Food Consumption/Biomass Ratios of the Pelagic Fish Community of Lake Malaŵi/Niassa

Rapports consommation alimentaire/biomasse chez les poissons pélagiques du lac Malawi/Niassa

B.P. Ngatunga and E.H. Allison

Abstract

An empirical model relating food requirements to morphometric indices of metabolic rate was used to calculate consumption/biomass ratios (Q/B) for 16 species of fish that make up the pelagic fish community in Lake Malaŵi/Niassa. The Q/B/year varied from 3.31 to 9.82, with the large catfish (*Dinotopterus nyasensis*) having the lowest and a small cyprinid (*Engraulicypris sardella*) having the highest Q/B ratio. Direct estimates of Q/B for four of the most abundant species, based on analysis of diel feeding patterns, ranged from 4.20 to 24.70; the extreme values in this range representing replicate studies on the same species, the predatory cichlid *Rhamphochromis longiceps*. Previous studies that indicated exceptionally low Q/B ratios (≤ 1.0) in pelagic cichlids from Lake Malaŵi are not supported by this more recent work.

Résumé

*Un modèle empirique rapprochant les besoins alimentaires et les indices morphométriques des taux métaboliques a permis de calculer les rapports consommation/biomasse (Q/B) pour 16 espèces qui constituent la communauté pélagique de poissons du lac Malawi/Niassa. Des valeurs annuelles de Q/B variant de 3,31 à 9,82 ont été enregistrées, le grand poisson-chat (*Dinotopterus nyasensis*) donnant les valeurs les plus faibles et le petit Cyprinidé (*Engraulicypris sardella*) les valeurs les plus élevées. Les estimations directes de Q/B pour quatre des espèces les plus abondantes, étaient comprises, d'après les résultats d'une analyse des cycles nycthéméraux de prise d'aliments, entre 4,20 et 24,70, les valeurs extrêmes correspondant aux réplicats réalisés sur la même espèce, le Cichlidé prédateur* Rhamphochromis longiceps. *Les résultats de la présente étude ne confortent pas ceux de travaux précédents rapportant des valeurs Q/B exceptionnellement faibles (Q/B ≤ 1.0) chez les Cichlidés pélagiques du lac Malawi.*

Introduction

The holistic approach to managing tropical and subtropical ecosystems has heightened interest in constructing models for the assessment of multispecies fisheries (Pauly and Tsukayama 1987; Daan and Sissenwine 1991; Peters and Schaaf 1991; Christensen and Pauly 1993). Many fisheries are now assessed within the context of the overall ecosystem that supports them by using trophic interaction models. Population food consumption estimates are among the parameters required in these models.

Food consumption rates of fish populations are difficult and costly to estimate, and where there are many species it is seldom possible to estimate these rates for all species. For these reasons, Pauly (1989) searched for a simple index of metabolic rate in fish that would correlate well with the most useful measure of food consumption — the annual food consumption per unit biomass of the fish population (Q/B). Empirical models relating published Q/B estimates to various morphological attributes of fish that are related to metabolism and therefore to food requirements have been derived by Palomares and Pauly (1989); Pauly (1989); Jarre et al. (1991); and Palomares (1991).

As part of a wider study of the fishery potential and productivity of the pelagic zone of Lake Malaŵi/Niassa (Menz 1995), we have used Jarre et al.'s (1991) empirical model to obtain preliminary estimates of Q/B for 11 cichlid species (*Copadichromis quadrimaculatus, Diplotaxodon argenteus, D. limnothrissa, D. greenwoodi, D.* 'bigeye', *D.* 'holochromis' [two new species, not yet named], *Rhamphochromis esox, R. ferox, R. leptosoma, R. longiceps,* and *R. woodi*); three cyprinids (*Engraulicypris sardella, Opsaridium microcephalum, O. microlepis*); and two catfish (*Synodontis njassae* and *Dinotopterus nyasensis*). These species account for 98% of estimated fish biomass in the pelagic waters of Lake Malaŵi (Thompson et al., in press a, b).

