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SOME FEATURES OF FISH FOOD CONSUMPTION ESTIMATES USED BY ECOSYSTEM MODELERS*

by

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ABSTRACT

A comparative study of the food consumption rates for fish used in thirteen different ecosystem models is presented. The aim is to see if the independent estimates possess the attributes one can expect of proper estimates of food consumption of fishes, i.e.,

1. food consumption should increase with temperature, and have a reasonable Q_{10};
2. pelagic fish should eat more than demersal fish;
3. herbivores should eat more than carnivores;
4. large fish should eat relatively less than small fish.

A first, rough analysis was conducted based on multiple regression techniques, and it was found that the emerging picture is as expected from (1) to (4) above. As the various consumption rates can be assumed to be largely independent of each other, it is concluded that the body of data used by the ecosystem modelers is coherent and well-structured.

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INTRODUCTION

The brief review presented here is a by-product of a comparative study of trophic ecosystem models published in the last 3 decades (Christensen and Pauly, this vol.).

In the course of that work, we became increasingly intrigued by the apparent ease with which the authors of ecosystem models appear to obtain or somehow generate the food consumption estimates needed to link the fish "boxes" of such models with their corresponding prey boxes.

The first question asked was thus: how do they know, i.e., what are the sources of the estimates used. However, our limited library resources and time did not allow a follow up on all the sources of the estimates of fish food consumptions in the models assembled.

Besides, in the course of our data compilation, a more interesting question (at least for us) emerged, i.e., whether the independent food consumption estimates used by independent modelers possess the attributes one can expect of proper estimates of food consumption of fishes, i.e.,

1. food consumption rates should increase with temperature, and have a reasonable Q_{10} (Regier et al., in press);

2. pelagic fish should eat more than demersal fish per unit biomass (higher activity level);

3. herbivores should eat 3-4 times more than carnivores (Brett and Groves 1979);

4. large fish eat relatively less than small fish (Dickie et al. 1987).

Confirmation of these simple hypotheses can be viewed as confirmation that the authors of various multispecies ecosystem models have drawn their estimates from a coherent, structured body of data, reflective of reality and therefore useable for further generalized inferences.

MATERIALS AND METHODS

We scanned the literature for ecosystem models which included "fish" as components, either as a single species (e.g., *Engraulis ringens*) or a functional group (e.g., "small planktivores") and reexpressed, for each group included in a model, the (mean) annual food consumption (Q) in relation to population biomass (B), i.e., as relative population food consumption (Q/B) *sensu* Pauly (1986). Only models with consumption estimates that we deemed independent have been used.

The main food item was also noted for the different fish boxes of each model and used to assign each fish or fish group to one of the following four feeding types:

BC :	Benthic carnivores
PF :	Apex and/or pelagic predators and/or zooplankton feeders
HD :	Herbivores and detritivores

These categories are crude and some groups may have been misassigned; however, this may be in part compensated by the fact that some species (e.g., cod) had different diets in different models and hence ended up being assigned to several categories. Note that all flatfish were assigned to BC and a few detritivores to HD.

In the multiple regression models presented below, these four groups were identified using two dummy variables (PF and HD, with BC serving as default).

Next, a rough measure of the peak of the biomass curve was assigned to each species (group). This measure was found from 0.3 times the maximum weight normally observed in the population. For groups including several species, a weighted average was used. The information was log transformed before it was included in the regression.

Mean annual habitat temperatures (T, in ^{o}C) were estimated for each of the areas from which a model was available.

Temperature was used as log transformed values in a multiple regression only to obtain an estimate of Q_{10}, i.e., the change in Q/B caused by a 10^{o}C temperature increase (Winberg 1956). For prediction purposes however, temperature (T) was transformed as suggested by Regier et al. (in press) i.e., by using the physiologically better inverse Kelvin scale where TK = (1/K) x 1000 (recall that K = C + 273.1).

