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Food consumption by tropical and temperate fish populations: some generalizations

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Published estimates of ration and/or food conversion efficiency of various size groups of fishes from 75 different stocks belonging to 56 tropical and temperate species were standardized and re-expressed as annual fish food consumption (Q) per unit biomass of the age-structured population (B). Although derived from extremely heterogeneous sources, these estimates of Q/B show surprisingly regular patterns. These allow confirmation of some earlier hypotheses, e.g. that Q/B increases with water temperature and decreases with asymptotic weight. More interestingly, it is shown that the aspect ratio of the caudal fin of fishes that use the carangiform and related swimming modes (i.e. subcarangiform and thunniform) correlates closely with Q/B, when other factors are accounted for. A brief discussion of some implications of these and related results is provided.

Key words: fish populations; modelling; food consumption; body shape; caudal fin; caudal peduncle; aspect ratio; swimming behaviour.

I. INTRODUCTION

Theoretical advances, notably by Ulanowicz (1986), and the necessity to manage marine ecosystems such as, e.g. the North Sea or the Gulf of Thailand, on a multispecies basis have recently heightened the interest of ecologists and fisheries scientists in constructing trophic models of such systems.

Among the parameters of such models, the food consumption rate of the various fishes considered is one that is most difficult and/or costly to estimate (as compared with food and feeding habits, which are straightforwardly assessed by stomach contents analysis).

In this contribution, I propose an approach to obtain rough estimates of the relative food consumption of a marine fish population. This is achieved by:

i. standardizing published food consumption estimates of a large number of marine species and populations;
ii. identifying and defining some easy-to-obtain predictors of food consumption;
iii. deriving an empirical (multiple linear regression) model linking the predictors in (ii) with the standardized rates in (i);
iv. 'explaining' the food consumption rates of marine fishes as expression of their activity (i.e. metabolic) levels.

The model in (iii) also tests the hypothesis that the body shape of fish, and especially the shape of the caudal fin, relates to their food consumption, because the shape of fishes reflects their metabolic level (Fig. 1).

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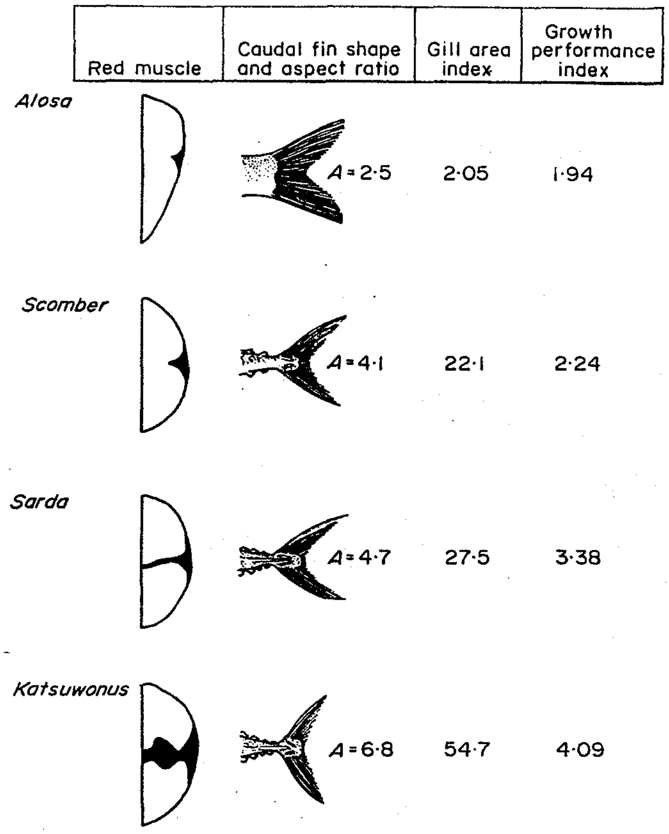

FIG. 1. Some pelagic fish genera illustrating the relationships between development of some organs (here: red muscle and gills), shape-related indices (here: the aspect ratio of the caudal fin) and indices of metabolic activity (here: growth performance). See text for food consumption as correlate of, e.g., aspect ratio. Red muscle areas are from Bone (1978) and Sharp & Dizon (1978); aspect ratios estimated as shown in Fig. 2; gill area index = estimated surface area (cm^2) of a 1-g fish (Pauly, 1979); growth performance index = sum of the $\log_{10}$ of the von Bertalanffy parameters (year^{-1}) and W_∞ (g) (Pauly, 1979).

