

Estimates of Relative Food Consumption by Fish and Invertebrate Populations, Required for Modelling the Bolinao Reef Ecosystem, Philippines*

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Abstract

Estimates of food consumption per unit biomass in five important invertebrate groups and eight species of fish are presented for taxa which either occur or can be used to represent major elements of the coral reef ecosystem of Bolinao, Pangasinan, Philippines. A brief discussion is presented on how these estimates can be used to construct a steady-state trophic model of the Bolinao reef ecosystem, and of the application of the methods used therein to other taxa and/or ecosystems.

Introduction

When studying the trophic structure, i.e., energy flow and predator-prey relationships of coral reef ecosystems, it is of vital importance to relate the food consumption (Q), biomass (B) and production (P) of each reef organism to the production of its food resource (Winberg and Duncan 1971; Mann 1978; Polovina 1984; Olson and Mullen 1986). Furthermore, the evaluation of the magnitude and nature of these interactions

are relevant aspects of ecosystem and multispecies fisheries management (Palomares and Pauly 1989 and see contributions in this volume).

This paper (of which Sambilay et al. 1992 is a summary version) provides estimates of the food consumption of some fish and invertebrate groups occurring in Bolinao Reef in Lingayen Gulf, Pangasinan, Philippines. The results can be used as initial estimates of input parameters to an ecosystem model as constructed using the ECOPATH or ECOPATH II models and software. Details of the procedures on how these estimates were obtained are also provided to serve as example for approaches such as used here for taxa and/or areas not considered here.

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Materials and Methods

Materials

The estimates of the food consumption per unit biomass (Q/B) of five invertebrate groups and eight species of fish presented here were derived using growth and feeding data obtained from the literature, except for two species of coral reef fishes (*Zebрасoma scopas* and *Myripristis murdjan*) which are based on experiments conducted (by S. Opitz) at the Institut für Meereskunde, Kiel University, Germany.

Except for recent estimates of food consumption of *Siganus fuscescens* by Hernandez et al. (1990) and Espinosa (1991), food consumption studies based on samples obtained in the Bolinao area are currently unavailable. However, the estimates presented here refer to tropical or subtropical species of the Indo-Pacific faunal zone (except for two datasets, pertaining to an Atlantic sea urchin and an octopus) of which most have been recorded from the Bolinao area (Aprieto and Viloso 1982; Mines 1986; M. Lopez, unpubl. data).

Methods

ESTIMATION OF CONSUMPTION FROM DATA ON FOOD CONVERSION EFFICIENCY

Gross food conversion efficiency (K_1 , Ivlev 1961) is defined as

$$K_1 = (\text{growth increment}/\text{food intake}) \quad \dots 1$$

for any period of time. The relationship of K_1 with the size of the organism can be expressed as a function of weight (Pauly 1986; Silvert and Pauly 1987), i.e.,

$$K_1 = 1 - (W/W_\infty)^\beta \quad \dots 2$$

where W_∞ is the asymptotic weight of the organisms in the population in question, as also used in the von Bertalanffy growth function (VBGF), which has the form

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^\beta \quad \dots 3$$

where K is the rate (dimension: time⁻¹) at which W_∞ is approached; t_0 is the theoretical age the organisms would have at length zero if they had always grown according to the VBGF; and β is the exponent of a length-weight relationship of the form

$$W = a \cdot L^b \quad \dots 4$$

(see below for the estimation of the VBGF parameters). Equation (2) can be written:

$$-\log_{10}(1-K_1) = \beta \log_{10} W_\infty - \beta \log_{10} W \quad \dots 5$$

which has the form of a linear regression, from which W_∞ and β can be estimated. Alternatively, when W_∞ is known, β can be estimated from

$$\beta = (\overline{-\log_{10}(1-K_1)}) / (\log_{10} W_\infty - \overline{\log_{10} W}) \quad \dots 6$$

If several factors other than size (W) affect K_1 , (5) can be extended to the multiple linear regression

$$-\log_{10}(1-K_1) = a - \sum_{i=1}^n \beta \log_{10} W + \sum b_i v_i \quad \dots 7$$

where for $i=1$ to n , b_i is the partial slope associated with the factor v_i , affecting the growth of the organisms studied, such as, e.g., temperature, food type, etc. (Pauly 1986; Palomares 1987; Palomares and Pauly 1989).

From (2), one can express the rate of food consumption (dq/dt) at age t as

$$dq/dt = (dw/dt)/(K_{1(t)}) \quad \dots 8$$

where $K_{1(t)}$ is the conversion efficiency expressed as a function of age, as can be obtained by combining (2) and (3), and in which the growth rate (dw/dt) is the first derivative of the VBGF, or

$$dw/dt = W_\infty b K (1 - e^{-K(t-t_0)})^{b-1} e^{-K(t-t_0)} \quad \dots 9$$

Cumulative food consumption (Q_c) from any age t_r to t_{\max} can therefore be estimated from

$$Q_c = \int_{t_r}^{t_{\max}} \frac{(dw/dt) dt}{K_{1(t)}} \quad \dots 10$$

Food consumption per unit biomass per unit time (Q/B) in an age-structured steady-state population (Pauly 1986) can thus be computed by

$$Q/B = \frac{\int_{t_r}^{t_{\max}} (dw/dt) e^{-z(t-t_r)} dt}{1 - (1 - e^{-K(t-t_0)})^\beta} \bigg/ \int_{t_r}^{t_{\max}} W_t e^{-z(t-t_r)} dt \quad \dots 11$$

where t_r and t_{\max} are the ages at recruitment and exit from the population, respectively; Z is

the instantaneous mortality between ages t_r and t_{max} ; and the exponential terms ($e^{-Z(\dots)}$) express the decay of the population through time, starting from an arbitrary number of recruits (here set equal to 1). Apart from allowing the estimation of Q/B , this model also enables the estimation of maintenance ration (R_m) and of trophic efficiency (E_T). This is because maintenance ration is defined as "Q/B at W_∞ " and trophic efficiency (E_T , production per unit of food consumed) can be reexpressed as

$$E_T = Z \cdot (B/Q) \quad \dots 12$$

A few of the Q/B values estimated below originally referred to habitat (or experimental) temperatures (T) of less than 27°C. The appropriate upward adjustment was performed by multiplying the original estimates of Q/B by a factor "V" obtained from

$$V = 27^{0.6121/T} \quad \dots 13$$

where 27 refers to the temperature at Bolinao in °C, and 0.6121 is the partial regression coefficient associated with temperature in the empirical model of Palomares and Pauly (1989).

Throughout this paper, Q/B values will be expressed either on an annual or daily basis; in the latter case, we shall express Q/B as % BWD, i.e., per cent of body weight per day. Unless otherwise mentioned, the consumption rates in this contribution refer to live or wet weight (ww).

ESTIMATION OF RELATIVE POPULATION CONSUMPTION FROM ESTIMATES OF INDIVIDUAL RATION

When daily ration (R_d), i.e., the daily food consumption of the fish of a certain size is known, the concepts presented above can be used, when growth parameter and mortality estimates are also available, to estimate population food consumption per unit biomass (Q/B).

Thus, substituting R_d for "food intake" and dw/dt for "growth increments" in (1) gives

$$K_1 = (dw/dt)/R_d \quad \dots 14$$

and the estimation of β and Q/B can proceed as outlined above.

