EDITORIAL

"Progress in any field depends primarily on our ability to synthesize previous experience". This is the opening remark from Hilborn and Liermann's recent plea for meta-analysis in fisheries, published in a Beverton and Holt Jubilee (40 years young) special issue of Reviews in Fish Biology and Fisheries. Ray Hilborn and Martin Liermann emphasize that fisheries models should strive to incorporate experience and not simply ignore it as most often the case. They find comfort, however, in the pioneering compilations of Daniel Pauly on natural mortality, in Ram Myers and colleagues' stock-recruitment work, and they conclude that the most critical need for meta-analysis is availability of databases, citing FishBase (www.fishbase.org) as a good example. Another good example is given in this issue of FishByte. Tom Brey of AWI has for years been collecting and analyzing information on productivity of benthic invertebrates and his Opus Major from 1995 is indeed a gold mine for ecological modelers in need of reliable productivity estimates. We are happy to present a Brey potpourri of empirical relationships here. As ecological modeling is becoming more and more useful for fisheries research, the need for information on all aspects of aquatic life is increasing. Reflective of this is that we are including a variety of empirical relationships in the Ecopath with Ecosim software system (www.ecopath.org) and welcome more inputs from you.

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A Collection of Empirical Relations for Use in Ecological Modelling[1]

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Abstract

This study summarizes previously published and updated empirical relations for the estimation of production/biomass ratios in benthic invertebrates; of natural mortality in benthic invertebrates and finfish; and of respiration from production and vice versa in animal populations. A MS-EXCEL spreadsheet containing these equations is available from the author via Email. They are also included in the Ecopath with Ecosim software.

Introduction

Any ecological model aims for an appropriate description or simulation of a set of ecological processes. The quality of the model depends on, among other factors, the quality of the data entered. Information on the dynamics of the major populations of a system such as respiration, production, productivity or mortality is crucial for successful modelling. However, producing valid estimates of these parameters is costly, time consuming and often impossible under the constraints of a project.

Many attempts have been made to establish empirical relations which allow for the derivation of this information from other, easy-to-obtain parameters. This paper summarizes single and multiple linear regression models for the estimation of respiration, production, production/biomass ratios and natural mortality rate in various taxonomic groups. The relationships presented here are included in the Ecopath with Ecosim software (www.ecopath.org).

Preliminary Remarks

In the empirical relations described below, the independent variables explain about 70-90% of the variance of the dependent variable. This indicates that predictions made by these models are reasonable. It should be noted, however, that almost all models work with log-transformed variables. Hence, seemingly small confidence intervals of log-transformed predictions translate into rather wide confidence intervals when de-transformed, i.e., the accuracy of these models may be below acceptable limits for modelling purposes (Brey et al. 1996). To help visualize this problem, the spreadsheet version of models (A1), (B1) and (B3) also indicate the 95% confidence intervals of the predicted parameter.

Predictions become more reliable when several independent estimates (e.g., production of each bivalve species in the ecosystem) are combined into one estimate (e.g., production of bivalves), because the deviations of estimates from true values are ran-

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of estimates from true values are randomly distributed and tend to cancel out each other when estimates of several populations are pooled (Brey et al. 1996).

Empirical Relations

(A) Production and production/biomass ratio of benthic invertebrate populations

(A1) P/B RATIO OF BENTHIC INVERTEBRATE POPULATIONS

The model (N = 933; r^2 = 0.756) established by Brey (1995) estimates somatic **P/B** ratio (y^{-1}) of benthic invertebrate populations from three continuous and seven discrete (dummy) variables. It covers all taxa from marine as well as freshwater habitats. The spreadsheet implementation of the model delivers the estimate of **P/B** and its lower and upper 95% confidence limits.

Model parameters:

	Coefficient	Parameter	Explanation
log(P/B) =	10.154	Intercept	
	-0.271	* log(M)	Mean individual body mass (kJ)
	-2824.247	* 1/(T+273)	Bottom water temperature (°C)
	-0.063	* log(D+1)	Water depth (m)
	+0.130	* DLife-ME	Motile epifauna? yes:1; no: 0
	+0.076	* DDiet-C	Carnivorous? yes:1; no: 0
	-0.311	* DTaxon-M	Mollusca? yes: 1; no: 0
	-0.154	* DTaxon-C	Crustacea? Yes: 1; no: 0
	-0.266	* DTaxon-P	Polychaeta? yes: 1; no: 0
	-0.472	* DTaxon-E	Echinodermata? yes: 1; no: 0
	-0.150	* DHabitat-L	Habitat = Lake? yes: 1; no: 0

Note: For taxa which belong neither to Mollusca, Crustacea, Polychaeta, Echinodermata nor to Insecta-larvae, set Polychaeta = 1 and the other three taxon dummy variables to zero.

(A2) PRODUCTION OF MARINE BENTHIC INVERTEBRATE POPULATIONS

The model (N = 125; r^2 = 0.86) established by Tumbiolo and Downing (1994) estimates annual somatic production (g Dry Mass $m^{-2}y^{-1}$) of marine benthic invertebrate populations from biomass, maximum individual body mass, surface water temperature and water depth.