II. MATERIALS AND METHODS

METHOD FOR THE ESTIMATION OF THE FOOD CONSUMPTION OF FISH POPULATIONS

The scientific literature on marine fish biology was scanned for contributions presenting, for a given fish species (or population of a given species), information on individual growth, natural mortality, daily ration, food conversion efficiency and habitat temperature.

The von Bertalanffy growth function (VBGF) was used to reduce and express all growth data. The VBGF has, for weight, the form:

$$W_t = W_\infty (1\text{-}\exp^{-(K(t-t_0))})^b \tag{1}$$

where W_t is the weight at age t (here: wet weight), W_∞ the asymptotic weight, K a growth coefficient, t_0 the theoretical 'age' of the fish at weight zero, and b the exponent of a length–weight relationship of the form:

$$W = a \cdot L^b \tag{2}$$

which was used to convert the VBGF for length (L) into that for weight.

TABLE I. Some shape-related indices of the metabolic level of fishes using the carangiform and related modes of locomotion

Index	Definition and remarks
Depth ratio (D)	Body length (from tip of snout to end of caudal peduncle, as used to define standard length)/Maximum body depth ($D_{\max}$)
Aspect ratio (A)	Height of caudal fin squared/surface area of caudal fin (Fig. 1)
Acceleration index (C)	$C = \sum_{i=1}^{10} (f_i/D_{\max})i$, where f_i are the depths of ten successive slices of the body, from $D_{\max}$ to the narrowest part of the caudal peduncle (Fig. 2)
Relative depth of caudal peduncle (P)	Depth of caudal peduncle/$D_{\max}$ (Fig. 2)

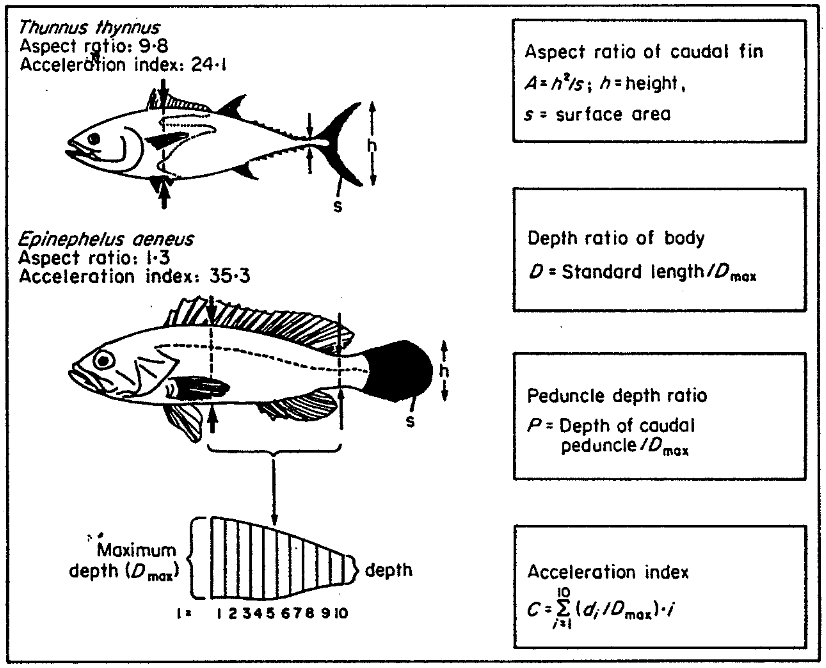

FIG. 2. Schematic representation of methods for estimation of shape-related indices of fish activity discussed in the text, as illustrated by bluefin tuna, highly specialized for sustained swimming, and by white grouper, specialized for burst swimming.