There are numerous methods for estimation of ration in fishes (see Elliott and Persson 1978; Mann 1978; Windell 1978; Palomares and Pauly 1989; and references therein). A method which seems particularly applicable to Bolinao reef fishes is the analysis of diurnal cycles of stomach

contents (Sainsbury 1986 as modified by Jarre et al. 1991).

ESTIMATION OF GROWTH PARAMETERS (W_∞ , K and t_0)

Estimates of the parameters of the VBGF were obtained predominantly from literature data and a number of conversions. Of these, the conversion of estimates of asymptotic length (L_∞) to asymptotic weight (W_∞) was the most important. This was performed based on (4), with approximate values of L_∞ estimated from

$$L_\infty \approx L_{max}/0.95 \quad \dots 15$$

where L_{max} is the maximum length reported from the population in question (Pauly 1984).

When length-weight relationships with appropriate estimates of the parameters "a" and "b" were not available, values of "a" were obtained from length-weight data pairs and setting $a = W/L^3$, assuming isometric growth, i.e., $b = 3$. Through this contribution, we use cm for lengths and g for (wet) weight.

Estimates of K were obtained by either fitting the VBGF to length-at-age data, using the program of Gaschütz et al. (1980), which also yielded estimates of L_∞ and of t_0 , or from the equation

$$\log_{10} K = \bar{\phi}' - 2 \log_{10} L_\infty \quad \dots 16$$

In this, $\bar{\phi}'$ is the mean of several values of

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty \quad \dots 17$$

where K and L_∞ are growth parameter estimates for taxa (preferably species or genera) related to the one for which an estimate of K is to be obtained (Pauly 1979; Pauly and Munro 1984).

Rough estimates of t_0 were obtained, finally, from an empirical equation derived by Pauly (1979), i.e.,

$$\log_{10}(-t_0) = -0.40 - 0.28 \log_{10} L_\infty + 1.04 \log_{10} K \quad \dots 18$$

where K is expressed in year⁻¹, L_∞ in cm (total length) and t_0 is a very preliminary estimate of "age" at length zero. Pauly (1986) performed a sensitivity analysis of (11) which showed that t_0 , t_r and t_{max} have very little influence on the estimation of Q/B ; hence, the use of (18) appears acceptable.

Some estimates of food consumption for echinoderms (sea urchins, holothurids) taken from the literature referred to specimens of "average"

size. We have assumed this to correspond to half the asymptotic length.

ESTIMATION OF TOTAL MORTALITY OF EXPLOITED ORGANISMS OF BOLINAO REEF

The edible organisms of Bolinao reefs (holothurids, sea urchins, molluscs, shrimps, fishes, etc.) are all strongly exploited, and we shall assume here that their level of fishing mortality (F) is about equal to that of their natural mortality M (see Pauly 1984 for a discussion of this assumption). Hence, since $Z = F + M$, we have $Z = 2M$.

In fishes and invertebrates with high metabolic rate (octopus, squid and shrimp), M (year⁻¹) was estimated from

$$\log_{10} M = -0.211 - 0.0824 \log_{10} W_{\infty} + 0.6757 \log_{10} K + 0.4687 \log_{10} T \quad \dots 19$$

where W_{∞} refers to asymptotic wet weight in g, K refers to year⁻¹ and T is expressed in °C (Pauly 1980): T is set here at 27°C.

In the case of the low-metabolism echinoderms (sea urchins and holothurids), M was assumed to be lower than implied by (19), i.e., about equal to K (as is demonstrably the case in tropical sea urchins, see Longhurst and Pauly 1987, Fig. 10.2).

Note that the values of "Z" obtained as described above should not be used for fisheries assessment, although they might assist in obtaining reasonable estimates of Q/B when used in conjunction with equation (11).

Results

Sea Cucumbers

Sea cucumbers (holothurids) are ecologically important components of coral reef ecosystems; marketed as "trepang" or "bêche-de-mer," they are also of great economic importance (Conand 1989).

We present here estimates of growth, mortality and food consumption for two groups of sea cucumbers: (1) "*Holothuria* spp." and (2) "other holothurids".

Table 1 presents available growth parameter estimates for two *Holothuria* species. From these, we estimated for *H. pulla* the values $L_{\infty} = 30.7$ cm and $K = 0.238$ year⁻¹ which imply, if one relies on a relationship established from data on fishes, that $t_0 = -0.7$ year⁻¹. The assumption that $M = K$ and $Z \approx 2M$ leads to $Z = 0.6$ year⁻¹.

Table 1. Growth parameter estimates of three species of the genus *Holothuria*.

Species	L_{∞} (cm)	K(year ⁻¹)	ϕ'	Source
<i>H. atra</i>	32.4	0.110	2.06	Conand (1989)
<i>H. scabra</i>	29.0	0.524	2.64	This study ^a
<i>H. pulla</i>	30.7	0.238	2.35	Means

^a Based on the analysis of the length-frequency data in Fig. 6 of Shelley (1985), using the Compleat ELEFAN software of Gayanilo et al. (1989).

Pinto (1982) performed feeding experiments with *H. pulla* sampled in Talin Bay, Batangas, Philippines. He estimated that "average"-sized specimens consumed 1.35 g of seagrass per day.

Assuming "average" to correspond to $L_{\infty}/2$ (i.e., 15.4 cm), one can use the length-weight relationship established by Conand (1989) for *H. atra* (which resembles *H. pulla*), i.e.,

$$W = 0.486 L^{2.13} \quad \dots 20$$

to estimate as 164 g the weight of Pinto's "average" specimens. From the above data, one can estimate $Q/B = 0.88\%$ of body weight·day⁻¹ (BWD) and $R_m = 0.59\%$ BWD.

Table 2 presents growth parameter estimates for "other holothurids". They lead to rough estimates of L_{∞} and K for *Opheodesoma spectabilis* of 32.6 cm and 0.178 year⁻¹, respectively, with the estimate of asymptotic length matching the reported maximum size of 30 cm for *Opheodesoma* spp. (Reyes-Leonardo 1984) and the rule of thumb $L_{\infty} \approx L_{\max}/0.95$.

This leads to $t_0 = -0.8$ year and $M = 0.2$ year⁻¹ given the assumption that $M/K = 1$ (see above).

A length-weight relationship for *O. spectabilis* is not available. We assume it is the same as from *H. atra* (which has a similar body shape); thus $L_{\infty} = 32.6$ cm corresponds to $W_{\infty} = 812$ g.

Pinto (1982) estimated from his seagrass-feeding experiments a ration of 2.2 g·day⁻¹ for "average"-sized *O. spectabilis*. Making the same assumption as above with regard to their length leads to a mean weight of 186 g for the

Table 2. Growth parameter estimates of miscellaneous holothurids, as used to infer L_{∞} and K in *Opheodesoma spectabilis*.

Species	L_{∞} (cm)	K(year ⁻¹)	ϕ'	Source
<i>Actinopyga echinites</i>	29.5	0.090	1.894	Conand (1989)
<i>Actinopyga mauritana</i>	34.0	0.120	2.142	Conand (1989)
<i>Holothuria</i> spp.	-	-	2.350	See Table 1
<i>Stichopus chloronotus</i>	34.2	0.450	2.721	Conand (1989)
<i>Opheodesoma spectabilis</i>	32.6	0.178	2.277	Means

experimental animals, which would thus have a ration of 1.18% BWD. These parameters, combined with the growth parameters above, and $Z \approx 2M = 0.4 \text{ year}^{-1}$, lead to $Q/B = 1.22\% \text{ BWD}$ and $R_m = 0.88\% \text{ BWD}$.

