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Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity

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Abstract. A large data set of relative food-consumption estimates (Q/B) of marine and freshwater fish populations ($n = 108$ populations, 38 species) is documented and used to derive a predictive model for Q/B, using asymptotic weight, habitat temperature, a morphological variable and food type as independent variables. Salinity is shown to have no effect on Q/B in fish well adapted to fresh or salt water (other things being equal), while mortality (Z), has a strong, positive effect on Q/B and on gross food-conversion efficiency (defined by $GE = Z/(Q/B)$), by affecting the ratio of small:large fish. The empirical models thus derived should be useful for parameterization of trophic models of ecosystems and similar applications.

Introduction

One of the most important parameters required for trophic models of ecosystem is the amount of food ingested (Q) by a population over a period of time (conventionally a year) relative to its biomass (B), or Q/B (Polovina 1984; Christensen and Pauly 1992). This parameter is usually difficult to obtain and is often replaced by arbitrary guesses.

This paper derives multiple regression models for the prediction of Q/B from easily obtainable population parameters. These models also test the hypothesis of no difference between the Q/B values of freshwater and marine fishes once shape, size, habitat, temperature and food type are accounted for.

Materials and methods

Pauly (1986) proposed for the estimation of Q/B the model

$$Q/B = {}_{tr}\!\int^{tmax}(dW/dt)/K_{1(t)} / {}_{tr}\!\int^{tmax} W_t N_t dt \qquad (1)$$

where N_t is the number of fishes of age t, W_t their mean individual weight, $K_{1(t)}$ (see Eqns 7–10) their gross food conversion efficiency, t_r the age at which fish recruit, and t_{max} the maximum age in the population. Eqn (1) expresses Q relative to the biomass of age-structured populations, but can be solved for a single representative fish by setting the number of recruits (N_r) equal to unity. The key assumptions of Eqn (1) then are *(i)* that the population studied is in equilibrium, i.e. that, over all, recruitment compensates for mortality, as must often be assumed in mass-balance models (Polovina 1984; Christensen and Pauly 1992); and *(ii)* that the fishes in this population grow according to the von Bertalanffy (1934, 1939) growth formula (VBGF), expressed by the relationship:

$$W_t = W_\infty\{1 - \exp - [K(t - t_0)]\}^b \qquad (2)$$

where W_t is the mean predicted weight at age t, W_∞ is the asymptotic weight, i.e. the mean weight the fish would reach if they were to grow indefinitely, K the rate (dimension time^{-1}) at which W_∞ is approached, t_0 the theoretical age at length zero, and b the exponent of a length–weight relationship of the form

$$W = aL^b \qquad (3)$$

The parameter b of the length–weight relationship usually takes values between 2.5 and 3.5 (Carlander 1950, 1969, 1977). When no b value is available, growth is assumed to be isometric and b is set at 3, while a is set equal to the condition factor [c.f.] $= W/L^3$ (Pauly 1984).

The first derivative of the VBGF expresses the rate of growth, dW/dt and can be written as

$$dW/dt = W_\infty\, 3K\{1 - \exp - [K(t - t_0)]\}^{b-1} \qquad (4)$$

while the number of individuals in the population from time periods t_1 to t_2 is expressed by

$$N_2 = N_1 \exp - [Z(t_2 - t_1)], \qquad (5)$$

whose parameter Z is the coefficient of mortality between t_1 and t_2. It is assumed that Eqn (5) reasonably describes the survivorship patterns of juveniles and young adults, i.e. of those stages contributing most to the biomass of the population.

The baseline values of Z used here are estimates of natural mortality (M), obtained from the empirical equation of Pauly (1980), i.e.

$$\log M = 0.0066 - 0.279 \log L_\infty + 0.65431 \log K + 04631 \log T, \qquad (6)$$

where L_∞ is total length (TL) in cm, K is expressed on an annual basis, T is temperature in °C (see Table 1) and where 'log', as elsewhere in this
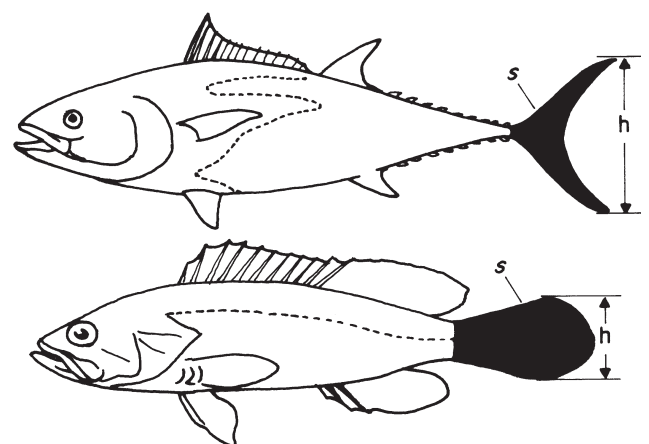
Fig. 1. Aspect ratio of the caudal fin for two generic fish, a very active tuna ($A = 6.7$) and a less active grouper ($A = 0.7$).