TABLE II. Data on morphometrics, food consumption (Q/B)[*] and related statistics of 75 stocks of temperate and tropical marine fish as used to derive model for prediction of Q/B (see text)[†]

No.	Species	Location	Temp. (° C)	W_α (g)	K (year^{-1})	Aspect ratio	Acceleration index	Depth ratio	Peduncle ratio	Q/B (year^{-1})
1	*Cetorhinus maximus*	North Sea	12·0	13 820 000	0·045	4·5	32·4	5·72	0·22	3·70
2	*Isurus oxyrinchus*	New England coast	10·0	377 535	0·229	4·2	27·3	5·48	0·15	9·64
3	*Squalus acanthias*	British Columbia	10·0	4773	0·063	2·1	29·9	7·00	0·27	4·77
4	*Alosa pseudoharengus*	Georges Bank	10·0	481	0·216	2·7	29·0	3·15	0·28	8·62
5	*Clupea harengus*	Georges Bank	10·0	400	0·270	1·9	31·2	4·13	0·30	4·59
6	*Clupea harengus*	Clyde, Scotland	10·0	439	0·200	1·9	31·2	4·13	0·30	10·10
7	*Sprattus fuegensis*	Falkland	10·0	93	0·380	1·8	31·2	4·66	0·33	8·57
8	*Argentina silus*	Georges Bank	10·0	747	0·156	3·5	34·6	5·73	0·38	10·17
9	*Synodus englemani*	Great Barrier Reef	26·0	250	1·400	2·5	35·6	6·17	0·37	29·60
10	*Hygophum proximum*	West Central Pacific	25·0	2	0·760	1·7	33·6	4·63	0·35	34·60
11	*Hygophum reinhardtii*	West Central Pacific	25·0	1	0·540	1·1	32·6	5·49	0·37	26·80
12	*Lampanyctus alatus*	Gulf of Mexico	25·0	2	0·500	1·6	33·2	4·75	0·46	11·90
13	*Myctophum asperum*	West Central Pacific	25·0	8	0·340	1·3	30·7	4·12	0·29	26·50
14	*Myctophum aurolaternatum*	West Central Pacific	25·0	10	0·170	1·1	31·0	4·98	0·40	16·70
15	*Myctophum nitidulum*	West Central Pacific	25·0	11	0·260	0·9	32·9	4·10	0·33	12·20
16	*Myctophum spinosum*	West Central Pacific	25·0	13	0·237	1·3	29·5	4·38	0·03	26·50
17	*Symbolophorus evermanni*	West Central Pacific	25·0	4	0·310	1·2	35·5	5·38	0·38	20·90
18	*Gadus morhua*	Baltic, East	5·0	10 834	0·154	0·9	31·3	5·08	0·23	2·17
19	*Gadus morhua*	Georges Bank	10·0	30 451	0·130	0·9	31·3	5·08	0·23	2·19
20	*Gadus morhua*	NW Atlantic	8·0	16 387	0·180	0·9	31·3	5·08	0·23	3·43
21	*Gadus morhua*	Baltic, West	10·0	12 356	0·220	0·9	31·3	5·08	0·23	2·70
22	*Gadus morhua*	Iceland	4·0	124 745	0·049	0·9	31·3	5·08	0·23	4·08
23	*Gadus morhua*	Irish Sea	8·0	16 350	0·190	0·9	31·3	5·08	0·23	3·41
24	*Gadus morhua*	Barents Sea	5·0	24 000	0·100	0·9	31·3	5·08	0·23	2·34
25	*Gadus morhua*	North Sea	12·0	15 714	0·300	0·9	31·3	5·08	0·23	2·29
26	*Gadus morhua*	Faeroe Is.	8·0	16 350	0·190	0·9	31·3	5·08	0·23	4·36
27	*Gadus morhua*	North of Norway	5·0	24 000	0·100	0·9	31·3	5·08	0·23	1·41
28	*Gadus morhua*	Scotland	8·0	16 350	0·190	0·9	31·3	5·08	0·23	4·55
29	*Gadus morhua*	Kattegat	8·0	21 908	0·180	0·9	31·3	5·08	0·23	1·94
30	*Melanogrammus aeglefinus*	North Sea	12·0	1858	0·205	1·7	33·6	4·58	0·24	5·69
31	*Melanogrammus aeglefinus*	Faeroe's Sea	8·0	7350	0·157	1·7	33·6	4·58	0·24	3·97
32	*Melanogrammus aeglefinus*	Georges Bank	10·0	5400	0·220	1·7	33·6	4·58	0·24	3·00
33	*Melanogrammus aeglefinus*	Scotland	12·0	5400	0·220	1·7	33·6	4·58	0·24	12·76
34	*Melanogrammus aeglefinus*	Iceland	4·0	6087	0·228	1·7	33·6	4·58	0·24	4·96
35	*Micromesistius poutassou*	Iceland	4·0	284	0·360	0·9	36·8	6·93	0·29	9·06
36	*Pollachius virens*	Faeroe and Georges Bank	8·0	10 114	0·158	2·3	30·5	5·28	0·24	4·76