Finally, combining our estimates for *Holothuria* spp. and "other holothurids" gives $Q/B = 1.05\% \text{ BWD}$ and $R_m = 0.73\% \text{ BWD}$ as mean value for sea cucumbers as an ecological group.

Sea Urchins

Sea urchins (echinoids) are ecologically important grazers in coral reef ecosystems, besides representing, in many areas, a valuable export commodity (Kato and Schroeter 1985). The account below, which presents the basis for our estimates of the relative grazing rate of a generic sea urchin population, is based on data from four groups: (1) *Echinometra mathaei*, (2) *Diadema* spp., (3) *Tripneustes* spp., and (4) *Echinometra picta*.

1. *Echinometra mathaei*. Ebert (1982) published the following growth parameter estimates for *Echinometra mathaei*: $L_\infty = 4.1 \text{ cm}$ (S_∞ in Ebert's notation, referring to ambitus length or largest diameter), $K = 0.29 \text{ year}^{-1}$; the corresponding values of asymptotic weight, t_0 and Z ($\approx 2M \approx 2K$, see above) are 31.3 g (assuming $b = 3$ and $a = 0.456$), -0.01 year and 0.58 year^{-1} , respectively.

2. *Diadema* spp. Downing and El-Zahr (1987) presented data (in their Table 1) on the gut content of *E. mathaei* specimen of 3.71 cm on the average (23 g), which allowed estimate of a mean gut content (over one daily cycle) of 1.53 g, of which 93% is CaCO_3 , or 0.09 g organic matter.

They also performed experiments to assess the time needed for their specimens of *E. mathaei* to empty their guts. From their data (Fig. 1), we estimated an instantaneous gut evacuation rate of 1.91 day^{-1} .

3. *Tripneustes* spp. Elliott and Persson (1978) showed that

$$R_d = \text{mean gut content} * \text{evacuation rate} \quad \dots 21)$$

Both *T. gratilla* and *T. ventricosus* (for which ration estimates are available, see below) reach sizes of up to 15 cm (George and George 1979); hence, $L_\infty = 15.8 \text{ cm}$ ($\approx 15 \text{ cm}/0.95$) will be used here together with $K = 0.841 \text{ year}^{-1}$, as derived from ϕ' above. We also have $t_0 = -0.22 \text{ year}$ and $Z \approx 2K = 1.7 \text{ year}^{-1}$.

Ebert (1975) gave for *T. gratilla* a complex length-weight relationship, which reexpressed to the format used here, reads

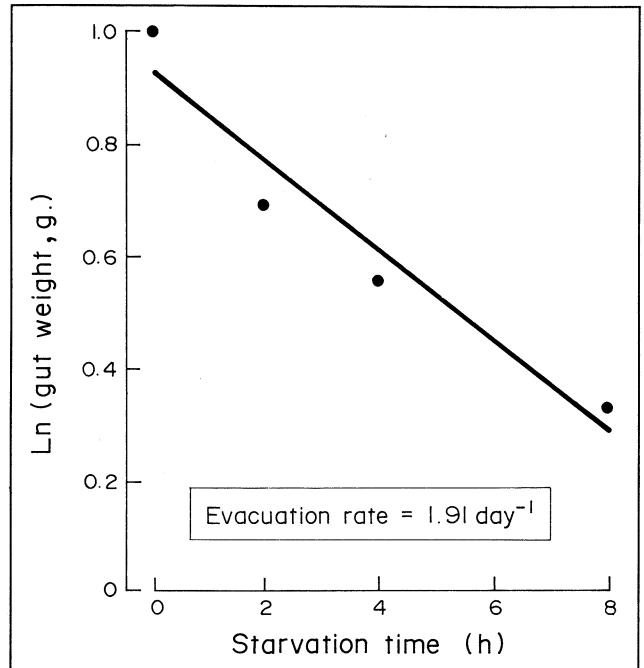


Fig. 1. Evacuation of gut contents in the sea urchin *Echinometra mathaei* as used to estimate the instantaneous evacuation rate (based on data point in Fig. 4 of Downing and El-Zahr 1987).

$$W = 0.959 L^{2.62} \quad \dots 22)$$

Combining the available growth and mortality estimates with the ration estimate in Table 3 gives $\beta = 0.276$, and hence, $Q/B = 1.34\% \text{ BWD}$ and $R_m = 0.83\% \text{ BWD}$.

Table 3. Estimates of daily feeding rates in *Tripneustes ventricosus*.

S (cm)	WW (g)	Feeding rate (g-day ⁻¹)	R _d (% BWD)	Source
7.5	177	4.40 (ww)	2.49	Ebert (1975)
12.1	742	1.44 (dw)	0.61 ^a	Tertsching (1989)

^aComputed from dry weight equivalent of 742 g, i.e., sea urchins are assumed to contain 68% water (see Appendix 1).

4. *Echinometra picta*. Pinto (1982) presented an estimate of seagrass consumption by "average"-sized *E. picta* which, if combined with appropriate growth parameters and Z estimates, leads to $Q/B > 90\% \text{ BWD}$. This is unrealistically high and will not be considered in further analyses.

Hence, combining (1), (2) and (3), values of $Q/B = 0.98\% \text{ BWD}$ and $R_m = 0.64\% \text{ BWD}$ can be suggested for sea urchins as an ecological group.

Penaeid Shrimps

Various crustaceans occur in or about coral reefs. The account below aims at providing an estimate of the relative food consumption of a population of penaeid shrimps, as represented by (1) *Penaeus monodon* and (2) *Metapenaeus monoceros*.

1. *Penaeus monodon*. This species is reported to reach 33.6 cm total length (Holthuis 1980), and hence we shall use, for $L_{\max}/0.95 \approx L_{\infty}$, an asymptotic length of 35 cm. Direct estimates of the value of the parameter K were not available, and hence, we estimated it via ϕ' and the data for *Penaeus* spp. in Table 4, as 0.35 year^{-1} .

Table 4. Growth parameters of miscellaneous penaeid shrimps as used to estimate ϕ' and K values for *Penaeus monodon*. M = male, F = female (adapted from Pauly et al. 1984).

Species		TL _∞ (cm)	K (year ⁻¹)	ϕ'
<i>Penaeus duorarum</i>	(M)	17.6	1.45	2.652
		17.6	1.20	2.570
<i>P. kerathurus</i>	(F)	21.0	0.80	2.548
	(M)	18.0	0.90	2.465
<i>P. setiferus</i>	(F)	22.5	1.25	2.801
	(M)	19.2	1.55	2.757
<i>P. monodon</i>	(-)	35.0	0.35 ^a	2.632 ^b

^aSee text.

^bMean of other values.

For the length-to-weight conversion, we used the generalized relationship for penaeid shrimps of Pauly et al. (1984)

$$W = 0.008(\text{TL})^3 \quad \dots 23)$$

which provides $W_{\infty} = 343 \text{ g}$. The other estimates used here are $t_0 = -0.46 \text{ year}$, $Z \approx 2M = 1.8 \text{ year}^{-1}$.

Vijayaraghavan et al. (1988) fed juvenile *P. monodon* of 0.15 g mean weight with *Artemia* cysts and nauplii. The mean observed weight increment and amount of feed ingested were 0.197 g and 0.790 g, respectively, and hence $K_1 = 0.25$.

From (6), $\beta = 0.0371$; the Q/B value derived from (11) is 4.48% BWD; maintenance ration is 2.58% BWD.

