitude of the standard errors of the TL estimates based on $^{15}\text{N}/^{14}\text{N}$ data was similar to those of the Ecopath estimates.

Applying $^{15}\text{N}/^{14}\text{N}$ data from PWS to an Ecopath model of the Alaska Gyre System resulted in a reduced correlation ($r = 0.755$, for $n = 16$), suggesting that TL estimates may be transferred between ecosystems, though at the cost of reduced precision. These encouraging results warrant further exploration.

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Introduction

While the trophic level concept existed since the beginning of ecosystem research (Golley 1993), controversy has raged as to its operational validity. Particularly, some ecologists could not reconcile this concept, articulated in form of integers (primary producers = 1; first order consumers = 2, etc.), with the observation that many organisms derive their food from widely different parts of food webs (e.g., Rigler 1975). This problem was overcome by the introduction, through Odum and Heald (1975), of fractional trophic levels (*TLs*). These are computed as weighted means from disparate diet compositions, and their variance can be interpreted as an omnivory index (*OI*), in agreement with Pimm (1982), who defined omnivory as "feeding on more than one trophic level" (Pauly et al. 1993, Pauly and Christensen 1995). Until the late 1980s, however, estimation of trophic levels continued to be largely definitional for lower levels (see above), or based on crude, and often grossly erroneous guesses for higher levels. (See Pauly 1996 for the a discussion of such guesses by Ryther 1972 and other authors.)

In recent years, two methods have emerged that are capable of reliably estimating *TL* and related statistics: (1) the ¹⁵N/¹⁴N method (DeNiro and Epstein 1981, Fry 1988, Wada et al. 1991, and see below), and (2) the construction of mass-balance trophic models of ecosystems (Christensen and Pauly 1992, and see below). The former estimates are identified as *TL_N*, the latter as *TL_E*. In this study, we present a first comparison of results obtained by these two approaches, using a preliminary mass balance model of the Prince William Sound (PWS) ecosystem (Dalsgaard and Pauly 1997) as a starting point. Another model, describing the Alaska Gyre System (AGS; Pauly and Christensen 1996) is then used to test whether estimates of *TL* and *OI* may be transferred from one ecosystem to the other.

Materials and Methods

The trophic mass-balance model of PWS used here was constructed using the Ecopath approach of Polovina (1984) and Christensen and Pauly (1992); this is based on the system of linear equations

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

where, for any conventional period without massive change of system structure:

B_i is the mean biomass of functional group i (e.g., a group of species with similar vital statistics, diet compositions and consumers); B_j is the mean biomass of the consumers of i ; $(P/B)_i$ is the production/biomass ratio of i (equivalent to its instantaneous rate of mortality; Allen 1971); EE_i is the fraction of production $\{P_i = B_i \times (P/B)_i\}$ that is consumed within the

system; Y_i is the catch of i by the fishery, if any; $(Q/B)_j$ the consumption per unit biomass of j ; and DC_{ij} is the contribution of i to the diet of j .

The Ecopath software (Christensen and Pauly 1992) was used to solve this system of equations, after estimation of values of B , P/B , etc, from the literature on PWS and related systems. The assumptions made when estimating the inputs, and for their subsequent adjustment when establishing mass-balance, are documented in Dalsgaard and Pauly (1997). The other trophic mass-balance model used here, representing the Alaska Gyre system, was constructed in similar fashion and is documented in Pauly and Christensen (1996).

For both models, estimation of the *TL* values was performed by Ecopath, based on

$$TL_{Ei} = (1 + \text{mean trophic level of prey}) \quad (2)$$

Omnivory indices (OI_{Ei}) were computed as the variance of the TL_{Ei} estimates (Christensen and Pauly 1992); the square root of the OI_{Ei} values was then treated as standard error of the TL_{Ei} estimates ($S.E._{Ei}$).

Further details on Ecopath, including its ability to account for uncertainty in input values through a Monte Carlo resampling scheme interpreted in a Bayesian context, are provided in Walters (1996) and other contributions in Pauly and Christensen (1996).

Stable isotope measurements are unique in that they trace assimilated material. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988, Wada et al. 1991, Hobson and Welch 1992, Kiriluk et al. 1995). The heavy isotope of nitrogen, ¹⁵N, is enriched by about 0.34 ‰ (or 3.4 ‰ in conventional delta units) with each trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984) and has been shown to accurately indicate the "realized" trophic level of species within an ecosystem (Kling et al. 1992, Cabana and Rasmussen 1994). Thus, the set of TL_N values used for comparison was derived from samples collected in 1994-1995 in PWS (Kline 1997), and based upon the trophic bioconcentration of ¹⁵N.