37	*Urophycis tenuis*	Gulf of St Lawrence	10·0	23 972	0·454	1·0	26·6	4·81	0·21	3·10
38	*Merluccius bilinearis*	Georges Bank	10·0	942	0·246	1·5	29·5	5·87	0·21	4·26
39	*Merluccius bilinearis*	Nantucket	10·0	2564	0·116	1·5	29·5	5·87	0·21	3·85
40	*Merluccius capensis*	SW Africa	16·0	9200	0·140	0·8	34·1	5·69	0·28	7·53
41	*Merluccius productus*	Northwest Pacific	10·0	1083	0·311	1·2	28·1	5·58	0·26	1·85
42	*Hyporhamphus melanochir* (Crust.)	Australia	14·0	243	0·320	2·8	37·4	10·14	0·38	5·41
43	*Fundulus heteroclitus*	North Carolina	20·0	42	0·278	1·5	37·7	3·47	0·53	3·65
44	*Sebastes inermis*	Hokkaido, Japan	4·0	708	0·317	1·9	32·0	2·74	0·30	3·44
45	*Sebastes mentella*	Georges Bank	10·0	1972	0·058	1·3	30·0	3·04	0·26	7·97
46	*Lates calcarifer*	SE Asia	27·0	30 743	0·128	2·0	40·8	3·34	0·36	5·63
47	*Epinephelus aeneus*	NW Africa	19·0	47 089	0·171	1·3	34·6	4·68	0·40	4·01
48	*Epinephelus guttatus*	Bermuda	28·0	1880	0·240	1·4	32·8	3·25	0·30	2·77
49	*Epinephelus merra*	Indonesia	27·0	955	0·400	1·7	32·9	3·09	0·31	2·03
50	*Epinephelus tauvina*	Thailand	27·0	900	0·292	1·9	35·2	3·23	0·35	5·93
51	*Caranx ruber*	Cuba	27·0	3036	0·143	3·9	28·2	3·39	0·12	10·60
52	*Trachinotus teraia*	West Africa	29·0	7931	0·310	2·7	25·0	1·83	0·16	3·81
53	*Coryphaena hippurus*	Hawaii	25·0	147 000	0·566	3·3	28·0	5·04	0·20	8·48
54	*Lutjanus campechanus*	Gulf of Mexico	20·0	13 000	0·100	1·4	33·3	2·49	0·31	5·21
55	*Lutjanus erythropterus*	Indo-West Pacific	27·0	3229	0·310	2·4	32·6	2·60	0·32	6·65
56	*Lutjanus johnii*	Indonesia	27·0	8844	0·152	4·4	32·9	2·72	0·32	3·90
57	*Haemulon aurolineatum*	Bermuda	23·0	436	0·227	5·7	31·2	3·16	0·30	7·46
58	*Haemulon flavolineatum*	Bermuda	23·0	136	0·850	3·9	30·5	2·82	0·32	7·98
59	*Haemulon sciurus*	Bermuda	23·0	920	0·260	3·0	36·5	2·96	0·27	7·01
60	*Cynoscion striatus*	Argentina	14·0	2027	0·150	1·7	33·7	2·94	0·27	4·67
61	*Pagrus ehrenbergi*	Ghana	22·0	1104	0·495	2·5	29·7	2·27	0·24	9·37
62	*Sparus aurata*	Mediterranean	24·0	9617	0·130	2·8	31·3	2·51	0·23	4·66
63	*Liza subviridis*	Thailand	28·0	922	0·395	1·6	38·2	3·50	0·49	13·39
64	*Crenilabrus cinereus*	Black Sea	15·0	62	0·318	1·4	37·1	3·27	0·45	2·63
65	*Crenilabrus ocellatus*	Black Sea	15·0	22	0·774	1·0	36·3	3·10	0·45	5·53
66	*Callionymus pauciradiatus*	Florida	20·0	1	0·800	0·6	37·8	6·05	0·30	5·41
67	*Neogobius melanostomus (female)*	Azov Sea	11·0	55	0·547	1·4	30·2	4·09	0·40	3·63
68	*Neogobius melanostomus (male)*	Azov Sea	11·0	169	0·446	1·4	30·2	4·09	0·40	9·06
69	*Pomatoschistus microps*	Gullmar Fjord	8·0	14	0·295	0·9	38·3	5·93	0·54	5·68
70	*Pomatoschistus microps*	Lake Grevelingen	8·0	14	0·295	0·9	38·3	5·93	0·54	1·91
71	*Pomatoschistus minutus*	Northeast Atlantic	8·0	7	0·928	0·7	38·0	6·14	0·52	3·21
72	*Katsuwonus pelamis*	Pacific	24·0	15 433	0·596	7·2	25·5	3·92	0·07	32·57
73	*Sarda chiliensis*	Peru	22·0	5917	0·455	4·7	25·9	4·73	0·09	29·45
74	*Scomber scombrus*	Georges Bank	10·0	763	0·280	4·1	29·0	4·79	0·18	4·40
75	*Thunnus albacares*	Eastern Pacific	24·0	81 920	0·310	9·3	25·0	3·58	0·09	11·20