Table 1. Data used for deriving multiple regression models to predict relative food consumption by fish populations (Q/B; year^{-1}). Details on derivation of these parameters are on the FishBase CD-ROM (Froese and Pauly 1997). Sources and other information may be accessed from the FishBase CD-ROM by searching for entries in the 'POPQB' table with number 002939 or 012676 in the 'MainRef.' field, and 'Ref. 013343' in the 'Remarks' field

	Species	Locality	T (°C)	TL_∞ (cm)	W_∞ (g)	K (year^{-1})	M (year^{-1})	A	D	P	S	h	d	p	QB (year^{-1})
1	*Alosa pseudoharengus*	Lake Michigan	20.0	19.9	63	0.47	1.05	2.32	0.334	0.353	0	0	0	0	8.23
2	*Brevoortia patronus*	Gulf of Mexico	25.0	25.3	362	0.48	1.10	1.41	0.350	0.383	1	0	0	0	8.10
3	*Brevoortia tyrannus*	Atlantic Ocean	18.0	40.0	1216	0.30	0.75	1.89	0.326	0.357	1	1	0	0	31.42
4	*Engraulis encrasicholus*	Atlantic Ocean	15.0	14.3	28	1.15	1.80	1.31	0.161	0.415	1	0	0	0	9.13
5	*Oncorhynchus kisutch*	Lake Ontario	13.0	80.0	7500	0.98	0.94	2.40	0.261	0.330	0	0	0	0	6.50
6	*Oncorhynchus kisutch*	applied to marine population	13.0	98.0	10541	0.65	0.68	2.06	0.261	0.330	0	0	0	1	4.08
7	*Salmo salar*	applied to freshwater population	10.0	20.0	141	0.17	0.38	2.06	0.250	0.338	0	0	0	0	7.14
8	*Salmo trutta*	Brandstrup Brook, Norway	15.5	27.0	230	0.30	2.60	2.21	0.217	0.352	0	0	0	0	8.63
9	*Salmo trutta*	Dartmoor Stream, UK	9.0	37.8	605	0.21	0.36	2.21	0.217	0.352	0	0	0	0	5.22
10	*Salmo trutta*	France, applied to canal population	16.0	55.0	1824	0.18	0.38	2.21	0.217	0.352	0	0	0	0	11.73
11	*Salmo trutta*	France, applied to river population	16.0	47.8	1206	0.31	0.57	2.21	0.217	0.352	0	0	0	0	12.27
12	*Esox lucius*	England	15.0	111.0	13312	0.23	0.36	1.50	0.182	0.429	0	0	0	0	2.03
13	*Esox lucius*	Frome, Dorset, UK	15.0	108.0	10925	0.35	0.60	1.50	0.182	0.429	0	0	0	0	6.43
14	*Esox lucius*	Lake Windermere (mean), UK	7.0	87.5	6049	0.23	0.25	1.50	0.182	0.429	0	0	0	0	2.96
15	*Esox lucius*	Lake Windermere (females), UK	7.0	100.0	8810	0.24	0.26	1.50	0.182	0.429	0	0	0	0	1.61
16	*Esox lucius*	Lake Windermere (males), UK	7.0	75.0	3288	0.22	0.24	1.50	0.182	0.429	0	0	0	0	0.58
17	*Hygophum proximum*	West Central Pacific	25.0	6.1	2	0.76	2.13	1.03	0.216	0.474	0	0	0	0	33.87
18	*Hygophum reinhardii*	West Central Pacific	25.0	7.2	1	0.54	1.61	0.78	0.183	0.500	1	0	0	0	24.31
19	*Lampanyctus alatus*	Gulf of Mexico	25.0	7.5	2	0.50	1.53	0.75	0.211	0.611	1	0	0	0	12.12
20	*Myctophum asperum*	West Central Pacific	25.0	9.1	8	0.34	1.13	1.02	0.238	0.429	1	0	0	0	37.60
21	*Myctophum aurolaternatum*	West Central Pacific	25.0	13.0	10	0.17	0.64	0.83	0.188	0.516	1	0	0	0	16.24
22	*Myctophum nitidulum*	West Central Pacific	25.0	10.3	11	0.26	0.92	0.81	0.235	0.472	1	0	0	0	11.96
23	*Myctophum spinosum*	West Central Pacific	25.0	10.9	13	0.24	0.84	1.00	0.238	0.412	1	0	0	0	26.92