2. *Metapenaeus monoceros*. This is reported to reach 17.25 cm total length, from which, according to (15), $L_{\infty} \approx 18 \text{ cm}$. No direct estimate of K is available, and hence we have estimated this parameter indirectly, using growth parameter estimates for other species of the

genus *Metapenaeus* and the corresponding estimates of ϕ' (Table 5).

This resulted in $K = 0.67 \text{ year}^{-1}$ and the related estimates of $t_0 = -0.27$, and $Z \approx 2M = 3.2 \text{ year}^{-1}$. Asymptotic weight was derived via (23) and equaled 47 g.

Table 5. Some estimates of growth parameters in *Metapenaeus* spp. (from Pauly et al. 1984).

Species	TL _∞ (cm)	K (year ⁻¹)	ϕ'
<i>Metapenaeus brevicornis</i>	13.3	0.93	2.216
	14.2	0.90	2.262
<i>M. affinis</i>	17.5	1.20	2.565
<i>M. kutchensis</i>	14.0	1.15	2.353
	14.0	1.20	2.371
<i>M. monoceros</i>	13.5	1.05	2.282
	13.8	1.10	2.321
	18.0	0.67	2.338

Table 6 summarizes the results of feeding experiments with *M. monoceros* used here. As might be seen, the wide variety of feeds and experiment conditions led to widely varying values of K_1 , even after adjusting for the effect of body weight on K_1 . Here, we have ignored this variability and derived a single value of $\beta = 0.0249$, applicable to intermediate food and experimental conditions.

This value of β , combined with the growth parameters above, leads to $Q/B = 11.38\% \text{ BWD}$ and $R_m = 7.37\% \text{ BWD}$.

Based on the estimates for the two species above, "shrimp" as an ecological group, have a $Q/B = 7.93\% \text{ BWD}$ and $R_m = 4.98\% \text{ BWD}$.

Octopus

Various species of octopus occur on tropical reefs, inclusive of Philippine coral reefs (Roper et al. 1984). It is not certain whether *Octopus vulgaris*, the "common octopus," which is reported for the South and East China Seas, actually occurs on Philippine coral reefs but it is possible, given that "this species, or species-complex is widely distributed around the world (with) taxonomic and geographic parameters (that) still are not precisely defined" (Roper et al. 1984).

Growth parameters for *O. vulgaris* have been published by Guerra (1979) based on samples collected off Northwest Africa and in the Mediterranean (near Barcelona). We used the latter sets of parameters because these refer to warmer waters and hence, more akin to the condition prevailing in the Philippines.

Table 6. Food intake of *M. monoceros* on different diets.

No. ^a	Diet	dw (g) initial	dw (g) final	Food (g dw)	K ₁	ww ^b mean
1.	mangrove leaves	0.091	0.124	0.321	0.103	0.44
2.	mangrove leaves	0.089	0.114	0.251	0.100	0.42
3.	mangrove leaves	0.085	0.117	0.225	0.142	0.41
4. ^c	dry pellets	12.746	13.697	2.512	0.379 ^d	13.22
5. ^c	dry pellets	3.653	4.292	2.051	0.311 ^d	3.97
6. ^c	dry pellets	5.303	8.953	3.443	1.060 ^d	7.13
7. ^c	dry pellets	5.546	8.992	6.805	0.506 ^d	7.27
8. ^c	dry pellets	4.787	8.029	5.547	0.584 ^d	6.41
9. ^c	dry pellets	2.741	5.130	4.237	0.564 ^d	3.94
10.	trash fish	0.507	0.562	0.418	0.132	2.19
11.	low protein pellets	0.096	0.111	0.228	0.066	0.42
12.	Artemia	0.103	0.189	0.287	0.300	0.60
13.	Formula 5	0.167	0.271	0.851	0.122	0.90
14.	Formula 7	0.099	0.175	0.462	0.164	0.56
15.	Formula 8	0.072	0.136	0.471	0.136	0.42
16.	fish meal	0.200	0.201	0.465	0.002	0.82
17.	fish meal	0.239	0.299	1.010	0.060	1.10
18.	fish meal	0.394	0.505	2.104	0.053	1.84
19.	Cooper 6	0.185	0.192	0.521	0.014	0.77
20.	Cooper 6	0.253	0.337	1.175	0.071	1.21
21.	Cooper 6	0.407	0.500	2.750	0.034	0.64
22.	Formula 10	0.259	0.365	0.985	0.108	1.28
23.	Formula 10	0.443	0.630	2.970	0.063	2.20
24.	Tamil Nadu	0.156	0.148	0.505	-0.017 ^d	0.30
25.	pellet 7	0.262	0.299	1.532	0.024	1.15
26.	pellet 7	0.392	0.466	4.515	0.016	1.76

^a Nos. 1-3, Ramadhas and Vijayaraghavan (1979); 4-15, Royan et al. (1977); 16-26, Vijayaraghavan et al. (1978).

^b Weight conversion based on body water composition of *M. monoceros* = 75.6% (see Appendix 1).

^c Originally presented as ww.

^d Not used, unrealistically high (or negative).

The growth parameter estimates are $L_{\infty} = 30$ cm (mantle length, ML), $K = 0.72 \text{ year}^{-1}$ and $t_0 = -0.25$. Guerra (1979) also presented a length-weight relationship for western Mediterranean specimens of *O. vulgaris*, i.e.,

$$W = 0.42 (\text{ML})^{2.987} \quad \dots 24$$

Hence, $W_{\infty} = 10,850 \text{ g}$. From this, $M = 0.82 \text{ year}^{-1}$ and $Z \approx 1.64 \text{ year}^{-1}$.

Some estimates of K_1 for *O. vulgaris* are given in Table 7.

Combined with the growth parameter estimates presented above, this leads to $\beta = 0.2312$, which, when used in conjunction with the estimate of Z above, leads to $Q/B = 1.39\%$

Table 7. Estimated conversion efficiencies of *O. vulgaris* (from O'Dor and Wells 1987, based on experiments by Mangold and Boletzky 1973).

Weight range (g)	\bar{W} (g)	Temperature (°C)	K ₁
112-1,267	690	20	0.48
82-450	266	15	0.55
80-461	271	10	0.56

BWD and $R_m = 0.856\% \text{ BWD}$, both of which pertain to a mean temperature of 15°C . Conversion to the temperature prevailing at Bolinao leads to $Q/B \approx 2.0\% \text{ BWD}$ and $R_m \approx 1.23\% \text{ BWD}$ for octopus as an ecological group.

Squids

Squids occur in the pelagic areas of and around coral reefs, including Bolinao reef (Balgos 1990) and can be expected to consume a sizeable proportion of the secondary production of such areas, as is also the case in other ecosystems they inhabit (see contributions in Boyle 1987).

Estimates of food consumption of squids presented here are based on parameter estimates adapted from Longhurst and Pauly (1987), who combined population data pertaining to tropical with experimental data pertaining to temperate squids (Table 8).

These estimates, however, refer to low temperatures and thus need to be adjusted such that increased metabolism at higher temperatures, i.e., tropical reef areas, is accounted for. The adjusted estimates of Q/B and R_m are $6.53\% \text{ BWD}$ and $4.23\% \text{ BWD}$ for L .

Table 8. Parameters used in the estimation of Q/B and R_m of squids (adapted from Longhurst and Pauly 1987).