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*Q/B is the number of times the population in question consumes its own weight, per year.

†Details on data sources and methods used are available on request from the author.

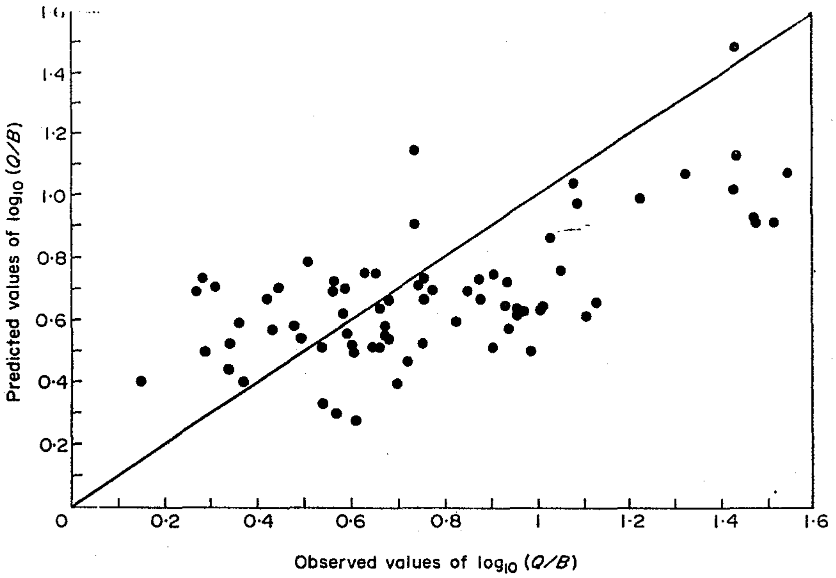

FIG. 3. Predicted *v.* observed food consumption per unit population biomass in 75 stocks of fishes using the subcarangiform, carangiform and thunniform modes of swimming; predicted values based on equation (13) (see text).

When not given in the original sources, rough estimates of the parameter t_0 were obtained from:

$$\log_{10}(-t_0) = -0{\cdot}3922 - 0{\cdot}2752 \log_{10} L_\infty - 1{\cdot}038 \log_{10} K \tag{3}$$

where K is as defined above and L_∞ is the length corresponding to W_∞ as defined above (Pauly, 1979).