Table 1 presents the Q/B values extracted from thirteen trophic models, along with ancillary data. Several of the models gave data for more than one time period or sub-area, but only one set of data was used from each model.

The estimates of Q/B in Table 1 were used to estimate the parameters of a multiple regression of the form,

$$\log_{10}Q/B = a + b_1\log_{10}TK + b_2\log_{10}W + b_3PF + b_4HD \quad ...1)$$

For estimates of Q_{10}, another regression similar to (1) was estimated; hence however $\log_{10}TK$ was replaced by $\log_{10}(T)$.

Various other standard statistical methods were applied to the data in Table 1, both in "testing" and in "exploratory" modes.

RESULTS AND DISCUSSION

The multiple regression model derived from the 75 estimates of Q/B in Table 1 is

$$\log_{10}Q/B = -5.04 + 1.94\log_{10}TK - 0.151\log_{10}W + 0.178\,PF + 0.291\,HD \quad ...2)$$

which has all signs as hypothesized and for which the correlation coefficient r = 0.66; no outliers (residual > 3 * standard deviation of residuals) were identified in preliminary runs. The residuals were normally distributed. Fig. 1 shows observed *v.s.* predicted estimates.

Table 2 shows that all the partial regression coefficients are significant at the 5% level. For an exploratory analysis like the present, this should be considered very promising.

The confidence intervals of the slopes are, as expected, rather wide, but it must be noted that the numerical values of the partial slopes are largely as expected (Regier et al., in press).

The Q_{10} estimate is surprisingly high, 5.0, but the 95% confidence interval from 2.3 to 11.0 signals a warning not to draw too firm conclusions with the present cursory data set. It should though be noted that Regier et al. (in press) reports Q_{10} values of 5.3 for penaeid shrimp yield, 3.7 for phytoplankton production, and 4.0 for crustacean plankton biomass, so perhaps our general assumption "Q_{10} is 2" needs validation.

The slopes associated with the feeding type variables have the ranking we expected, i.e., in terms of food consumption: BC < PF < HD.

The antilog of the associated slopes (b_2, b_3, b_4), are 1 : 1.5 : 2.0, indicating that the PF and HD groups eat 1.5 and 2 times as much as the BC group, respectively.

Of these estimates, the last (2.0) can be assumed to reflect the nutritive value of the food of herbivores compared to that of carnivores. This is quite a low estimate compared to those of Brett and Groves (1979) who found that "the protein fraction of plant diets is frequently one-fourth to one-third of meals". This difference is, however, only what should be expected, as none of the three feeding types are "clean" groups, the benthic carnivore group includes some plants in the diets and the herbivores group, some animal diet. And of course, the estimates reflect activity level as well as difference in the food nutritive values, and this may also partly explain the rather small difference in the Q/B values.

It was attempted to separate apex/pelagic carnivores and zooplanktivores but this was not justified by the results of an initial regression and it was concluded that in this rough analysis the separation did not improve the predictions, it only added undesired complexity. Consequently, the groups were merged for the final regression.

The partial slope caused by the size of fish indicates that a tenfold increase in size (between species, not within species) leads to a reduction in the consumption/biomass ratio of around 30%. This is comparable with the estimate obtained by Pauly (1989), using a different approach, of approximately 22% reduction.

As the various Q/B values used to make the above inferences are assumed to be largely independent of each other, we further conclude that the body of data used by the ecosystem modelers in Table 1 is coherent and well-structured.

This however suggests that more detailed studies than that presented here, preferably based on a more extended data set, could help identify and quantify a number of other variables linked to and hence allow for reasonable predictions of Q/B values (e.g., variables derived from the shape of fishes, as shown by Palomares and Pauly (1989) and Jarre et al. (in press) to strongly correlate with Q/B).

In this context, a subsidiary hypothesis may emerge, related to the difference between "raw" Q/B estimates, derived from estimates of ration and/or related parameters in single-species assessments, and "refined" estimates of Q/B, i.e., estimates of Q/B that have been found reliable enough for inclusion in a multispecies model.