Parameter units	<i>Loligo duvaucelli</i> / <i>L. opalescens</i>	<i>Sepioteuthis lessoniana</i> / <i>Illex illecebrosus</i>
ML_∞ (cm)	29.00	27.00
W_∞ (g)	150.00	650.00
K (year ⁻¹)	1.00	0.73
t_0 (year)	set = 0	set = 0
Z (=2M, year ⁻¹)	3.16	1.70
β	0.083	0.230
Q/B (% BWD)	5.094	1.414
R_m (% BWD)	3.300	0.869
Temp. (°C)	18.0	10.0

- Start of second feeding period : 12h24'
- End of second feeding period : 23h42'
- Food ingestion rate : 0.16 g·h⁻¹
- Stomach evacuation rate : 0.35 h⁻¹
- Asymptotic weight of stomach contents : 0.42 g
- Daily ration : 2.43 g (=1.04% BWD)

A graph showing the fit of the model to the data is given as Fig. 2. As might be seen, the fit is "good," but there are few data points, and the results are thus tentative.

The ration estimates, combined with the growth and mortality parameters given above, lead to Q/B = 1.17% BWD and R_m = 0.49% BWD.

duvaucelli and 2.60% BWD and 1.60% BWD for *S. lessoniana*.

Combining these results in Q/B = 4.56% BWD and R_m = 2.92% BWD for squids as an ecological group.

Saurida undosquamis

The brushtooth lizardfish *Saurida undosquamis* (Synodontidae) is reported to reach "about 40 cm (and) to feed on bottom-feeding invertebrates and fishes" (Abe and Pathansali 1974).

The growth parameters of *S. undosquamis* population in the Visayan Sea, Philippines, were estimated by Ingles and Pauly (1984) as FL_∞ = 30.5 cm (TL = 33.7 cm) and K = 0.8 year⁻¹. The corresponding estimate of t_0 = -0.2 year.

Data in SEAFDEC (1979) allowed estimates of the length-weight relationship

$$W = 0.043 (TL)^3 \quad \dots 25)$$

which, combined with the estimate of asymptotic length, yields W_∞ = 1,646 g. From this, M = 1.35 year⁻¹, and hence, Z ≈ 2.7 year⁻¹.

Data on the diel feeding pattern of *S. undosquamis* off Oman coast were presented by Budnichenko (1977). These data, reproduced here as Table 9, suggest that *S. undosquamis*, like numerous other piscivores, feeds mainly at dusk and dawn (Hobson 1972).

Jarre et al. (1991) presented a method to analyze such data. The presentation of their model would require too much space for inclusion here, and we refer therefore to their paper and the accompanying software. Some of the results obtained from the analysis of Table 9 and pertaining to fishes with a mean standard length of 15 cm (=17.6 cm TL; 234 g) are:

- Start of first feeding period : 03h48'
- End of first feeding period : 07h30'

Table 9. Data on the diel cycle of stomach content of *Saurida undosquamis* sampled off Oman (adapted from Budnichenko 1977, Fig. 2).

Time	Mean stomach contents (g) ^a
01h30'	0.441
05h30'	0.317
09h30'	1.199
13h30'	0.264
17h30'	0.090
21h30'	0.362

^a Converted from relative weights (in %); the value for 13h30' is a mean of two observed stomach content weights taken during this period.

Myripristis murdjan

The big-eye soldierfish *Myripristis murdjan* (Holocentridae) feeds at night on large zooplankton and small fishes; it reaches a length of about 30 cm (De Graaf 1977) which shall be used here as estimate of asymptotic (total) length.

Growth data for this species are not available, but growth parameter estimates for the related *M. amaena* are given in Dee and Radtke (1989). However, they suggest a much slower growth than in other holocentrids, which may be an artifact of the method they used for ageing (otolith microstructures presumed to be daily). For this reason, we have used, for the estimation of K from L_∞ , a value of ϕ' estimated as the mean of the single value for *M. amaena* and that for *Holocentrus* spp. (see Table 10). This yielded, for TL_∞ = 30 cm, the estimate of K = 0.239 year⁻¹.

These estimates allow computation of t_0 = -0.69 year. The length-weight relationship of *M. amaena* derived by Dee and Radtke (1989), of the form

$$W = 0.031 (SL)^{3.042} \quad \dots 26)$$

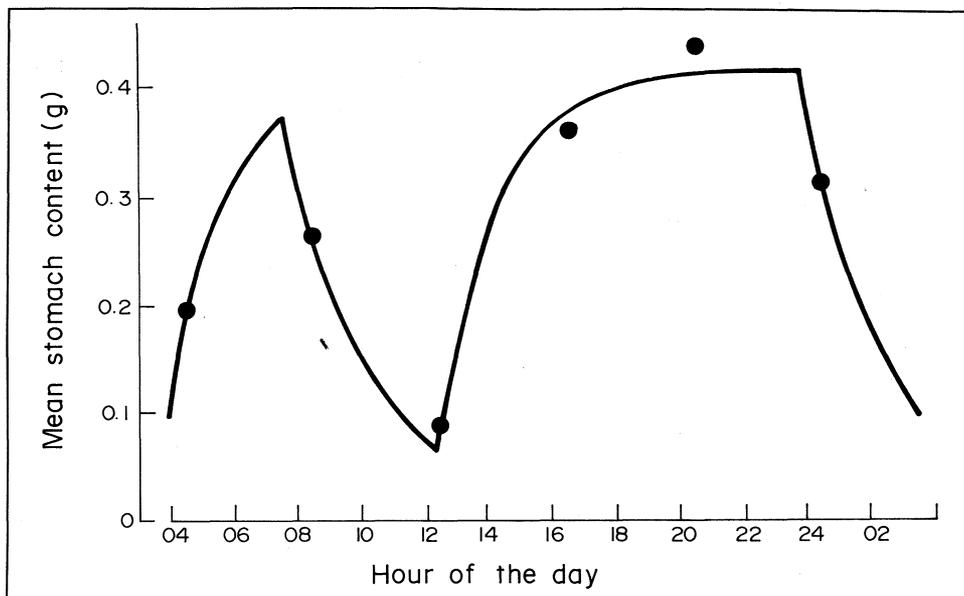


Fig. 2. Diurnal changes of stomach contents in lizardfish *Saurida undosquamis* off Aden; the data points (from Budnichenko 1977), fitted with the model of Jarre et al. (1991), suggest that this fish feeds mainly at dusk and dawn. The estimate of daily ration is 2.43 g or 1.04% BWD (see text).

Table 10. Published growth parameters of some soldierfish, as used to infer an approximate value of K in *Myripristis murdjan*.

No.	Species	FL_{∞} (cm)	K (year ⁻¹)	ϕ'	Source
1.	<i>Holocentrus sciurus</i>	40	0.26	2.62	Nicholson and Hartsuijker (1983)
2.	<i>H. ascensionis</i>	30	0.26	2.37	Nicholson and Hartsuijker (1983)
3.	<i>H. diadema</i>	14.7 ^a	1.13	2.39	Pauly (1978), based on Gundermann and Popper (1975)
4.	<i>H. rufus</i>	23	0.29	2.19	Nicholson and Hartsuijker (1983)
5.	<i>Holocentrus</i> spp.	-	-	2.393	ϕ' mean of Nos. 1-4
6.	<i>Myripristis amaena</i>	21.5 ^b	0.239	2.043	Dee and Radtke (1989)
7.	<i>M. murdjan</i>	26.3	0.239	2.218	ϕ' mean of Nos. 5 and 6

^aReferred to as *Sargocentron diadema* in Dee and Radtke (1989).