The conventional delta notation used to express a stable isotope ratio is reported relative to international standards (air for N) and defined by the following expression:

$$\delta^{15}N = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000\text{‰} \quad (3)$$

where $R = ^{15}N/^{14}N$. The isotope standard has a delta value of zero by definition, i.e., $\delta^{15}N = 0$ for atmospheric N_2 . Naturally occurring $\delta^{15}N$ values observed in biota range from ~ 0 to $\sim +20$.

TL_N is estimated by relating observed $\delta^{15}N$ values to a reference value (TL_{ref}), and to the trophic enrichment factor, 3.4 (Minagawa and Wada 1984, Kline 1997), via:

$$TL_{Ni} = 1 + (\delta^{15}N_i - \delta^{15}N_{ref})/3.4 \quad (4)$$

Where TL_{Ni} is the trophic level of functional group i , $\delta^{15}N_i$ is the mean $\delta^{15}N$ of functional group i , and $\delta^{15}N_{ref}$ is the mean $\delta^{15}N$ value of the herbivorous copepod (with $TL = 2$, by definition) used as reference, here *Neocalanus cristatus* (Kline 1997). The standard deviations of the $\delta^{15}N_i$, $S.D._{Ni}$ were multiplied by the trophic enrichment factor, 3.4 (Minagawa and Wada 1984, Kline 1997), to estimate $\delta^{15}N$ -based omnivory indices, OI_{Ni} . Given their relative magnitudes, we compared the OI_{Ni} estimates with the $S.E._{Ei}$, rather than with the OI_{Ei} .

Isotope sampling and data acquisition procedures were described elsewhere (Kline et al. 1993, Kline 1997). To account for the different definitions of the functional groups in the two ecosystem models (PWS and AGS), the available isotopic databases were arranged differently for each comparison. For example, in the PWS model, herring are considered separately (Table 1), while they are included in the small pelagics group of the AGS (Table 2).

Results and Discussion

Table 1 presents our results for PWS, i.e., the estimates of TL and omnivory index (OI) derived by the two methods under comparison. As might be seen, the fit between the estimates of TL_E and TL_N is very tight, even if one omits the reference data point, pertaining to *Neocalanus*, and for which $TL_E = TL_N = 2$ by definition (see arrow in Fig. 1A). Moreover, the data points are close to the 1:1 line, as they should if TL_E and TL_N measure the same underlying quantity. Figure 1B shows that the magnitude of the omnivory index estimates are similar for both methods compared here, except for the reference group (see arrow), which cannot, by definition, take a value of $S.E._E$ other than zero, while the estimate of OI_N can be quite large. This feature precludes correlation analysis.

The good match between the two types of TL estimates for functional groups in the PWS model is due, we believe, to the taxonomic correspondence between the Ecopath groups and the groups for which $\delta^{15}N$ were available. Another factor is scope of the sampling for stable isotope data, which involved numerous samples (Table 1) and which was very broad for all groups except birds. (Bird isotopic data were collected within a limited spatial and temporal range and included few of the common duck-like shorebirds; pers. comm., M.A. Bishop, U.S. Forest Service).

The Ecopath model of PWS was based almost exclusively on data collected prior to the 1989 *Exxon Valdez* oil spill, while the $\delta^{15}N$ data were collected after the spill. The good match between the two data sets implies that the basic structure of the food web has not been modified by the spill, at least as far as can be detected within the scope of this comparison. On the other hand, $\delta^{15}N$ data are not available for marine mammals

Table 1. Comparison of trophic level (TL) and omnivory index ($S.E._E$ and OI_N) estimates for seven functional groups in the Prince William Sound ecosystem.

Ecopath group ^a	Corresponding taxa with $\delta^{15}N$ data	Data source ^b	N ^c	TL_E^d	TL_N	$S.E._E^e$	OI_N
Mesozooplankton	<i>Neocalanus cristatus</i> ^f	1	938	2	2	0	0.54
Macrozooplankton	Euphausiids, amphipods, chaetognaths, etc.	1,2	329	2.8	2.81	0.43	0.49
Salmon fry	Young-of-the-year chum, sockeye and pink salmon	3	285	3.2	3.18	0.32	0.31
Herring	<i>Clupea pallasii</i> (Pacific herring)	1,3	385	3.3	3.33	0.37	0.21
Small pelagics	Smelts, juvenile gadids	3	273	3.3	3.08	0.34	0.32
Demersal fishes	Flatfish, rockfishes, greenlings, gadids, cottids	3	459	3.9	3.88	0.53	0.40
Birds	Seabirds	4	191	4.1	3.81	0.45	0.44

^a Model is described in Dalsgaard and Pauly (1997), including details of species included in each functional group.