The estimates of Q/B from the empirical model are compared with recent estimates from models fitted to diel stomach content data for four of the most abundant pelagic fish species: *D.* 'bigeye', *D. limnothrissa, R. longiceps,* and *S. njassae* (Allison et al. 1996), and earlier estimates for one of these (*D. limnothrissa*) and three other species (*C. quadrimaculatus, E. sardella* and *O. microcephalum*) (Walczak 1982).

Materials and Methods

The following regression model (Jarre et al. 1991) was used to estimate Q/B for all pelagic fish species:

$$\log_{10}Q/B = 4.885 - 1309.139(1/T) + 0.423 \log_{10}A + 0.285 \log_{10}D - 0.111 \log_{10}W_\infty - 0.445 \log_{10}CP$$

where T = temperature in Kelvin, A = aspect ratio of the caudal fin (= fin height^2/fin surface area), D = depth ratio (standard length/maximum body depth), W_∞ = maximum live weight (g) in the population, and CP = caudal peduncle depth/maximum body depth.

Fish used in this study were sampled from throughout the pelagic zone of Lake Malaŵi between August 1992 and November 1993 using gillnets and a mid-water trawl. The height of caudal fin and its surface area were determined by tracing the fully stretched fin on paper and measuring its image using a computer image-analysis system (OPTIMAS: BioScan 1989). Maximum body depth and caudal peduncle depth were measured using a diel caliper. Mean habitat temperature for Lake Malaŵi is 24.5°C (Patterson and Kachinjika 1995).

Studies of diel feeding periodicity were undertaken in October 1992 for *R. longiceps* and August 1993 for four species which are reported in detail in Allison et al. (in press). Here we present graphically the results of the August 1993 study so that readers may assess the quality of the estimates, to aid comparison with those derived empirically.

Daily ration, the fraction of food ingested relative to body weight of individual fish per day, was estimated from diel stomach contents data using the methods of Sainsbury (1986), as generalized by Jarre et al. (1991). Ingestion (feeding) and

evacuation rates were estimated simultaneously from stomach contents weight, sampled regularly over one or more feeding cycles. We used the MAXIMS software (Jarre et al. 1990) to fit the appropriate models.

As daily rations are size-specific (Pauly 1986; Pauly 1989; Palomares and Pauly 1989) and we did not have sufficient data to model each size-category of fish separately, we expressed stomach contents relative to fish body weight (mg/g) and used the entire size-distribution of fish in fitting the model. Our estimates of 'relative daily ration' were therefore estimates of population consumption (Q) to biomass (B) ratios (per day) weighted by the size-distribution of the population. As the size-distributions of the populations sampled during the food consumption studies were similar to average size-distributions

throughout the open waters, our Q/B ratios should be reasonably unbiased in this respect.

Results

Morphometric data (mean ± s.d.) used to estimate food consumption values are presented in Table 1. Some of the errors are quite large, indicating both morphometric variability within fish species and practical difficulties, particularly in determining aspect ratio, where there is some uncertainty about how much to stretch out the caudal fin before measuring.

The Q/B values (± s.d.) for the 11 pelagic cichlids, three cyprinids, and two catfishes, calculated from the empirical relationships of Jarre et al. (1991), are shown in Table 2. Note that the errors are derived from variability in the

Table 1. Morphometric data (mean with s.d. in parentheses) for the most abundant species of pelagic fish in Lake Malaŵi/Niassa, used for the empirical estimation of Q/B values in this study using the model of Jarre et al. (1991).