24	*Symbolophorus evermanni*	West Central Pacific	25.0	9.5	4	0.31	1.04	0.93	0.187	0.421	1	0	0	0	19.89
25	*Alestes baremoze*	Lake Chad, Chad	25.8	34.8	250	0.60	1.16	2.52	0.232	0.323	0	0	0	0	6.37
26	*Astyanax eigenmanniorum*	Lake San Roque, Argentina	15.4	12.3	32	0.44	1.02	2.13	0.443	0.345	0	0	0	0	2.50
27	*Colosoma macropomum*	Amazon	24.5	107.3	32000	0.23	0.45	2.37	0.489	0.291	0	0	0	1	1.61
28	*Catla catla*	Reservoir, Pakistan	31.7	36.7	615	1.42	2.24	1.94	0.378	0.457	0	0	0	1	4.24
29	*Cirrhinus mrigala*	Reservoir, Pakistan	30.8	48.3	808	0.98	1.61	1.51	0.221	0.524	0	0	0	1	5.58
30	*Labeo rohita*	Reservoir, Pakistan	30.8	42.7	883	1.52	2.22	1.98	0.289	0.400	0	0	0	1	6.26
31	*Mirogrex terraesanctae*	Lake Kinneret, Israel	14.0	18.1	60	0.19	0.50	1.41	0.273	0.503	0	0	0	0	15.93
32	*Rutilus rutilus*	Lake Pareloup, S.W. France	9.0	26.8	316	0.46	0.63	1.49	0.303	0.427	1	0	0	0	13.63
33	*Rutilus rutilus*	Lake Sovdeborgssjön, Sweden	14.0	30.7	766	0.09	0.27	1.49	0.303	0.427	0	0	0	1	2.68
34	*Bagrus dormac*	Lake Victoria, Kenya	25.5	90.0	6650	0.17	0.40	1.44	0.303	0.427	0	0	0	0	22.07
35	*Clarias gariepinus*	Africa (mean)	25.0	157.0	21887	0.08	0.22	1.26	0.256	0.477	0	0	0	0	1.32
36	*Clarias gariepinus*	Lake Malawi, Malawi	22.5	90.3	6074	0.14	0.34	1.26	0.247	0.421	0	0	0	0	1.73
37	*Clarias ngamensis*	Lake Malawi, Malawi	22.5	57.1	1688	0.27	0.58	1.01	0.161	0.414	1	0	0	0	1.33
38	*Gadus morhua*	Western Baltic	10.0	105.0	12356	0.16	0.23	0.77	0.178	0.67	0	0	0	0	2.59
39	*Gadus morhua*	North Sea	12.0	114.8	15714	0.30	0.20	0.77	0.181	0.368	1	0	0	0	2.26
40	*Gasterosteus aculeatus*	Lake Frongoch, UK	10.0	6.7	2	0.64	0.90	1.69	0.181	0.368	0	0	0	0	3.85
41	*Sebastes melanops*	Eastern Pacific, USA	13.0	60.0	3776	0.14	0.28	1.78	0.181	0.368	1	0	0	0	1.09
42	*Lates niloticus*	Lake Chad, Chad	25.0	88.8	16595	0.24	0.50	1.09	0.300	0.279	0	0	0	0	4.26
43	*Luciolates strappersii*	Lake Tanganyika, East Cent. Africa	26.0	48.0	1006	0.39	0.82	2.40	0.361	0.396	0	0	0	0	4.31
44	*Epinephelus aenus*	Northwestern Africa	19.0	144.0	47000	0.17	0.31	0.69	0.365	0.543	0	0	0	0	4.02
45	*Epinephelus fuscoguttatus*	Eastern Samar, Philippines	28.0	91.7	12338	0.19	0.45	1.54	0.214	0.292	0	0	0	1	4.02
46	*Epinephelus guttatus*	Bermuda	28.0		1880	0.24	0.64	1.07	0.250	0.392	0	0	0	0	2.77
47	*Epinephelus tauvina*	Thailand	28.0	102.0	17940	0.12	0.89	0.92	0.250	0.392	0	0	0	1	2.34
48	*Lepomis gulosus*	USA	27.0	30.0	702	0.15	0.52	1.49	0.275	0.600	1	0	0	0	15.40
49	*Micropterus salmoides*	Minnesota, USA (mean)	27.0	54.7	2296	0.22	0.56	1.69	0.349	0.410	0	0	0	0	6.22
50	*Micropterus salmoides*	USA (mean)	27.0	61.5	3290	0.20	0.51	1.69	0.314	0.481	0	0	0	0	20.30
51	*Perca flavescens*	Lake Washington, USA	10.0	33.6	380	0.25	0.44	1.64	0.312	0.508	1	0	0	0	2.79
52	*Perca fluviatilis*	Lake Bojörn, Sweden	9.0	18.6	173	0.22	0.59	1.94	0.516	0.437	0	0	0	0	5.99