^b Numbers in this column indicate sources of $\delta^{15}N$ data, viz. 1 = Kline (in press); 2 = Kline (unpublished data); 3 = Kline (1997); 4 = M.A. Bishop (U.S.F.S., Cordova, unpublished data).

^c Number of $\delta^{15}N$ measurements.

^d As given on Table 23 of Dalsgaard and Pauly (1997).

^e From Ecopath file of PWS, available from second author.

^f Reference group for $^{15}N/^{14}N$ as discussed in text.

and many bird species that experienced large mortalities, and this conclusion may thus change when the issue is revisited.

Table 2 and Fig. 1C show that using $\delta^{15}N$ data from one system (PWS) to estimate trophic levels in another, adjacent system (AGS), leads to predictions that are less precise than when inferences are drawn within the same system. Moreover, the omnivory index values become completely uncorrelated (Fig. 1D), partly because of overaggregation of functional prey groups, which leads to predators that appear to feed at only one trophic level.

A likely reason for the differences between TL_E in AGS and TL_N estimates from PWS is the shoe-horning of taxa with $\delta^{15}N$ data into the "boxes" of the AGS model. For example, the TL_N estimate for demersal fish in PWS is compared with a TL_E estimate for "large fish" in the AGS, though these consist of large pelagic fish (Pauly and Christensen 1996).

Table 2. Comparison of estimates of TL_E and $S.E._E$ for functional groups in the Alaska Gyre system with TL_N and OI_N estimates derived from Prince William Sound organisms.

Ecopath group ^a	Corresponding taxa with $\delta^{15}N$ data	Data source ^b	N^c	TL_E^d	TL_N	$S.E._E$	OI_N
Small herb. zoopl.	<i>Neocalanus cristatus</i> ^e	1	938	2	2	0	0.54
Microzooplankton	Bulk net samples	1	195	2	2.17	0	0.34
Carnivorous zoopl.	Amphipods, chaetognaths, decapod larvae, etc.	1,2	159	3	2.89	0	0.52
Jellies ^f	Gelatinous zooplankton	2	4	3	2.35	0	0.35
Krill	Euphausiids	1	170	2.05	2.74	0.22	0.45
Squids	Squids	3	104	3.15	3.44	0.37	0.25
Small pelagics	Herring, smelts, juvenile gadids	1,3	545	3.16	3.24	0.36	0.27
Sockeye salmon	Sockeye salmon	4	118	3.91	2.88	0.45	0.13
Chum salmon	Chum salmon	2	1	4	3.05	0	
Pink salmon	Pink salmon	2	4	3.99	2.94	0.38	0.18
Steelhead	Dolly Varden ^g	2	6	4.12	3.46	0.20	0.31
Mesopelagics	Myctophids, smoothtongue, glass shrimp, snailfish	3	73	3.04	3.12	0.05	0.39
Large fish	Flatfishes, rockfishes, greenlings, gadids, etc.	2	459	4.04	3.88	0.30	0.40
Sharks	Dogfish, salmon shark	2	5	4.49	3.66	0.45	0.40
Pinnipeds	Copper R. Delta Harbor seals & Steller sea lions	5	22	4.33	4.92	0.36	0.08
Marine birds	Seabirds	6	191	4.08	3.81	0.28	0.44

^a Model described in Pauly and Christensen (1996), including details of species included in each functional group.

^b Numbers in this column indicate sources of $\delta^{15}N$ data, viz. 1 = Kline (in press); 2 = Kline (unpublished data); 3 = Kline (1997); 4 = Kline and Ewald (unpublished data); 5 = Hobson et al. (1997); 6 = M.A. Bishop (U.S.F.S., Cordova, unpublished data).

^c Number of $\delta^{15}N$ measurements.

^d From Ecopath file of Alaska gyre, available from the second author.

^e Reference group for $\delta^{15}N$.

^f Diet composition, omitted in Pauly and Christensen (1996), consisted of 88% herbivorous zooplankton, and 12% microzooplankton.

^g Presumed analogous to steelhead because both are iteroparous salmonids; see text.

