Hydrobiologia **332**: 175–181, 1996.

Secondary production and energetics of the shrimp *Caridina nilotica* in Lake Victoria, East Africa: model development and application

Marcy Ignatow, Godfrey Mbahinzireki & John T. Lehman
Department of Biology and Center for Great Lakes and Aquatic Sciences, Natural Science Building, University of Michigan, Ann Arbor, MI 48109, USA; Fisheries Research Institute, P.O. Box 343, Jinja, Uganda

Received 8 August 1995; in revised form 9 January 1996; accepted 16 February 1996

Key words: tropical zooplankton, bioenergetics, assimilation efficiency

Abstract

Measurements of body mass, carbon content, respiration, growth, and egestion are combined in a model of secondary production by the tropical freshwater shrimp *Caridina*. The model is developed to permit its direct application to empirical data for abundances and size frequency distributions of field populations. Model calculations combined with population data for offshore Lake Victoria over a period of two years indicate that *Caridina* consume the equivalent of 2.2% of annual lake primary production. Present net annual secondary production by the shrimp is an order of magnitude greater than the present fishery yield of the lake. Detritus-fed experimental organisms evidently had assimilation efficiencies as low as 10% by model calculation.

Introduction

The atyid shrimp, *Caridina nilotica*, is a conspicuous inhabitant of many freshwater ecosystems in Africa. A primitive decapod, *Caridina* attains adult maximum total lengths of 2.5 cm (Fryer, 1960). Small individuals appear transparent and virtually colorless. Most large specimens are darkly pigmented, appearing primarily dark brown; others are so densely pigmented that they appear dark blue or black.

C. nilotica is abundant in equatorial Lake Victoria, the world's second largest freshwater lake (68800 km^2), which has a surface elevation of 1240 m and a mean annual water temperature of about 25 °C. In African lakes *C. nilotica* has given rise to a slender form with attenuated appendages, which could be correlated with the existence of thick flocculent mud on the bottom of the lake (Fryer, 1960). *Caridina* is frequently found in littoral regions wherever there are weed beds of submerged vegetation (Fryer, 1960), and it also occurs as an epibenthic, vertically migrating member of the offshore community (Lehman et al., 1996).

Caridina is a primary source of food for juvenile Nile perch (Ogutu-Ohwayo, 1990), and also for birds, mainly heron (Begg, 1973). Nile perch larger than 67 cm in length have gill raker spacing exceeding the mean body depth of *C. nilotica*, and consequently Hughes (1992) has argued that gill raker spacing is the constraint that prevents perch larger than 70 cm in length from being effective prawn predators.

Feeding habits of *Caridina* reportedly include the ingestion of submerged macrophytic vegegation, algae, and plants. *Caridina* has a complicated and specialized feeding mechanism. Fryer (1960) described *Caridina* in Lake Victoria as a 'macrophagous chelate raptatory feeder', and as 'detritus feeders, eating the material which accumulates on the bottom of the lake and on submerged macrophytic vegetation'. Fryer's examination of the gut revealed an amorphous mass of gray-green material along with minute alga cells, inorganic particles, and fragments of higher plants. Fryer also reported that the gut fills and empties rapidly, suggesting that the animals rely on a constant abundance of food. Much of the organic matter ingested is loose and flocculent and is released in a partially digested condition or in compact, elongated fecal pellets.

Although *Caridina* has been characterized as an epibenthic detritivore (Fryer, 1960) and not pelagic in habitat, early surveys have encountered atyid shrimp in

the plankton (Worthington, 1931). Recent study of *C. nilotica* in Lake Victoria has demonstrated the presence of shrimp not only in littoral regions but in offshore locations as well. Offshore populations (Lehman et al., 1996) were mainly planktonic both day and night and they exhibited diel vertical migration to surface waters in the darkness. Although Fryer characterized littoral *Caridina* as strict detritivores, Lehman et al. suggest that offshore populations may be facultative consumers of living planktonic algae and other suspended particles, and that the shrimp probably migrate to avoid visual predators.

In this paper we develop a method to calculate the secondary production of pre-reproductive *Caridina* by application of bioenergetic mass balance modeling. We use the basic equation

$$I = G + E + R + M, \tag{1}$$

where I is rate of ingestion, G is growth rate, E is egestion rate, R is the respiration rate and M is molting rate, all expressed in units of carbon mass (μg C d^{-1}). Model development relies heavily on the comprehensive studies of Hart (1980a, 1980b, 1981). We combined Hart's metabolic relationships and equations with original data for abundance and size distributions of *Caridina* collected from Lake Victoria, and thereby constructed temperature-dependent relationships among age, carapace length, weight, growth, ingestion, egestion, respiration, and molts. From these relationships and data, we developed an algorithm to compute production rates from field data.

Methods

Model equations for secondary production.

Length and length–weight relationships

We adopted the empirical length–weight regression developed by Lehman et al. (1996) for Lake Victoria *Caridina*:

$$W(\mu\text{gDW}) = 1.429L^{3.021} \tag{2}$$

where L (mm) is measured from midpoint of the eyes to the base of the telson. We also determined the empirical relationship between individual *Caridina* length (L, mm), and carapace length (CL, mm), measured from midpoint of the eyes to the margin of the cephalothorax and urosome, by nonlinear regression ($r^2 = 0\,987$, $n = 85$; SYSTAT 5.0):

$$\text{CL} = 0.387(\text{SE} = 0.029)L^{0.913(\text{SE}=0.037)}. \tag{3}$$

Animals used to construct the regression were collected from offshore Lake Victoria on 24 October 1992.