No.	Species	Location													
53	*Perca fluviatilis*	Lake Ladoga, USSR	15.4	33.9	897	0.18	0.44	1.94	0.307	0.387	0	0	0	0	6.25
54	*Perca fluviatilis*	Lake Vitalampa, Sweden	9.0	17.9	154	0.41	0.50	1.94	0.307	0.387	0	0	0	0	4.57
55	*Perca fluviatilis*	Loch Leven, UK	16.5	32.2	336	0.44	0.81	1.94	0.304	0.313	0	0	0	0	5.06
56	*Caranx ruber*	Cuba	27.0	56.0	3036	0.14	0.41	1.21	0.285	0.323	0	0	0	0	10.55
57	*Coryphaena hippurus*	Hawaii	25.0	151.0	147000	0.57	0.70	1.21	0.285	0.323	0	0	0	0	8.47
58	*Lutjanus campechanus*	Gulf of Mexico	20.0	90.0	13000	0.10	0.25	1.28	0.285	0.323	0	0	0	0	5.26
59	*Lutjanus erythropterus*	Indo-West Pacific	27.0	60.0	3229	0.31	0.55	1.68	0.285	0.323	0	0	0	0	6.64
60	*Sparidentex hasta*	Kuwait	24.0	80.6	7400	0.38	0.35	1.19	0.292	0.159	1	0	0	0	2.34
61	*Sparus aurata*	Adriatic Sea	16.0	59.0	4000	0.28	1.00	1.97	0.206	0.156	1	0	0	0	1.61
62	*Sparus aurata*	Southeastern Mediterranean	24.0	84.5	9617	0.13	0.33	1.97	0.412	0.491	1	0	0	0	4.67
63	*Plagioscion squamosissimus*	Lake Janauaca, Central Amazon	27.0	41.7	1093	1.04	0.72	0.91	0.387	0.431	1	1	0	0	19.93
64	*Haplochromis nigripinnis*	Lake George, Central Africa	30.0	11.0	16	1.30	2.90	0.76	0.369	0.404	1	1	0	0	17.47
65	*Oreochromis alcalicus grahami*	Lake Nakuru, Kenya	20.5	20.0	153	0.50	1.10	1.32	0.415	0.302	1	1	0	0	29.62
66	*Oreochromis aureus*	Virgin Islands, USA	25.0	35.7	479	3.55	3.65	1.20	0.415	0.302	0	1	1	0	7.50
67	*Oreochromis mossambicus*	Malawi, Africa	22.5	43.2	1144	0.22	0.54	1.17	0.415	0.302	0	1	0	0	2.70
68	*Oreochromis mossambicus*	mean, applied to tank stock	27.0	20.6	242	5.19	5.63	1.17	0.267	0.474	0	0	0	0	30.34
69	*Oreochromis mossambicus*	mean, applied to pond stock	27.0	23.8	348	5.04	5.31	1.17	0.361	0.600	0	0	0	0	31.63
70	*Oreochromis mossambicus*	mean, applied to natural population	27.0	37.1	1193	0.22	0.62	1.17	0.381	0.592	0	0	0	0	2.24
71	*Oreochromis mossambicus*	Parakrama Samudra, Sri Lanka	27.0	38.1	996	0.25	0.68	1.17	0.454	0.592	0	1	0	1	75.52
72	*Oreochromis niloticus*	aquaria, applied to cage stock	26.0	23.8	271	5.05	5.23	1.28	0.413	0.562	0	0	0	0	27.99
73	*Oreochromis niloticus*	aquaria, applied to natural population	26.0	45.9	2495	0.33	0.75	1.28	0.413	0.562	0	0	1	1	3.56
74	*Oreochromis niloticus*	Bangkok, Thailand, Asia	26.5	16.3	95	7.27	7.40	1.28	0.413	0.562	0	0	1	1	65.08
75	*Oreochromis niloticus*	Bouaké, Côte d'Ivoire	28.5	64.6	5700	0.17	0.46	1.28	0.413	0.562	0	0	0	1	3.30
76	*Oreochromis niloticus*	Bouaké, Côte d'Ivoire, applied to cage stock	28.5	20.6	361	4.81	1.16	1.28	0.413	0.562	0	0	0	0	24.78
77	*Oreochromis niloticus*	Lake Awasa, Ethiopia	24.5	44.7	2036	0.33	0.74	1.28	0.457	0.510	0	1	0	1	49.88
78	*Oreochromis niloticus*	Lake George, Uganda	30.0	40.0	1517	0.24	0.10	1.28	0.457	0.510	0	1	1	1	12.76
79	*Oreochromis niloticus*	Lake Kossou, Côte d'Ivoire	28.5	46.0	2056	0.33	0.78	1.28	0.457	0.510	0	0	0	1	2.08
80	*Oreochromis niloticus*	Lake Kossou, Côte d'Ivoire, applied to cage stock	28.5	29.5	545	3.67	0.41	1.28	0.457	0.510	0	0	0	1	15.58