Our hypothesis here is that "model-tested", or "refined" estimate of Q/B should, when used to derive multiple regressions analogous to (1), generally lead to significant models, with well-behaved residuals, while "raw" estimates of Q/B should lead to more unstable models. If upheld, this hypothesis would support the notion that multispecies models, among their many uses, may contribute to validating single-species estimates of vital statistics of fish.

In the present case no outliers were identified, i.e., no observations with residuals differing from the predicted values with more than three times the standard deviation of the residuals. Two observations (marked on Fig. 1) were however very close, i.e., bonito in the Peru model Jarre et al. (in press) and haddock in the North Sea Multispecies VPA (Anon. 1989).

We acknowledge, of course, that the "multispecies" model filter of questionable Q/B values is used on data that have already been filtered several times (e.g., by non-publication of results, indicated by a "physiological" filter to be thermodynamically unlikely). We have thus often found that gross efficiency (i.e., the ratio between production and consumption) is a powerful filter pinpointing problematic data. Had this filter been used on the North Sea Multispecies VPA (Anon. 1989) it would, we are certain, have shown that the Q/B ratio of around 0.7 used in this model is unrealistically low.

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Table 1. Estimates of annual consumption/biomass ratios (Q/B) from 13 multispecies models. "Type" indicates specific feeding types (i.e., "1" being benthic carnivores; "2" apex and/or pelagic predators and/or planktivores; and "3" herbivores detritivores). "Temp" is mean annual habitat temperatures and "W_{max}" pertains to maximum weights for the various groups/species.

Model[a]	Group/species	Type	Q/B (year)	Temp. (°C)	W_{max} (kg)
9	Haddock	1	0.7	9.5	1.8
13	Cod	1	1.2	7.0	1.2
5	Plaice	1	1.3	9.5	1.5
6	Saithe	2	1.4	9.5	10.0
6	Dab	1	2.0	9.5	0.8
9	Cod	1	2.1	9.5	16.0
6	Cod	1	2.2	9.5	15.0
6	Long rough dab	1	2.2	9.5	0.7
9	Saithe	2	2.6	9.5	10.0
6	Haddock	1	2.6	9.5	10.0
9	Mackerel	2	2.6	9.5	0.8
2	Intermediate predators	1	2.7	27.6	2.0
6	Whiting	1	2.8	9.5	1.0
1	Sharks	2	2.8	25.3	626.0
10	Cod	1	2.8	8.0	15.0
10	Redfish	1	3.0	8.0	2.0
9	Whiting	1	3.0	9.5	0.9
12	Cod	2	3.6	5.7	12.0
10	Haddock	1	3.6	8.0	5.4
1	Mackerel	2	3.6	25.3	27.0
6	Herring	2	3.7	9.5	0.4
12	Other fishes	1	4.0	5.7	2.0
10	Other finfish	1	4.1	8.0	2.0
10	Red hake	2	4.1	8.0	0.8
10	Other flounders	1	4.1	8.0	1.2
10	Pollock	2	4.1	8.0	10.0
10	Mackerel	2	4.1	8.0	0.8
6	Mackerel	2	4.2	9.5	0.8
10	Herring	2	4.5	8.0	0.4
10	Yellowtail flounder	1	4.6	8.0	1.2
8	Herring	3	4.7	7.0	0.4
6	Sandeeel	2	4.8	9.5	0.1
10	Silver hake	2	4.8	8.0	0.9
4	Menhaden	2	5.1	13.9	1.2
5	Temporary planktivores	2	5.5	9.5	0.4
7	Other demersal fishes	1	5.5	19.6	2.0
4	Summer flounder	1	5.8	13.9	5.3
4	White perch	1	5.9	13.9	9.0
2	Large zoobenthos feeders	1	6.1	27.6	15.0
7	Hake	2	6.3	19.6	10.0
6	Norway pout	1	6.5	9.5	0.1
4	Catfish	1	6.6	13.9	2.3

Table 1 Cont'd...