Natural mortality estimates (M) were either obtained from contributions dealing with the species (or population) in question, or estimated from the empirical equation of Pauly (1980).

Throughout, weights are expressed in grammes live (wet) weight, length (usually total length) in centimetres, time in years, and rates (M and K) as per year.

Published estimates of daily ration (R_d) were matched against the corresponding fish sizes and re-expressed (due to lack of sufficient data on energy contents) as percent body weight per day (% BWD). Standard conversion factors were used for this purpose (e.g. Brey *et al.*, 1988). Also, ration estimates were adjusted to account for seasonality, e.g., 'winter' estimates were averaged with 'summer' estimates to obtain annual means.

Gross food conversion efficiency (K_1) was defined for any time interval by Ivlev (1939) as:

$$K_1 = \text{growth increment/food ingested,} \tag{4}$$

which can be generalized and solved as:

$$\text{ration} = \text{growth rate at age } t/K_{1(t)}. \tag{5}$$

The growth rate of equation (5) can be expressed by dw/dt, i.e. the first derivative of equation (1), while K_1 can be expressed as a function of weight (W) using:

$$K_1 = 1\text{-}(W/W_\infty)^\beta. \tag{6}$$

Equations (5)–(7) imply that values of K_1 and ration can be used interchangeably, given a set of growth parameters (Pauly, 1986; Silvert & Pauly, 1987; Palomares & Pauly, 1989). Thus, either ration or K_1 estimates can be used to parameterize the model:

$$Q/B = \int_{t_r}^{t_{\max}} [(\mathrm{d}w/\mathrm{d}t)\exp(-M(t-t_r))/1-(1-\exp(-K(t-t_0)))^{b/\beta}]\,\mathrm{d}t \Big/ \int_{t_r}^{t_{\max}} [W_t\cdot\exp(-M(t-t_r))]\,\mathrm{d}t \quad (7)$$

where Q is the population-weighted food consumption, B is population biomass, t_r and $t_{\max}$ are the ages at recruitment into and of derecruitment from the stock, respectively, and all other parameters are as defined in equations (1)–(6). This equation was obtained by combining equation (1) and its derivative with equations (5) and (6), and was used here to condense the available growth, mortality and feeding-related information in the form of population-weighted food consumption estimates per unit population biomass.

A sensitivity analysis (Pauly, 1986) showed that the estimates of Q/B obtained via equation (7) are very sensitive to β and b, less so to K and M, and relatively insensitive (over a broad range of reasonable values) to the specific estimates of t_r, $t_{\max}$ and t_0 used (hence the use of equation (3) above).

The properties of the model summarized by equation (7) have been discussed in detail by Pauly (1986). Thus, it may suffice here to stress that equation (7) allows direct comparisons of (annual) food consumption rate among different populations because the resulting estimates of Q/B are weighted over an entire population and are not size-specific (as are estimates of R_d commonly presented in the literature).

DERIVATION OF SIMPLE SHAPE-RELATED INDICES OF FISH ACTIVITY

Elaborate classifications of the swimming modes of fishes exist (review: Lindsay, 1978). For the purposes of this contribution, three groups may be distinguished: I, anguilliform; II, subcarangiform, carangiform and thunniform; III, miscellaneous modes based on undulatory or oscillatory motions of fins other than the caudal.

In this contribution, only Group II fishes will be considered, i.e. fishes in which the shape of the caudal fin—the (main) organ of propulsion—can be used to infer metabolic levels (see below).

Webb (1984) proposed a scheme by which fishes, especially those of Group II, can be positioned onto a graph with three axes: specialization toward cruising (e.g. *Thunnus*); specialization toward accelerating (e.g. *Esox*); specialization toward manoeuvering (e.g. *Chaetodon*).