81	*Oreochromis niloticus*	Lake Nakuru, Kenya	20.5	63.0	5700	0.18	0.49	1.28	0.457	0.510	0	1	0	1	17.15
82	*Oreochromis niloticus*	Liège, Belgium	26.0	25.7	431	5.58	5.50	1.28	0.457	0.510	0	1	0	0	61.84
83	*Oreochromis niloticus*	Thailand, applied to tank stock	32.0	13.7	101	5.33	6.95	1.28	0.457	0.510	0	0	0	0	15.31
84	*Oreochromis niloticus*	Thailand, applied to tank stock	27.0	16.3	95	7.27	7.50	1.28	0.457	0.510	0	0	0	0	42.82
85	*Oreochromis niloticus*	Thailand, applied to pond stock	27.0	19.0	145	8.19	7.74	1.28	0.457	0.510	0	0	0	1	53.99
86	*Oreochromis niloticus*	Thailand, applied to pond stock	32.0	19.0	145	8.19	8.37	1.28	0.457	0.510	0	0	0	0	28.35
87	*Oreochromis niloticus*	Thailand, applied to natural population	27.0	45.9	2495	0.33	0.75	1.28	0.457	0.510	0	0	0	0	4.81
88	*Oreochromis niloticus*	Thailand, applied to natural population	32.0	45.9	2495	0.33	0.83	1.28	0.457	0.510	0	0	0	0	4.15
89	*Sarotherodon galileus*	Lake Chad, Chad	25.8	35.6	1396	0.33	0.80	1.56	0.457	0.510	1	1	0	1	15.70
90	*Sarotherodon melanotheron*	Sakumo Lagoon, Ghana	27.0	22.3	215	0.74	3.70	1.21	0.457	0.510	0	0	1	0	35.11
91	*Tilapia rendalli*	mean, applied to pop. in ponds	26.0	25.8	360	0.94	1.72	1.48	0.457	0.510	0	1	0	1	9.28
92	*Tilapia rendalli*	mean, applied to pop. in the nat. env.	26.0	37.4	1265	0.31	0.77	1.48	0.457	0.510	0	0	0	0	4.46
93	*Tilapia zillii*	mean, applied to pop. in the nat. env.	27.5	21.8	429	0.52	1.19	1.65	0.457	0.510	1	0	0	1	113.54
94	*Mugil cephalus*	Texas, USA	23.0	41.1	787	0.35	0.75	2.55	0.489	0.561	1	0	0	0	12.28
95	*Siganus canaliculatus*	Negros Oriental, Philippines	27.0	25.0	215	1.57	2.85	2.81	0.451	0.587	1	1	1	0	61.69
96	*Siganus spinus*	Indo-Pacific Ocean	27.0	24.4	234	2.32	3.31	1.92	0.479	0.477	1	1	1	1	41.98
97	*Thunnus albacares*	Eastern Pacific	24.0	160.0	81920	0.31	0.48	5.80	0.479	0.477	0	0	0	1	11.64
98	*Thunnus thynnus*	Japan	15.0	332.0	622000	0.41	0.20	6.70	0.458	0.501	0	0	0	0	3.94
99	*Limanda limanda*	North Sea	12.0		756	0.20	0.38	0.66	0.232	0.326	0	0	0	0	3.69
100	*Limanda limanda*	North Sea	12.0		149	0.48	0.78	0.66	0.232	0.326	0	0	0	0	7.04
101	*Pleuronectes platessa*	North Sea	12.0	70.0	3430	0.08	0.12	1.01	0.392	0.167	0	0	0	1	2.12
102	*Pleuronectes platessa*	North Sea	12.0	45.0	910	0.15	0.22	1.01	0.353	0.212	0	0	0	1	3.43
103	*Dicentrarchus labrax*	Marseille, France	15.0	68.0	3067	0.23	0.16	1.76	0.448	0.635	0	0	0	0	1.52
104	*Dicentrarchus labrax*	Thau Lagoon, France	15.0	68.0	3067	0.23	0.16	1.76	0.448	0.635	0	0	0	0	10.17
105	*Sparus auratus*	Thau Lagoon, France	15.0	71.4	3555	0.15	0.20	1.97	0.511	0.407	0	0	0	0	4.75
106	*Mugil cephalus*	Thau Lagoon, France	15.0	68.0	5877	0.32	0.51	2.55	0.511	0.407	1	0	0	1	4.74
107	*Ictalurus nebulosus*	Port Vieux, Garonne River, Toulouse, France	12.4	37.0	710	0.47	0.71	1.34	0.260	0.069	1	1	0	0	12.69
108	*Rutilus rutilus*	Port Vieux, Garonne River, Toulouse, France	12.4	48.8	1769	0.18	0.35	1.49	0.296	0.115	1	0	0	0	14.51