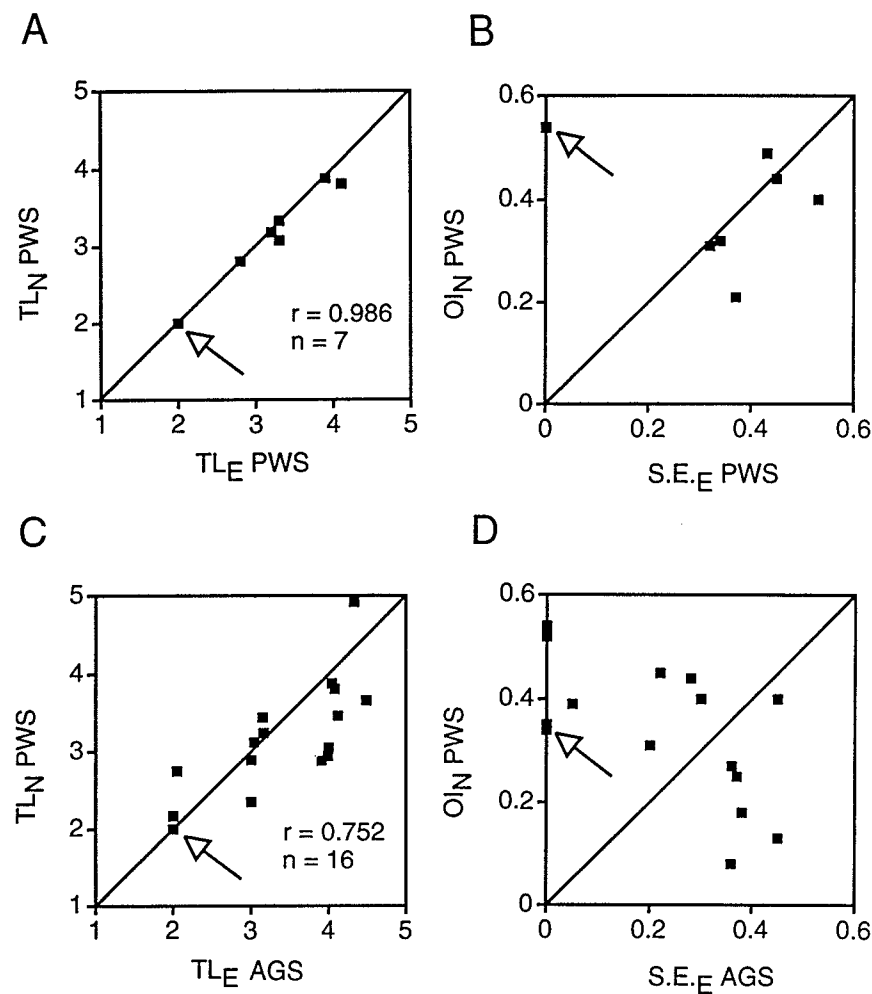


Figure 1. Relationships between estimates of trophic level derived from $\delta^{15}N$ data (TL_N) and Ecopath modeling (TL_E), and between the corresponding standard errors, for functional groups in Prince William Sound (PWS) and the Alaska Gyre System (AGS). (Arrows indicate reference group [*Neocalanus cristatus*]; see Tables 1 and 2 for details.) (A) Correlation between TL_N and TL_E estimates from PWS; (B) Relationship between OI_N and $S.E._E$ estimates from PWS; (C) Correlation between TL_N estimates from PWS and TL_E estimates from AGS; (D) Lack of relationship between OI_N estimates from PWS and $S.E._E$ estimates from AGS.

The $\delta^{15}\text{N}$ data on salmonids in Table 2 refer to adult specimens collected during their return migration through PWS and/or the Copper River, of which all would have done most of their feeding on the Gulf of Alaska shelf and/or in the AGS. However, having broadly similar life histories may not be sufficient for their TL values to be similar: the iteroparous salmonid, Dolly Varden (*Salvelinus malma*) had an estimated TL_N much lower than another iteroparous salmonid, steelhead (*Oncorhynchus mykiss*; Table 2), but close to the value of $TL_N = 3.54 \pm 0.21$ estimated for semelparous coho salmon (*O. kisutch*; $n = 12$). Thus, caution needs to be used when selecting "analog" species for cross-validation.

Still, we view the cross-validation exercise presented here as encouraging, in that the data we assembled led to coherent results, fully validating the independent, within-system estimates of TL . We also think that the lower correlation between the TL values from PWS and AGS were largely due to the lack of correspondence between the species included in the functional groups that were compared.

The next step is to refine our analyses, based on ecosystem models that are more detailed, thus requiring less "shoehorning," making better use of the available $\delta^{15}\text{N}$ data, and reducing the occurrence of misleadingly low estimates of $S.E._E$. Also, an important test will be to verify the high trophic level ($TL_E \sim 5$; Pauly and Christensen 1996) estimated for transient killer whales. Future work by both authors will be devoted to these and related issues, important in view of the recent demonstration (Pauly et al. 1998) that the trophic levels of global fisheries catches have been steadily declining in recent decades.

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