Species	n	Size range, SL (cm)	Aspect ratio (A)	Depth ratio (D)	Peduncle ratio (P)	W_ (g)
Copadichromis quadrimaculatus	12	13.1-16.0	2.26 (0.20)	2.81	0.34	97
Diploxalodon argenteus	7	10.2-18.5	1.52 (0.24)	3.59 (0.13)	0.37 (0.01)	144
Diploxalodon 'bigeye'	6	7.8-12.0	3.43 (0.19)	3.11 (0.25)	0.44 (0.09)	57
Diploxalodon limnothrissa	10	7.9-16.2	3.60 (0.71)	4.17 (1.08)	0.41 (0.05)	56
Diploxalodon greenwoodi	3	6.2-26.3	2.80 (0.73)	3.04 (0.27)	0.31 (0.01)	628
Diploxalodon 'holochromis'	8	13.5-15.0	1.79 (0.32)	3.40 (0.12)	0.39 (.02)	89
Rhamphochromis esox	3	17.6-18.5	2.84 (0.20)	5.83 (0.35)	0.47 (0.00)	686
Rhamphochromis ferox	11	21.6-41.4	2.74 (0.25)	4.17 (0.31)	0.36 (0.02)	1 477
Rhamphochromis leptosoma	3	21.8-25.8	2.14 (0.12)	5.02 (0.22)	0.40 (0.01)	623
Rhamphochromis longiceps	41	4.9-30.0	3.28 (0.29)	4.77 (0.38)	0.45 (0.03)	107
Rhamphochromis woodi	4	21.1-28.2	2.47 (0.21)	4.21 (0.32)	0.36 (0.01)	1 023
Engraulicypris sardella	13	3.5-9.8	3.77 (0.43)	6.96 (0.68)	0.50 (0.05)	11
Opsaridium microcephalus	8	14.1-29.2	3.24 (0.71)	4.55 (0.57)	0.38 (0.03)	359
Opsaridium microlepis	3	20.5-27.0	2.23 (0.30)	4.77 (0.08)	0.38 (0.01)	3 252
Synodontis njassae	15	8.7-11.5	4.64 (0.65)	4.87 (0.52)	0.42 (0.04)	67
Bathyclarias nyasensis	8	38.9-79.0	1.75 (0.27)	7.66 (0.87)	0.59 (0.07)	6 378

Table 2. Estimates of Q/B values (± s.d.) for common fish species from the pelagic zone of Lake Malaŵi obtained by the empirical and diel stomach contents analysis (DSCA) methods.

Species	Q/B/year		
	Empirical (this study)	DSCA Walczak (1982)	DSCA Allison et al. (1996)
Copadichromis quadrimaculatus	5.67 (0.23)	1.00	-
Diploxatodon argenteus	4.74 (0.61)	-	-
Diploxatodon 'bigeye'	6.68 (0.64)	-	12.79
Diploxatodon limnothrissa	7.46 (0.88)	0.394	5.87-7.13
Diploxatodon greenwoodi	5.32 (0.58)	-	-
Diploxatodon 'holochromis'	5.13 (0.42)	-	-
Rhamphochromis esox	5.33 (0.21)	-	-
Rhamphochromis ferox	4.96 (0.19)	-	-
Rhamphochromis leptosoma	4.96 (0.08)	-	-
Rhamphochromis longiceps	6.75 (0.37)	-	4.20-24.70 (mean, 11.56)
Rhamphochromis woodi	4.94 (0.11)	-	-
Engraulicypris sardella	9.82 (0.68)	9.63	-
Opsaridium microcephalus	6.21 (0.62)	6.61	-
Opsaridium microlepis	4.23 (0.29)	-	-
Synodontis njassae	8.50 (0.61)	-	6.45
Bathyclarias nyasensis	3.31 (0.25)	-	-

Estimates of Q/B for *D.* 'bigeye' and *R. longiceps* by Allison et al. (in press) are almost twice those predicted empirically, while those for *D. limnothrissa* and *S. njassae* are slightly lower than the empirical predictions (Table 2). Given the scatter in the diel stomach contents data and the variability in the empirical regression relationship of Jarre et al. (1991, Fig. 6), no significance can be attributed to differences of this magnitude. The difference of an order of magnitude between Walczak's and both our and Allison et al.'s estimates of Q/B for *D. limnothrissa* is, however, likely to be significant.

morphometric parameters only. These will be underestimates of the true errors, which should also include the error term in the regression model.

Values estimated from diel stomach content data for seven of the species (Walczak 1982; Allison et al. 1996) are also shown for comparison. Walczak's (1982) estimates of Q/B = 9.63 per year for post-larval *E. sardella* and 6.61 per year for *Opsaridium microcephalum* (reported in Degnbol 1993) are close to values of 9.82 per year and 6.21 per year estimated from the empirical model. The data set used by Pauly (1989) and Jarre et al. (1991) to derive the model did not include Walczak's (1982) estimates, or any freshwater fishes.