Model[a]	Group/species	Type	Q/B (year)	Temp. (°C)	W_{max} (kg)
5	Apex predators	2	6.7	9.5	4.0
4	Bluefish	2	6.7	13.9	14.0
4	Striped bass	2	6.9	13.9	9.0
12	Sprat	2	7.7	5.7	0.1
12	Herring	2	7.7	5.7	0.4
4	Shad	2	8.0	13.9	2.0
8	Cod	2	8.2	7.0	16.0
2	Small demersal zoobenthos feeders	1	8.3	27.6	0.2
2	Small demersal zooplankton feeders	2	8.3	27.6	0.2
7	Sardine	2	8.6	19.6	0.2
3	Piscivorous fishes	2	8.9	30.8	0.1
5	Small fishes	1	9.1	9.5	0.1
11	Fish - planktophages	2	9.4	26.0	2.0
2	Large predators	2	9.6	27.6	15.0
1	Demersal (Bottom fishes)	1	9.9	25.3	2.0
4	Atlantic croaker	1	10.1	13.9	6.8
4	Hog choker	1	10.7	13.9	0.5
5	Medium predators	1	11.3	9.5	2.0
7	Other pelagic fishes	2	12.0	19.6	2.0
11	Other benthophages	1	12.7	26.0	2.0
2	Pelagic fishes	2	13.5	27.6	0.2
4	Spot	1	13.8	13.9	0.5
7	Mackerel	2	13.8	19.6	4.5
7	Horse mackerel	2	14.2	19.6	3.0
3	Herbivorous fishes	3	14.6	30.8	0.4
7	Anchoveta	3	15.5	19.6	0.1
4	Alewife & blue herring	2	15.7	13.9	0.5
5	Permanent planktivores	2	17.1	9.5	0.2
3	Invertebrate feeders	1	18.8	30.8	0.2
4	Bay anchovy	2	19.2	13.9	0.4
1	Menhaden	3	19.5	25.3	1.2
3	Herbi-detrivorous fishes	3	20.1	30.8	0.4
7	Bonito	2	25.9	19.6	15.0

[a] Model sources: (1) Sheridan et al. (1984); (2) Liew and Chan (1987); (3) Siaw-Yang and Furtado (MS); (4) Baird and Ulanowicz (1989); (5) Nauen (1984); (6) Andersen and Ursin (1977); (7) Jarre et al. (in press); (8) Limburg et al. (1982); (9) Anon. (1989); (10) Cohen et al. (1982); (11) Nguyen Tac An (1990); (12) Elmgren (1984); (13) Mendoza (1990).

Table 2. Summary of parameter characteristics from multiple regression on food consumption estimates.

	Parameter	Coefficient	Antilog coefficient	Std. error	t-value	95% Confidence interval	Sign. level
a	(Constant)	-5.090	-	1.114	-4.57	-7.31 to -2.87	0.0000
b_1	(log TK)	1.950	-	0.388	5.03	1.18 to 2.73	0.0000
b_2	(logW)	-0.151	0.7	0.041	-3.67	-0.23 to -0.07	0.0005
b_3	(PF)	0.184	1.5	0.060	3.09	0.07 to 0.30	0.0029
b_4	(HD)	0.297	2.0	0.128	2.31	0.04 to o.55	0.0238
	Q10	0.695	5.0	0.174	3.99	2.2 to 11.0	0.0002

r^2 = 0.443 (adjusted for d.f.); r = .67; 75 observations.