contribution, refers to $\log_{10}$. To investigate the effect of mortality on Q/B, and to derive predictive models of Q/B taking explicit account of different mortalities, values of Q/B were calculated, via Eqn (1), for mortalities equal to $0.5M$, M, $2M$ and $4M$.

The food conversion efficiency (K_1) used in Eqn (1) is defined by

$$K_1 = \text{growth increment/food ingested} \qquad (7)$$

for any time period (Ivlev 1945). Pauly (1986) showed that K_1 depends, among other things, on the individual weight of fish (W) in a manner that can be summarized by

$$K_1 = 1 - (W/W_\infty)^\beta \qquad (8)$$

where β is an exponent estimated as the slope of a linear regression of log $1-K_1$ $v.$ log$W$. (Pauly 1986). Note that Eqn (8) predicts a K_1 value of zero at W as should be the case. On the other hand, a value of $K_1 = 0$ is predicted for $W = 0$, which is not realistic. However, this applies to weights that do not contribute more than a minuscule fraction of a population's biomass.

Combining Eqn (7) with the VBGF and simplifying allows expression of K_1 and dW/dt (see Eqns (4) and (7)) as a function of age t through

$$K_{1(t)} = 1 - \{1 - \exp -[K(t - t_0)]\}^{b\beta} \qquad (9)$$

The application of Eqn (1) is not limited to estimates of K_1 obtained from feeding experiments with captive fish. Daily ration (R_d) estimates can also be used by first converting them to K_1 through

$$K_1 = (\text{d}W/\text{d}t) / R_d \qquad (10)$$

as is implied from the very definition of K_1 (see Eqn 7).

Daily ration estimates may be obtained from: analysis of 24 h cycles of stomach contents data obtained from field studies (Jarre *et al.* 1991), from metabolic studies (Winberg 1956; Mann 1978), and from nitrogen and/or energy budget studies (Ivlev 1945; Gerking 1962, 1978).

The methods and equations presented above were applied to estimates of K_1 and R_d in 108 freshwater and marine populations of fishes and were used to estimate Q/B values. Then, multiple regression models were constructed which included various parameters earlier hypothesized to affect Q/B, i.e. the VBGF parameter W_∞ (in g), with a slope expected to be negative (Palomares and Pauly 1989; Pauly 1989); the mean annual temperature of the water body, expressed as $T' = 1000/\text{Kelvin}$ (Kelvin = °C + 273.15). A positive relationship between temperature and Q/B is expected. However, given the transformation used here, a negative slope should be estimated (Regier et al. 1990);

The aspect ratio of the caudal fin which is a measure A of the swimming and metabolic activity of the fish expressed as

$$A = h^2/s \qquad (11)$$

where A is the aspect ratio, h the height of the caudal fin and s the surface area of the caudal fin, extending to the narrowest part of the caudal peduncle (Fig. 1); a positive slope is expected (Pauly 1989); two morphometric ratios as indices of the body form of a fish, i.e. D = standard length / body depth, and P = caudal peduncle height / body depth. High Q/B values were previously hypothesized to be associated with intermediate values of D, while a negative slope was hypothesized for P (Pauly 1989); the types of food consumed, i.e. h for herbivores ($h = 1$, $d = 0$ and $p = 0$; positive slope); d for detritivores ($d = 1$, $h = 0$ and $p = 0$; positive slope); and p for cultured fish fed with commercial pellets ($p = 1$, $h = 0$ and $d = 0$; no prior hypothesis concerning slope); carnivores are identified by default ($h = 0$, $d = 0$ and $p = 0$) (Palomares 1991); and the salinity of the water body, i.e. $S = 1$ for marine or brackishwater and $S = 0$ for freshwater (no hypothesis concerning slope).

Estimates of Q/B obtained from the data in Table 1 were recalculated for values of Z derived by multiplying M by 0.5, 2 or 4. These were added, along with the other (unchanged) predictor variables, to the file containing the original Q/B values and related predictor variables, and in which $Z = M$ pertained. Then, multiple regression models were calculated from this artificially expanded data set by using either Z or the M-multiplication factor (f) as an additional predictor variable. The regression statistics in such cases are meaningless, because Q/B is statistically related to Z (and f) through the incorporation of Eqn (5) into (1), and because the expanded data set consists essentially of replicates of the data set in Table 1.

Results and Discussion

Table 1 presents the Q/B and related statistics assembled here for 108 populations of fish, distributed over 65 species in 25 families of teleosts, of which 40 occur in marine and 68 in freshwater. The exploratory multiple regression model, including all hypothesized variables, is documented in Table 2; the slopes associated with depth ratio, peduncle depth, pellets and salinity have extremely large standard errors, indicating that they do not have significant relationships with Q/B. The slope associated with aspect ratio, on the other hand, is a borderline case, notwithstanding a formal test. Given this, and the fact that it is the morphometric variable with the lowest standard error, it was kept in Eqn (12), the second model estimated

$$\log Q/B = 7.964 - 0.204\log W_\infty - 1.965T' + 0.083A \qquad (12)$$
$$+ 0.532h + 0.398d$$

which—except for A—includes only terms significant at $P<0.001$ (Table 2). All the signs in Eqn (12) are as previously hypothesized. Fig. 2*a* shows how the predicted values of Q/B correlate with the observed values, and Figs 2*b*–2*d* show that the residuals do not form patterns with regard to any of the re-expressed continuous variables. The residuals are normally distributed (Fig. 2*e*), thus suggesting that the key assumptions of linear regression were met.

Table 2. **Statistics of exploratory multiple linear regression, and of Eqns (12–14), linking Q/B and predictor variables ($n = 108$)**
(Intercepts in parenthesis)

|	Exploratory model		Eqn (12)		Eqn (13)	Eqn (14)
	estimate	s.e.	estimate	s.e.	estimate	estimate
Intercept	(6.972)	(0.340)	(7.964)	(0.339)	(8.056)	(5.847)
Slope						
Factor (log)	–	–	–	–	0.300	–
Z (log; year^{-1})	–	–	–	–	–	0.280
W_∞ (log; g)	–0.209	0.036	–0.204	0.033	–0.201	–0.152
T'(1000/K)	–1.729	0.476	–1.965	0.406	–1.989	–1.360
Aspect ratio	0.071	0.046	0.083	0.044	0.081	0.062
Depth ratio	0.291	0.417	–	–	–	–
Peduncle depth	0.372	0.330	–	–	–	–
Herbivore[A]	0.517	0.112	0.532	0.104	0.522	0.510
Pellets[A,B]	–0.060	0.095	–	–	–	–
Detritivore[A]	0.352	0.153	0.398	0.144	0.393	0.390
Salinity	–0.058	0.083	–	–	–	–
R^2	0.530	–	0.516	–	–	–
df	98	–	102	–	–	–

[A]Dummy variable.