The data from which Allison et al. (in press) derived their food consumption rate estimates appear reasonable; periodicity in feeding activity is clearly seen in three of the four species sampled (Fig. 1). *D.* 'bigeye' appear to have two feeding periods associated with diurnal vertical migration of their main prey, the larvae of lakefly (*Chaoborus edulis*). *D. limnothrissa* are generalized visual-feeding zooplanktivores and feed throughout daylight hours. On this occasion, *R. longiceps* were satiated following an intensive
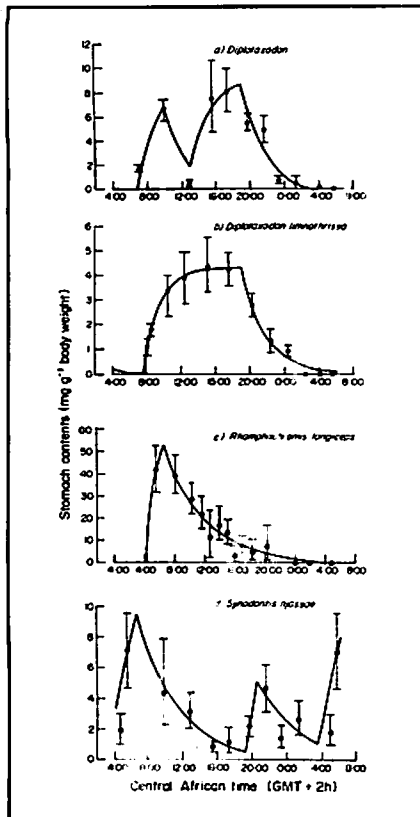
Fig. 1. Mean weights, with bootstrap 95% confidence intervals, of stomach contents (mg), relative to preda-tor body weight (g), of Diplotaxodon limnothrissa, D. 'bigeye', Rhamphochromis longiceps and Synodontis njassae sampled over 24-hour periods between 24 and 27 August 1993. Note the differences in scale on the y-axis. Fitted curves are models of ingestion and evacuation rates (from MAXIMS) used for calculation of daily ration. Sunrise and sunset times (Central African Time) were 0553 and 1730 hours, respec-tively.

period of feeding activity on emerging *C. edulis* pupae early in the morning. Feeding patterns may change according to the type of prey eaten (Allison et al., in press). *Synodontis njassae* also feed on lake flies, but are largely nocturnal and, unlike the cichlids, are not visual feeders. Feeding periodicity in this species is less clear, and stomach contents are likely to reflect fluctuations in prey availability rather than complete cessation of feeding activity.

Discussion

Pauly's (1989) ideas of relating fish morphology to metabolic rates, in the form of the empirical model of Jarre et al. (1991), have proven useful in two respects. First, for obtaining preliminary estimates of Q/B for the less important species of fish in the Lake Malaŵi/Niassa pelagic zone (and those which proved impossible to catch throughout a 24-hour cycle). Second, for providing an objective method of comparing estimates derived from stomach contents data by Walczak (1982) and Allison et al. (in press) against a global database of such values. We hope

this study provides an illustration of the usefulness of the comparative approach, and of the databases (e.g., FishBase) that facilitate such comparisons.

For the important species that we were able to catch throughout the 24-hour cycle, the MAXIMS software provided a useful tool for dealing with the complex model-fitting problems that result from having populations with more than one feeding period. However, in common with many other such algorithms, the error structures of the fitted models are difficult to interpret, and although we were able to estimate the errors associated with our data, we were unable to produce confidence intervals for the model parameters and for our estimated Q/B ratios.

Catching all fish species throughout the diel cycle proved difficult. *Rhamphochromis* spp. were readily caught in day-set gillnets, but were less common in night-set gillnets and were caught sporadically in trawls. Conversely, *Diplotaxodon* spp. were caught in sufficient numbers in night-time trawls, but in very small numbers by day-set gillnets. The small mid-water trawl was usually ineffective during daylight hours. It was therefore necessary to use a combination of gillnetting and trawling by day, and trawling by night, to obtain sufficient numbers of fish for analysis. A knowledge of the diurnal movements of fish was also required to determine the optimum sampling depth. Of course, each species has different depth preferences and, if one does not want to make a separate 24-hour sampling trip for each species, methods have to be devised to fish several depth bands at once (Allison et al. 1994). All this requires hard work, expensive boat time, and extensive reliance on high-tech electronics such as bridge echo-sounders and net sounders to locate fish and deploy gear optimally. Under such circumstances, and at around 0300 hours, one begins to see the attractions of the empirical approach.