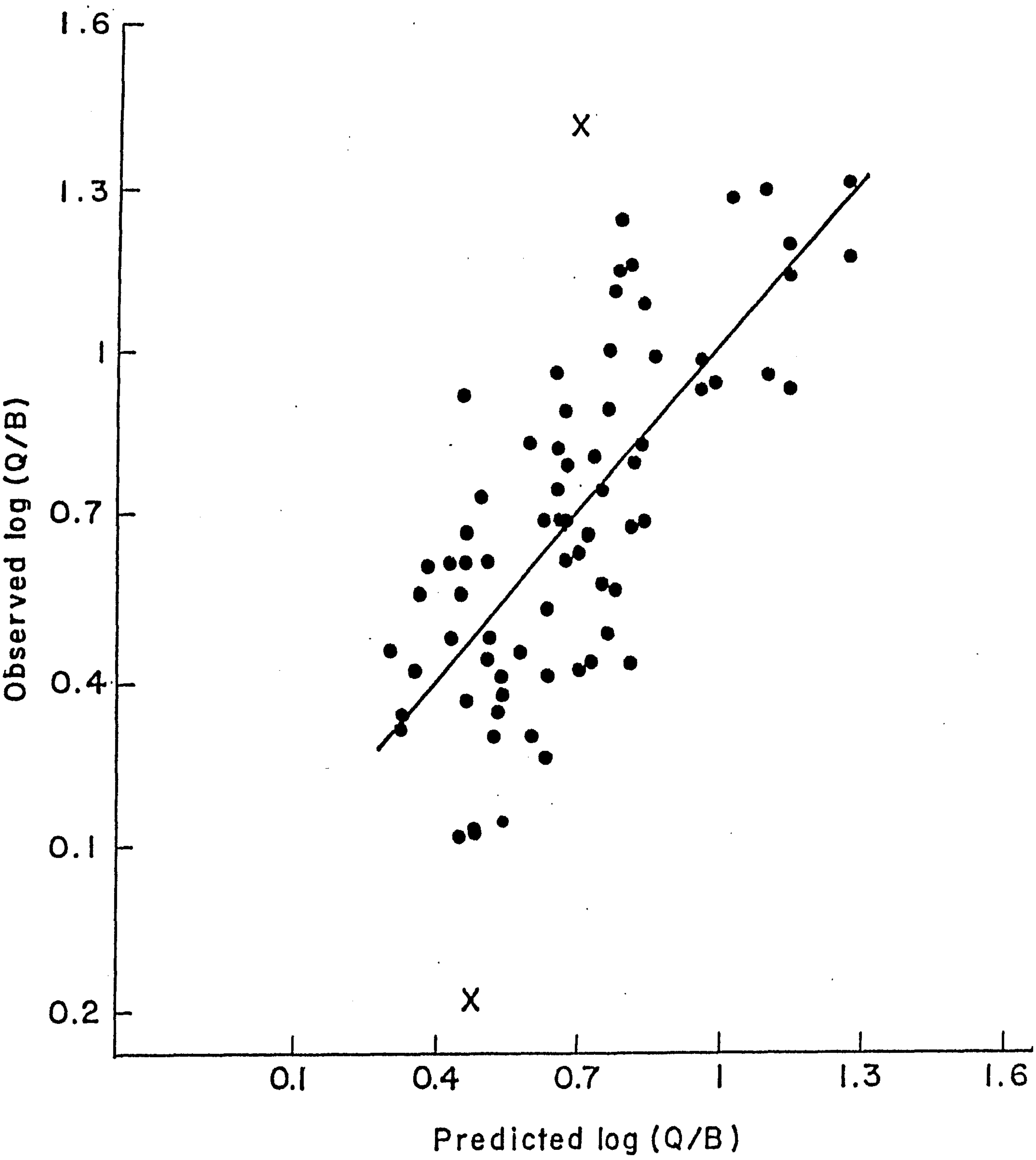

Fig. 1. Observed and predicted estimates of (log) consumption/biomass ratios for 75 fish groups. All estimates are used in the multiple regression, including the two estimates marked with crosses. These extreme estimates are for haddock in the North Sea Multispecies VPA (below regression line), and bonito in the Peru Upwelling Model (above regression line).