^bConverted from total to fork length via a ratio of 1.14:1.

was used for the conversion of our estimate of TL = 30 cm (= 22.5 cm SL) because these two species have very similar shapes (Tinker 1978). This led to an estimate of $W_{\infty} = 402$ g, which allowed estimation of $M = 0.67$ year⁻¹.

Growth and food conversion experiments were conducted at the IfM using six specimens of *M. murdjan*. These fishes yielded six positive values of K_1 , of which the upper three, pertaining to the less stressed fish, are presented in Table 11, along with the weights of the fish from which they were derived. Combined with the estimate of W_{∞} given above, these data led to an estimate of $\beta = 0.0216$.

Table 11. Partial results of aquarium growth experiments on *Myripristis murdjan* fed *Neomysis integer*.

Mean W (g)	Increment	Food intake (g)	K_1^a (g)
5.560	0.36	3.094	0.116
5.835	0.35	3.982	0.088
6.245	0.47	8.079	0.058

^aOnly highest three of six K_1 values obtained.

Combining this with an estimate of $Z \approx 2M = 1.34$ year⁻¹ leads to $Q/B = 5.29\%$ BWD and $R_m = 3.02\%$ BWD.

Epinephelus fuscoguttatus

The brown-marbled grouper *Epinephelus fuscoguttatus* (Serranidae) is reported to reach 120 cm and to feed on "bottom-living crustaceans and fishes" (Chan et al. 1974). The growth parameters for a Philippine population were estimated, using a combination of original and comparative data, as $TL_{\infty} = 91.7$ cm, $W_{\infty} = 12,338$ g, $K = 0.19$ year⁻¹, $t_0 = -0.66$ year (Palomares and Pagdilao 1988).

Cage experiments conducted in Guiuan, Eastern Samar, Philippines, with *E. fuscoguttatus* fed chopped trash fish led to a multiple regression for predicting food conversion efficiency from weight and food ingested, and corresponding to equation (7), of the form

$$C = 0.2838 - 0.05188 \log_{10} W - 0.00933 R_1 \quad \dots 27)$$

where $C = -\log_{10}(1-K_1)$; W is the mean weight of the fish during each of the 14 growth increments used to derive the model; and R_1 is the food ingested. Palomares and Pagdilao (1988) showed how this model led, after some manipulations, to $Q/B = 1.1\%$ BWD, for $Z \approx M = 0.44$ year⁻¹, as well as to $R_m = 0.8\%$ BWD. Palomares and Pagdilao (1988) also performed some simulations showing the dependence of Q/B on Z . From their Fig. 3, one can estimate, for $Z \approx 2M$, an approximate value of $Q/B = 5$ year⁻¹, or 1.37% BWD.

Epinephelus tauvina

The greasy grouper *Epinephelus tauvina* (Serranidae), which mainly feeds on "bottom-living crustaceans and fishes," is reported to reach up to 150 cm (Chan et al. 1974). Available estimates of asymptotic length are much lower, however, and their mean is 69 cm (Table 12).

The other growth parameter estimates used here are $W_{\infty} = 4,135$, estimated from $W = 0.0151 L^{2.96}$ (C. Pagdilao, unpubl. data), $K = 0.145$ year⁻¹ (see Table 12) and $t_0 = -0.94$.

Table 12. Growth parameters for *Epinephelus tauvina*.

L_{∞} (TL, cm)	K (year ⁻¹)	ϕ'	Source
36.0 ^a	0.292	2.578	Loubens (1980)
102.0	0.121	3.100	Mathews and Samuel (1985)
69.0 ^b	0.145	2.839 ^b	(Means)

^aFrom $TL = 1.16 SL$ (Chan et al. 1974), $SL_{\infty} = 30.7$ cm.

^bMean values.

Table 13 presents the results of three cage growth experiments with greasy groupers, for which we derived ten pairs of W, K_1 data.

These data, together with the estimate of W_{∞} above, lead to an estimate of $\beta = 0.154$ (see Fig. 3). Combining this with $Z \approx 2M = 0.78$ year⁻¹ yields an estimate of $Q/B = 0.56\%$ BWD and $R_m = 0.26\%$ BWD.

Table 13. Weight and gross food conversion efficiency (K_1) of *Epinephelus tauvina* in three separate feeding experiments: 1-4, from Tanomkiat and Pimoljinda (1986); 5 and 6, from Sugama et al. (1986b); and 7-10, from Danakusumah et al. (unpubl. data).

No.	Food type	Body weight (g) ^a			K_1
		W_i	W_f	\bar{W}	
1.	"Formula 1"	0.940	16.0	8.5	0.3531
2.	"Formula 2"	0.887	16.6	8.8	0.3611
3.	"Formula 3"	0.854	15.1	8.0	0.6969
4.	Minced fish	0.953	11.0	6.0	0.2529
5.	<i>Sardinella</i>	110.000	1,619.0	865.0	0.1316
6.	<i>Sardinella</i>	730.00	2,349.0	1,540.0	0.1960
7.	trash fish	129.00	248.0	188.5	0.2016
8.	trash fish	195.00	395.0	295.0	0.1299
9.	trash fish	266.00	411.0	338.5	0.1212
10.	trash fish	789.00	1,080.0	934.5	0.2616

^a W_i = initial; W_f = final; \bar{W} = mean.

Lutjanus johnii

John's snapper *Lutjanus johnii* (Lutjanidae) is reported to reach a maximum of 70 cm in Southeast Asia and to feed on "bottom-living invertebrates and fishes" (Talbot and Chan 1974). Estimates of L_{∞} and K were derived here from length-at-(relative)age data in Druzhinin (1970) for females and males separately, along with indirect estimates of t_0 ; means over both sexes were computed directly to L_{∞} and t_0 , and indirectly (via ϕ') for K (Table 14). The mean value of $L_{\infty} = 84.35$ cm was converted to an estimate of $W_{\infty} = 8,844$ g using

$$W = 0.007678L^{3.147} \quad \dots 28)$$

derived from data in Druzhinin (1970).

Table 14. Growth parameter estimates for *Lutjanus johnii*, as obtained from length-at-age data in Druzhinin (1970).

Sex	L_{∞} (cm)	K (year ⁻¹)	t_0 (year)	ϕ'
Males	94.00	0.122	-1.440	3.033
Females	74.70	0.195	-0.678	3.037
Means	84.35	0.152	-0.845	3.035

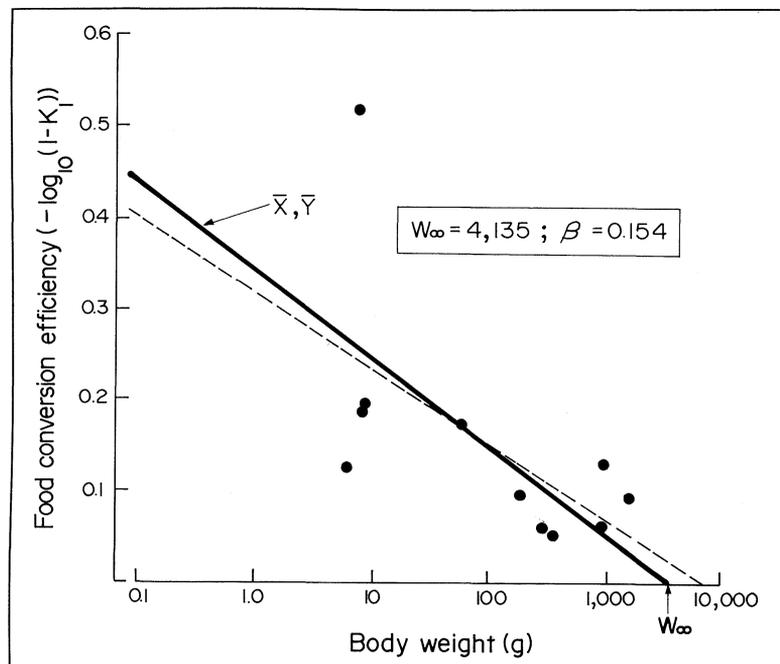


Fig. 3. Relationship between food conversion efficiency (K_1) and body weight (g-ww) in greasy grouper *Epinephelus tauvina*, as used to estimate the parameter $\beta = 0.154$. Dotted lines represents a Type I linear regression; solid line is forced through mean of x, y values and external estimate of asymptotic weight (based on data in Table 13; see text).