[B]Variable that identifies (aquaculture) populations for which only the amount of food given is known and not the amount actually consumed by the fish.
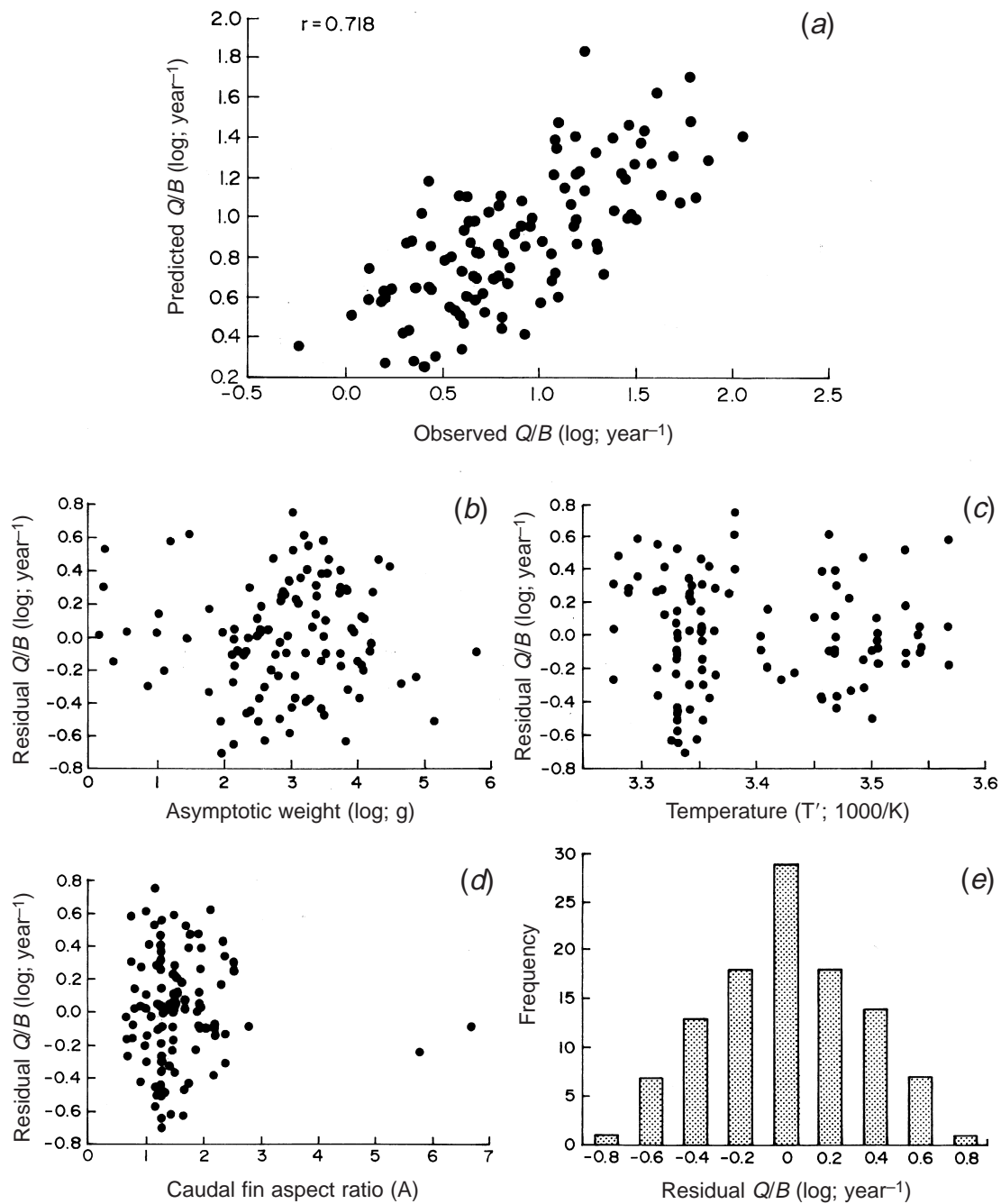
Fig. 2. Key features of the predictive model in Eqn (12). *(a)* Plot of log predicted *v.* log observed values; note relatively tight fit ($r = 0.718$, df 106). *(b)* Residuals (log predicted – log observed values) *v.* $\log W_\infty$; note absence of pattern, though W_∞ values between 100 and 10 000 g do predominate. *(c)* Residuals *v.* transformed temperature (1000/Kelvin); note faint vertical patterns due to preferences for 'round' values (in °C). *(d)* Residuals *v.* caudal-fin-aspect ratio; scarcity of high values (for tunas) explains the non-significant effect of this biologically important variable. *(e)* Frequency distribution of residual *Q/B* values; note normality of distribution.