Specialized cruisers have a deeply forked or lunate caudal fin with a high aspect ratio (A), a narrow caudal peduncle (P) and an intermediate ratio of maximum body depth to body length (D) (Table I). Other morphological adaptations include high gill surface areas (Hughes, 1970, 1980; Pauly, 1979, 1981; Longhurst & Pauly, 1987) supplying high quantities of oxygen to large masses of red muscle working aerobically in sustained fashion (Fig. 1), which indicates a high metabolic level and a high energy intake. Thus, the low relative depth of caudal peduncle and the high aspect ratio of caudal fin of these fishes (Fig. 2; Table I) can be hypothesized as indicating a high food consumption (Q/B), after higher-order effects have been taken into account (Sharp & Dizon, 1978).

Specialized accelerators include predators which stalk their preys, e.g. pike (*Esox lucius*). In these fishes, the muscle mass is concentrated nearer to the caudal fin than in cruisers, and the depth of the caudal peduncle is relatively greater. The ability of fishes to accelerate rapidly can also be assessed by an acceleration index loosely adapted from Webb & Weihs (1986):

$$C = \sum_{i=1}^{10} (f_i/D_{\max})\cdot i \quad (8)$$

where $D_{\max}$ is the maximum body depth of the fish in question (as also used to compute D) and f_1 the depths of ten successive ' slices ' of the body, from the maximum depth to the end of the narrowest part of the caudal peduncle (i.e. excluding the caudal fin to prevent multicollinearity with the variable A; see Fig. 2 and text below). The muscles of specialized accelerators work anaerobically, and these fishes are rather quiescent between strikes. One can thus hypothesize that high values of C or of P should correlate with a low overall metabolic level and hence with a low relative food consumption (Q/B).

Fish which specialize in manoeuvering, such as coral reef fishes and fishes living in other complexly structured habitats, generally have rounded or squared, low aspect ratio tails and a short body (disk-shaped in extreme cases) " which facilitate rotating movements in the median vertical plane" (Webb, 1984). They have high values of the ratio (D) of standard length to maximum body depth (Table I; Fig. 2).

All values of the shape-related indices used in this contribution were derived from illustrations of adult fishes, as published in, e.g. Fischer *et al.* (1981) and Whitehead *et al.* (1984).

STATISTICAL (MULTIPLE REGRESSION) MODELS USED

The model used to analyse the data presented here has the form:

$$Y = a + b_1 X_1 + b_2 X_2 \ldots + b_k X_k \tag{9}$$

wherein the dependent variable is $\log_{10} Q/B$ as defined above, a is the intercept, and the X_i-X_k are variables (i.e. their $\log_{10}$ transforms) hypothesized to be related with Q/B via the partial regression coefficients or slopes (b_i-b_k).

Palomares & Pauly (1989), based on 33 estimates of Q/B, identified the following variables as related to ($\log_{10}$) Q/B: ($\log_{10}$) W_∞, the asymptotic weight of the fishes of a given population, as an index of their size; ($\log_{10}$) T, temperature in ° C, the mean habitat temperature of the population in question; ($\log_{10}$) A, the aspect ratio of the caudal fin; and F, the food type (a dummy variable, set at 0 in carnivorous and 1 in herbivorous fishes).

The variables W_∞, T and A are used here in addition to the new variables introduced above (C, P and D, see Table I); the variable F is omitted because all fishes considered here are carnivorous. The statistical model to fit equation (9) to the data is the ordinary least square linear multiple regression model available in the Lotus 1-2-3 software package.

To assess which of the X_i in equation (9) has the greatest impact on Y (independently of the different units used), so-called "beta weight coefficients" (Blalock, 1972) were computed, using

$$\beta_{1,2.3\ldots k} = b_{1,2.3\ldots k} \frac{\text{S.D.}2}{\text{S.D.}1} \tag{10}$$

where $\beta_{1,2.3\ldots k}$ is the beta weight coefficient linking the dependent variable 1 and the independent variable 2 after the effect of the independent variables 3 to k has been eliminated, while S.D.1 and S.D.2 are the standard deviations of variables 1 and 2, and $b_{1,2.3\ldots k}$ the corresponding partial slope.

III. RESULTS AND DISCUSSION

Table II lists the fish species and stocks used for the present exercise, along with their corresponding values of T, W_∞, K and M, either compiled from, or estimated from, data in the literature. Details on data sources and computations, which could not be presented for lack of space, are available from the author, along with the sources for the estimates of Q/B.