The results of the floating cage growth and feeding experiments used here to obtain W, K_1 data are summarized in Table 15.

They lead to an estimate of $\beta = 0.0535$ which, combined with $Z \approx 0.76 \text{ year}^{-1}$, yields $Q/B = 1.34\% \text{ BWD}$, and $R_m = 0.74\% \text{ BWD}$.

Table 15. Summary of growth and feeding data on *Lutjanus johnii*, as obtained by Sugama et al. (1986a).

Body weight (g) ^a			Ingested food (g) ^b	K_1
W_i	W_f	\bar{W}		
145.0	206.2	175.6	442	0.1385
206.2	306.0	256.1	584	0.1709
306.0	472.0	389.0	814	0.2039
472.0	601.3	536.6	1,102	0.1173
601.3	752.8	677.0	1,200	0.1262
752.8	915.0	833.9	1,286	0.1261
915.0	1,128.0	1,021.5	1,661	0.1282

^a W_i = initial; W_f = final; \bar{W} = mean.

^b*Sardinella* spp. fed twice daily to satiation.

Zebrasoma scopas

The blue-line sailfin-tang *Zebrasoma scopas* (Acanthuridae), of which *Z. flavescens* is a commonly used synonym, is reported to feed, near Okinawa, on filamentous microalgae (Sano et al. 1984). Direct estimates of growth parameters for this fish, which reaches about 20 cm, do not appear to have been published.

Following an initial attempt by Dalzell (1989), we estimated a value of K for *Z. scopas* from (1)

average growth parameters in acanthurids, and (2) growth parameter estimates reported from the related *Z. veliferum* and a set value of L_∞ (Table 16).

Table 16. Preliminary growth parameter estimates in two species of *Zebrasoma*.

Species	FL_∞ (cm)	K (year^{-1})	ϕ'	Source/remarks
<i>Z. veliferum</i>	25	0.330	2.31	From R. Withrow, Waikiki Aquarium, Hawaii, pers. comm. to Dalzell (1989)
<i>Z. scopas</i>	19	0.876	2.50	Dalzell (1989) setting $L_{\max} = L_\infty$, and using the mean ϕ' of all acanthurids for which he had growth estimates
<i>Z. scopas</i>	20	0.628	2.40	Intermediate values used in this study

The estimate of $TL_\infty = 20 \text{ cm}$, combined with the estimate of K , allows the estimation of $t_0 = -0.285 \text{ year}$.

Dalzell (1989) derived for *Z. scopas* the length-weight relationship

$$W = 0.123 \cdot FL^{2.41} \quad \dots(29)$$

from which W_∞ was estimated as 168 g; this leads to $M = 1.38 \text{ year}^{-1}$.

The food conversion experiments conducted with two specimens of *Z. scopas* (at the IfM) yielded very variable results, including negative growth and conversion efficiencies. Table 17 presents the few positive growth increments that were obtained.

Table 17. Food conversion efficiency of an aquarium-held specimen of *Zebrasoma scopas*. The food was almost exclusively mysids; some algae were provided to balance the food, but their energetic contribution can be neglected.

Mean fish weight during increment (g)	Growth increments (g)	Food ingested (g)	K_1
21.2	1.55	11.4	0.136
22.0	1.71	43.3	0.039

The value of β derived from these data is 0.0453.

From this, the growth parameters derived above and $Z \approx 2M = 2.76 \text{ year}^{-1}$, we obtain $Q/B = 7.75\% \text{ BWD}$ and $R_m = 4.73\% \text{ BWD}$.

Siganus spinus

The little spinefoot *Siganus spinus* (Siganidae) which reaches a length of 20 cm is reported to "browse on a wide range of bottom algae" (Woodland 1984).

Pauly (1978), based on Horstmann (1975), estimated for this fish $TL_\infty = 24.4 \text{ cm}$, $K = 2.32 \text{ year}^{-1}$ and $t_0 = -0.21 \text{ year}$. The length-weight relationship

$$W = 0.012 TL^{3.077} \quad \dots 30$$

presented by von Westernhagen and Rosenthal (1976) allows estimation of $W_\infty = 234 \text{ g}$. The estimate of $Z \approx 2M$ used here is 6.5 year^{-1} .

Daily ration estimates for *S. spinus* in Guam (in % body carbon day⁻¹) are available (Table 18).

From these data, an estimate of $\beta = 0.07$ is obtained which, when combined with the above parameters, yielded $Q/B = 13.13\% \text{ BWD}$ and $R_m = 8.85\% \text{ BWD}$.

Scomber japonicus

The Japanese mackerel, which occurs in the Philippines (see Herre 1953), where it is listed under the synonym *Pneumatophorus japonicus*, is a zooplanktivore and piscivore, of which growth parameters are given in Table 19.

Table 18. Daily ration for *Siganus spinus*, adapted from Bryan (1975).

Fork ^a length (cm)	Weight (g)	Assimilation (% of body carbon day ⁻¹)
5.1	1.91	47
5.2	2.03	60
5.4	2.28	27
5.9	2.99	9
10.7	18.59	20
11.4	22.58	11
11.9	25.76	7
12.3	28.52	39
13.1	34.60	6
13.2	35.42	8
14.0	42.44	24

^aThe ratio FL:TL is 1:1.06.

Table 19. Selected sets of growth parameters of *Scomber japonicus*.^a

FL _∞ (cm)	K (year ⁻¹)	φ'	Location
46.4	0.400	2.935	Japanese waters
45.5	0.340	2.848	Northwest Pacific
44.0	0.441	2.931	Northwest Pacific, Russian waters
45.3 ^a	0.391	2.905	Means

^aFrom Pauly (1978).

Data in Frey (1936) allow computation of the length-weight relationship

$$W = 0.00979 FL^3 \quad \dots 31$$

and hence, given $FL_\infty = 45.3 \text{ cm}$, $W_\infty = 910 \text{ g}$. The empirical equations in the Methods section allowed, further, the estimation of $t_0 = -0.36 \text{ year}$ and $Z \approx 2M = 1.74 \text{ year}^{-1}$.

The food conversion data used here for estimating the food consumption of *S. japonicus* stem from Hatanaka and Takahashi (1956) and Hatanaka et al. (1957) who maintained their fish on a diet of either anchovies or euphausiids.