Model parameters:

	Coefficient	Parameter	Explanation
log(P) =	0.240	Intercept	
	+0.960	* log(B)	Biomass (g DM m^{-2})
	-0.210	* log(M)	Max. individual body mass (gDM)
	+0.030	* T	Surface water temperature (°C)
	-0.160	* log(D+1)	Water depth (m)

Note: For molluscs shell free dry mass (SFDM) has to be applied.

(A3) PRODUCTION OF STREAM BENTHIC INVERTEBRATE POPULATIONS

The model (N=291; r^2=0.87) established by Morin and Bourassa (1992) estimates annual somatic production (g Dry Mass $m^{-2}y^{-1}$) of stream benthic invertebrate populations from biomass, mean individual body mass and bottom water temperature.

Model parameters:

	Coefficient	Parameter	Explanation
log(P) =	-0.750	Intercept	
	+1.010	* log(B)	Biomass (g DM m^{-2})
	-0.340	* log(M)	Mean individual body mass (gDM)
	+0.037	* T	Surface water temperature (°C)

(A4) PRODUCTION OF LAKE BENTHIC INVERTEBRATE POPULATIONS

The model (N=137; r^2=0.79) established by Plante and Downing (1989) estimates annual somatic production (g Dry Mass $m^{-2}y^{-1}$) of lake benthic invertebrate populations from biomass, mean individual body mass and bottom water temperature.

Model parameters:

	Coefficient	Parameter	Explanation
log(P) =	-0.060	Intercept	
	+0.790	* log(B)	Biomass (g DM m^{-2})
	-0.160	* log(M)	Mean individual body mass (mgDM)
	+0.050	* T	Surface water temperature (°C)

(B) Mortality of benthic invertebrate and fish populations

(B1) NATURAL MORTALITY RATE **M** IN UNEXPLOITED BENTHIC INVERTEBRATE POPULATIONS

The model (N=103; r^2=0.961) established by Brey (1995) estimates natural mortality rate **M** (y^{-1}) from annual **P/B** ratio in unexploited invertebrate populations. When individual growth follows the von Bertalanffy growth function and mortality can be described by the single negative exponential mortality model, then **M** equals **P/B**, as demonstrated by Allen (1971).

Model parameters:

	Coefficient	Parameter	Explanation
M =	0.082	Intercept	
	+0.925	* P/B	Production/biomass ratio (y^{-1})

(B2) NATURAL MORTALITY RATE **M** IN BENTHIC INVERTEBRATE POPULATIONS

This is a two-step approach: (i) The **P/B** ratio (y^{-1}) is estimated from maximum age, maximum body mass and bottom water temperature by a model (N=907; r^2=0.880) established by Brey (1995). Alternatively, **P/B** can be obtained by model A1. (ii) This estimate of **P/B** is then entered into model B1 to obtain **M** (y^{-1}). The spreadsheet implementation delivers the estimate of **M** together with lower and upper 95% confidence limits.

***Model parameters*(i):**

	Coefficient	Parameter	Explanation
log(P/B) =	1.672	Intercept	
	+0.993	* log(1/Amax)	Maximum age (y)
	–0.035	* log(Mmax)	Max. individual body mass (gDM)
	–300.447	* 1/(T+273)	Bottom water temperature (°C)

(ii) Enter P/B into model B1 to obtain **M**.

(B3) NATURAL MORTALITY OF FISH POPULATIONS

The model (N=218; r^2=0.726) originally established by Pauly (1980), now modified and extended by 44 new data sets, estimates natural mortality rate **M** (y^{-1}) of fish from W_∞, L_∞ and **K** of the von Bertalanffy growth function and ambient water temperature. The spreadsheet implementation delivers the estimate of **M** together with lower and upper 95% confidence limits.

Model parameters:

		Coefficient	Parameter	Explanation
log(M) =		4.355	Intercept	
	-	0.083	* log(W_∞)	W_∞ of VBGF (g Wet Mass)
	+	6.390	* W_∞/L_∞^3	Condition factor (gWM cm^{-3})
	+	0.627	* log(K)	K (y^{-1})
	-	1190.43	* 1/(T+273)	Ambient water temperature (°C)

Note: W_∞ is usually computed from L_∞ and a size-mass relation.

(C) Relation between production and respiration

The models of Humphreys (1979) estimate population production **P** (somatic and reproductive production) (kJoule $m^{-2}y^{-1}$) from population respiration **R** (kJoule $m^{-2}y^{-1}$) and *vice versa*. The general models are log(**P**) = a + b * log(**R**) and log(**R**) = a + b * log(**P**). A new relation for aquatic

Model parameters:

Taxon	P→R		R→P		N	r^2
	a	b	a	b		
Mammal	1.483	1.007	-1.358	0.885	56	?
Fish or social insect	1.121	0.839	-0.958	0.912	22	?
Aquatic invertebrate	0.691	0.892	-0.317	0.941	91	0.838
Non-social insect	0.183	0.963	-0.111	0.969	61	?

invertebrates including Insecta larva based on Humphreys data collection and 32 new data sets was computed (Appendix 1).

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