Mitchell (1997) argued that the approach documented in Fig. 2 to validate a predictive model is inappropriate and suggested the use of the approach in Fig. 3 instead. This also suggests that Eqn (12) meets the expectations for a model such as sought here.

[Note also that the circularity affecting Z (and f; see above) is avoided in the case of W_∞, although this parameter enters Eqn (12) both as independent variable and as factor in Eqns (2) and (4), used to estimate Q/B, the dependent variable. This is so because the values of W_∞ cancel out when (2)
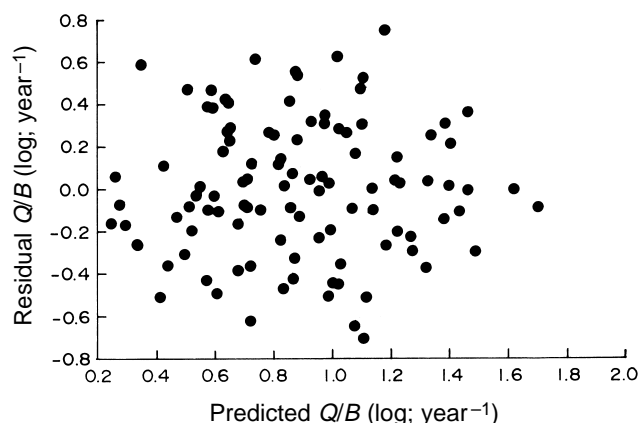
Fig. 3. Plots of residuals (log predicted – log observed values) *v.* predicted values. Note absence of pattern, which validates Eqn (12) by the criterion of Mitchell (1997).

and (4) are inserted into (1). The other independent variables of Eqns (12)–(16) are completely unrelated to Q/B.]

Thus validated, the statistics in Table 2 and Figs 2 and 3 lead to three major conclusions:

(1) Q/B can be predicted from population parameters that are relatively easy to estimate;

(2) morphometric variables for body depth and for caudal peduncle height, found by Pauly (1989) to have a significant effect on Q/B, have no relationship with Q/B once food type and temperature are properly accounted for; and

(3) for fish well adapted to fresh or salt water, salinity, other things being equal, does not have any significant effect on Q/B, contrary to a widespread, if often unstated, belief.

Re-expressing Eqn (12) in terms of path coefficients (Blalock 1972), i.e. of partial slopes standardized by the standard deviations of the variates, leads to the following values: $\log W_\infty = -0.455$; $h = 0.354$; $T' = -0.340$; $d = 0.193$ and $A = 0.141$. Thus, the effect of asymptotic weight on Q/B is about three times as strong as the effect of aspect ratio, with the other variables taking intermediate ranks.

The addition to our original data set ($n = 108$) to cover Q/B values recomputed for multiplication factors (f) of M equal to 0.5, 2 and 4 led to Eqn (13):

$$\log Q/B = 8.056 + 0.300\log f - 0.201\log W_\infty + 1.989T' \quad (13)$$
$$+ 0.081A + 0.522h + 0.393d$$

where all variables are defined as in Eqn (12), except for f, which has a positive slope, as expected. This model can be used to predict Q/B of exploited stock whose exact Z value is unknown, but for which total mortality can be approximated, based on natural mortality times a factor. Eqn (14) is supplied for cases where the exact value of Z is known:

$$\log Q/B = 5.847 + 0.280\log Z - 0.152\log W_\infty - 1.360T' \quad (14)$$
$$+ 0.062A + 0.510h + 0.390d$$

where Z is equal to $M + F$, the latter term representing fishing mortality.

Allen (1971) has shown that for a variety of expressions for growth and mortality (including Eqns 2 and 5) the instantaneous rate of total mortality Z is equal to production/biomass ratio (P/B), a key input in trophic models (Christensen and Pauly 1992).

In analogy to K_1, which expresses the food conversion efficiency of (a group of) animals of a given size, a gross conversion efficiency (GE) can be defined, for an age-structured population as

$$[GE] = (P/B)\,/\,(Q/B) \quad (15)$$

Thus, given the identity between Z and P/B, we can derive from Eqn (14) the model

$$\log[GE] = -5.847 + 0.720\log Z + 0.152\log W_\infty + 1.360T' \quad (16)$$
$$- 0.062A - 0.510h - 0.390d$$

which predicts GE as a function of Z, asymptotic weight, temperature and food-related parameters.

Here, as for Eqns (12)–(14), values of $A = 1$ may be used for fish which do not use their caudal fin as main organ of propulsion, and which will therefore tend to have low metabolic rates (Pauly 1989; see also Fig. 1 and Fig. 2*d*).

These equations will be useful for parameterization of trophic models. A previous model (Palomares and Pauly 1989) was widely used for such purposes (see, e.g., contributions in Christensen and Pauly 1993), although it did not include as many cases and as many variables as the models presented here.

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