For the 56 species in Table II, the relationship between relative peduncle depth (P) and acceleration index (C) was:

$$\log_{10} P = 24{\cdot}7 + 25{\cdot}6 \log_{10} C \tag{11}$$

with $r = 0{\cdot}778$ (d.f. $= 54$), which is significant ($P < 0{\cdot}01$). The high correlation between P and C suggests that relative peduncle depth in fishes using the subcarangiform, carangiform and thunniform swimming modes is a good index of the ability of these fish to accelerate and of the distribution of their muscle mass along their bodies. This high correlation also suggests that, to avoid multicollinearity, a multiple regression model such as equation (9) may include either P or C, but not both.

The relationship between caudal fin aspect ratio (A) and acceleration index (C) is, for the 56 species investigated:

$$\log_{10} A = 34{\cdot}9 - 1{\cdot}12 \log_{10} C \tag{12}$$

with $r = 0{\cdot}498$ (d.f. $= 54$), which is significant ($P < 0{\cdot}01$). The negative sign of this relationship confirms the suggestion of Webb (1984) that the specializations for cruising and accelerating involve a trade-off. Together, equations (11) and (12) confirm that the indices A, P and C are interrelated in a fashion that is compatible with contemporary theories on fish swimming modes.

Because P and C are interchangeable, the parameters of two multiple regression models were estimated from the data in Table II, i.e., $Q/B = f(T, W_\infty, A, D$ and $P)$ and $Q/B = f(T, W_\infty, A, D$ and $C)$. The former of these not only had a better fit ($R^2 = 0{\cdot}536$ *v.* $R^2 = 0{\cdot}498$) but also used P, a variable that is easier to estimate than C. Thus, the best multiple regression model derived from the data in Table II was

$$\log_{10} Q/B = -0{\cdot}102 + 0{\cdot}444 \log_{10} \mathrm{T} - 0{\cdot}115 \log_{10} W_\infty + 0{\cdot}427 \log_{10} A + 0{\cdot}577 \log_{10} D - 0{\cdot}464 \log_{10} P \tag{13}$$

with d.f. $= 69$ and $R = 0{\cdot}732$, and in which all partial slopes (T, W_∞, A and D) but one are significant at $P < 0{\cdot}01$, the other (P) being significant at $P < 0{\cdot}05$. This model explains 54% of the variance of the ($\log_{10}$) values in Table II.

Figure 3 shows a plot of predicted *v.* observed values of Q/B; this plot lacks structure, i.e. the deviations of the observed from the predicted values are random.

The beta weight coefficients corresponding to equation (13) are, in descending order, $\beta_{W_\infty} = (-)0{\cdot}4911$, $\beta_T = 0{\cdot}3354$, $\beta_A = 0{\cdot}3349$, $\beta_P = (-)0{\cdot}2852$ and $\beta_D = 0{\cdot}2302$. Thus, it appears that of the three shape-related indices included in equation (13), aspect ratio is the one whose variations have the greatest impact on variations of Q/B. These results confirm the earlier analysis of Palomares and Pauly (1989) who found the aspect ratio of the caudal fin of fishes to be an excellent predictor of Q/B (the beta weight coefficients for W_∞, A and T were $(-)0{\cdot}7056$, $0{\cdot}3095$, and $0{\cdot}1996$, respectively). The present study, based on more data points, established that, other things being equal, fishes with a high depth ratio tend to have higher food consumption rates than fishes with low depth ratios, while fishes that are specialized for rapid acceleration tend to have lower food consumption rates.

Overall, the data set presented here (a subset of a large database presently being assembled at ICLARM to support future comparative studies) documents the close relationships between the food consumption of fishes and their mode of locomotion as mediated by metabolic level.

The empirical relationships presented here may be useful for modelling. Thus, equation (13) can be used to obtain reasonable estimates of population-weighted food consumption for any species of temperate to tropical fishes in which the caudal fin is the (main) propulsive organ. This may be useful when multispecies trophic models are constructed, especially for less abundant species not justifying a major research effort.

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