The estimates of Q/B for three species of cichlid and one catfish obtained from diel stomach contents analysis by Allison et al. (in press) appear reasonable when compared with values in the literature (Pauly 1989) and, therefore, with those obtained from this

application of the empirical model. The values for two cyprinid species obtained by Walczak (1982) are also comparable to literature values. However, Walczak's estimates of Q/B for the cichlids *Copadichromis quadrimaculatus* and *Diplotaxodon* 'pallidorsalis' *nomen nudum* (now *D. limnothrissa*) are the lowest we have seen. *D. limnothrissa* was found to eat only 35% of its own body weight in a year. None of the 75 studies compiled by Pauly (1989), including data for a number of slow-growing arctic fish, indicated an annual Q/B of < 1, so it seems that Walczak's (1982) estimates for the two cichlid species may have been unrealistically low, by up to an order of magnitude. Walczak actually pointed this out, but his observation was subsequently overlooked, despite its implications for calculations of total consumption of zooplankton and lakeflies by fish, the estimation of which is crucial to arguments on the relative efficiency of Lake Malaŵi and other pelagic ecosystems (Turner 1982; Hecky 1984; Eccles 1985; McKay et al. 1985; Christensen and Pauly 1993; Degnbol 1993). These arguments centered around the perception that clupeids are much more efficient than cichlids as consumers of zooplankton. This must now be reassessed in the light of the findings presented here, as well as other observed discrepancies between recent and earlier studies on the Lake Malaŵi pelagic ecosystem (Menz 1995).

By combining the Q/B estimates reported here with studies of the prey composition in fish stomachs from throughout the lake, and with acoustic estimates of total fish biomass by species, then integrating these studies with estimates of production and biomass at each trophic level, we were able to summarize the trophic structure of the Lake Malaŵi pelagic ecosystem using an ECOPATH model (Allison et al. 1995). But that is another story.

Acknowledgements

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Comparative Growth Performance for Species of the Family Clupeidae of Sierra Leone

Croissance comparée des espèces de la famille des Clupéidés en Sierra Leone

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Abstract

Using length-frequency samples from the local fisheries and length-age data from otolith readings, von Bertalanffy growth parameters were estimated for the four species representing the Clupeidae family in Sierra Leone, *Sardinella aurita*, *S. maderensis*, *Ethmalosa fimbriata* and *Ilisha africana*. *E. fimbriata* and *I. africana* showed the highest and lowest values of ϕ', respectively, while *Sardinella* spp. were found to occupy the central position.

Résumé

Des données de fréquences de taille obtenues de pêcheries locales et des données sur l'âge par rapport à la longueur relevées par lecture des otolithes ont permis de calculer les paramètres de croissance de von Bertalanffy pour les quatre espèces constituant la famille des Clupéidés en Sierra Leone, Sardinella aurita, S. maderensis, Ethmalosa fimbriata *et* Ilisha africana. E. fimbriata *et* I. africana *ont respectivement donné les valeurs de ϕ' les plus élevées et les plus faibles alors que* Sardinella *spp. occupait la position centrale.*

Introduction

The Clupeidae constitutes one of the most abundant teleost families on the Sierra Leone shelf, and is represented by four species in three genera: *Sardinella aurita*, *S. maderensis*, *Ethmalosa fimbriata* and *Ilisha africana*. The spe-cies are pelagic and have extensive ranges in the East Central Atlantic. Maximum sizes are 30 cm for *S. maderensis* and *E. fimbriata* and 31 cm for *S. aurita* (Fischer et al. 1981).

In Sierra Leone, *S. aurita* occurs mainly in the northern part of the shelf, above latitude 8°N. *S. maderensis*, *E. fimbriata* and *I. africana*, which