The food conversion efficiencies were computed for each weight group; the temperature, food type and feeding status were tabulated; and a multiple regression was derived which had the form

$$C = 0.0145 - 0.0843 \log_{10} W + 0.1111 \log_{10} T + 0.0754P + 0.0344U \quad \dots 32$$

where $C = -\log_{10}(1-K_1)$, W the mean weight of the fish (in g) within a growth interval, T the water temperature (in °C), p the food type and U the

feeding status. The variables P and U were assigned values of 0 or 1, as follows:

- P = 0: the fish were fed euphausiids;
 P = 1: the fish were fed anchovies;
 U = 0: the fish were fed regularly; and
 U = 1: the fish were starved before the experiment.

The multiple correlation coefficient of equation (32) was $R = 0.492$ (d.f. = 138) and all four partial regression coefficients were significant ($P < 0.01$).

The equation was solved, following the method of Pauly (1986) for $W_{\infty} = 910$ g, $P = 0.5$, $U = 0$, and $T = 16^{\circ}\text{C}$, the mean temperature in the experimental tanks (the equation could have been solved for 27°C , as occurs in the Bolinao area, but this would have involved an extrapolation to outside of the temperature range covered by the experiments). This resulted in $\beta = 0.0629$ which, combined with the estimates presented above, yielded $Q/B = 2.95\%$ BWD and $R_m = 1.70\%$ BWD. These values, adjusted for a temperature of 27°C , are 4.06% BWD and 2.34% BWD, respectively.

Discussion

The food consumption estimates derived above for five groups of invertebrate and eight species of fishes are summarized in Table 20. The relative (population-weighted) estimates of food consumption range from 3.58 year^{-1} (in echinoids) to 47.9 year^{-1} (in herbivorous siganids). Our

results indicate that pelagic fishes and invertebrates have higher food consumption (Q/B) and lower ecological efficiencies (E_t) than demersals, with the same rule also applying to herbivores/detritivores in relation to carnivores.

Similar rules are embodied in the empirical equation of Palomares and Pauly (1989), derived from 33 fish populations

$$\ln Q/B = -0.1775 - 0.2018 \ln W_{\infty} + 0.6121 \ln T + 0.5156 \ln A + 1.26 P \quad \dots 33$$

where Q/B is as defined above, on a daily basis, W_{∞} is the asymptotic weight of the fishes in question, T the environmental temperature in $^{\circ}\text{C}$ (see also equation 13), A the aspect ratio of the caudal fin (as defined in Fig. 2 of Palomares and Pauly 1989) and P the food type, with $P = 0$ for carnivores, and $P = 1$ for herbivores.

Fig. 4, based on the data in Table 20, shows the relationship between the estimates of Q/B as presented for fishes in the Results section and estimates of Q/B obtained through the empirical model of Palomares and Pauly (1989). There is a good match between these two sets of estimates, the only clear outlier being No. 6 (*Zebrasoma scopas*).

Thus, as far as estimates of Q/B are concerned which pertain to using their caudal fin as (main) organ of propulsion, we conclude that the empirical model of Palomares and Pauly (1989) can be used to obtain reasonable estimate of Q/B . Indeed this model, being based on a large amount of data, may be more reliable than the results of simple feeding experiments, especially

Table 20. Summary of statistics related to the food consumption of the 13 taxa investigated in this contribution.^a

No.	Species group	Aspect ratio	E_t	R_m (% BWD)	Q/B (% BWD)	Q/B (year^{-1})
Invertebrates						
-	Sea cucumbers	-	0.1305	0.73	1.05	3.83
-	Sea urchins	-	0.2718	0.64	0.98	3.58
-	Shrimps	-	0.0864	4.98	7.93	28.94
-	Octopus	-	0.2942	1.23	2.00	7.30
-	Squids	-	0.1971	2.92	4.56	16.64
Fishes						
1.	<i>Saurida undosquamis</i>	1.96	0.6323	0.49	1.17	4.27
2.	<i>Myripristis murdjan</i>	3.53	0.0694	3.02	5.29	19.31
3.	<i>Epinephelus fuscoguttatus</i>	2.08	0.1760	1.00	1.37	5.00
4.	<i>E. tauvina</i>	1.54	0.3824	0.26	0.56	2.04
5.	<i>Lutjanus johnii</i>	1.91	0.1554	0.74	1.34	4.89
6.	<i>Zebrasoma scopas</i>	2.25	0.0976	4.73	7.75	28.29
7.	<i>Siganus spinus</i>	3.17	0.1356	8.85	13.13	47.92
8.	<i>Scomber japonicus</i>	5.85	0.1174	2.34	4.06	14.82

^aThis refers to food types mentioned in the text; note that herbivores/detritivores eat more than carnivores.

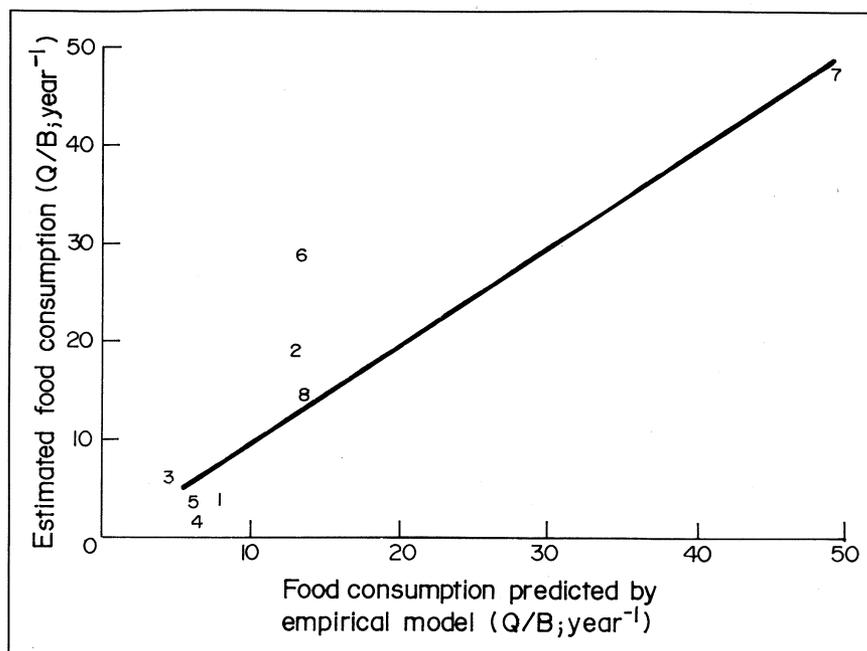


Fig. 4. Plot of the estimated food consumption (Q/B) of the fishes in Table 20 vs. Q/B values obtained through the empirical model of Palomares and Pauly (1989).

for active, easily stressed fishes such as *Z. scopas*, *Dascyllus trimaculatus* (Palomares 1987) or *Holacanthus bermudensis* (Menzel 1958).

The invertebrate groups in Table 20 do not represent all groups, or even the major groups - in terms of energy throughput - of coral reef ecosystems such as those near Bolinao. Thus, it will be necessary, when constructing a model of such reef, to consider the metabolic requirements of several taxa not considered here. An example of such group, to which the methodology presented above would be particularly applicable, are the sea hare (Family Aplysiidae), whose growth and mortality were reported upon by Pauly and Calumpong (1984), and whose feeding and general biology were studied by Carefoot (1967), Calumpong (1979), Kandel (1979) and others.

On the long run, however, empirical relationships linking Q/B and other rates, and/or with their shape will be required for major marine invertebrate groups, if coral reef modelling is to advance more rapidly than has hitherto been the case.

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