Respiration rate

Hart (1980a) investigated the influence of temperature and body size on oxygen consumption of *C. nilotica* by evaluating changes in routine metabolic rate. He reported a temperature-dependent regression relationship between oxygen consumption (R, μg O_2 h^{-1}) and body dry mass (M, mg) as:

$$R(\mu\text{g}O_2\text{h}^{-1}) = 0.008\text{T}^{1.829}M^{0.830}. \tag{4}$$

We converted respiration rates by Equation 4 into equivalent carbon units (μg C d^{-1}) by the following relationship:

$$R(\mu\text{gCd}^{-1}) = R(\mu\text{g}O_2\text{h}^{-1}) \cdot 24\text{hd}^{-1} \cdot 12/32 \cdot 0.949. \tag{5}$$

The scaling variables used in Equation 5 represent the ratio of molecular weights of C to O_2 (12:32), and the RQ value of 0.949 for ammonitelic organisms (Downing and Rigler, 1984).

Age, size and growth rates

Hart (1980b) evaluated growth trajectories and development rates of *C. nilotica* by investigating embryonic durations and post embryonic growth rates at experimental temperatures. We fit a non-linear regression model (SYSTAT 5.0) to Hart's (1980b) weight and age data for *C. nilotica* at 24°C:

$$W_{\text{rel}} = \exp[c \cdot \text{Age}/(\text{Age}+d)], \tag{6}$$

where Age is expressed in days, $W_{\text{rel}} = W/W_0$ (ratio of dry weight at any age to neonate weight), $c = 8.988$ (SE = 0.081), $d = 32.630$ (SE = 2.017), and $r^2 = 0.996$. We measured an empirical ratio of C:DW = 0.4442 (SE = 0.0056, $n = 3$ independent samples) for *Caridina* collected from Lake Victoria on 4 April 1995. Carbon body mass at any age (C) can be calculated from relative weight and neonate weight by the equation:

$$C = 0.4442 \cdot W_{\text{rel}} \cdot W_0. \tag{7}$$

Growth rates (G) were calculated by taking the first derivative of Equation 6 and combining with Equation 7:

$$G(\mu\text{gCd}^{-1}) = C \cdot [c/(\text{Age}+d)] \cdot [1-(\text{Age}/(\text{Age}+d)]. \quad (8)$$

Egestion rates

Hart (1981) estimated egestion rates of *Caridina nilotica* by quantitative recovery and gravimetric analysis of fecal pellets. His original analysis was reported as a linear regression between egestion rate (E, mg DW feces shrimp^{-1} d^{-1}) and W (mg DW) with a positive intercept, thereby potentially overestimating egestion by small juveniles. Hart generously supplied us with his original data, which we subjected to both linear and nonlinear regressions. We found that a linear model was appropriate but that the positive intercept was not significantly different from zero and consequently we substituted a simpler, one-parameter equation (SYSTAT 5.0), relating egestion rate to the dry weight of a shrimp ($r^2 = 0.925$, $n = 25$):

$$E = 0.6825 \cdot W \quad (9)$$

During April 1995, we collected fecal pellets from *Caridina* freshly isolated from nearshore Lake Victoria (Napoleon Gulf, Uganda). Feces were dried at 45 C for 24 h and were subjected to CHN analysis. Carbon content was 33.77% of DW. Thus, the egestion rate of *Caridina* in carbon mass (E_c, mg C shrimp d^{-1}) is:

$$E_c = 0.3377 \cdot 0.6825 \cdot W. \quad (10)$$

Molting losses

Hart and Allanson (1981) reported that the relationship between weight of a molt and carapace length was:

$$W_m = 21 \cdot \text{CL}^{3.086} \quad (11)$$

where W_m is the dry weight (μg) of an exuvium of carapace length CL (mm). According to this relationship, the molts lost by small shrimp equal almost 50% of their body mass, and larger shrimp have molting losses around 20% of body mass. The molt losses presented for *Caridina* seemed to be an unusually large component of the energy budget. By comparison, Parsons et al. (1984) summarized data for *Euphausia pacifica* and reported that from 7 to 15% of the animals' food intake could be required for molts.

We re-examined the relationship between molt weight and animal weight for *Caridina* from Lake Victoria. Live *Caridina* were collected from Napoleon Gulf, Uganda on 4 April 1995. The animals were sorted individually and were held in Lake Victoria water at ambient laboratory temperature (24 to 27 C). The animals were inspected at ca. 12 h intervals for up to 72 hours or until molting occurred. Upon molting, both the exuvium and molted animal were collected and were dried at 45°C on Teflon disks. The dried specimens were weighed by electrobalance. Analysis showed that the relationship between mass of the molt and the mass of molt and animal combined was linear ($r^2 = 0.910$, $n = 11$) over a range of animal masses from 0.4 mg DW to 18 mg DW:

$$W_m = 0.138(\text{SE} = 0.008) \cdot W. \quad (12)$$

Carbon content of the molts was 20.7% (SE = 0.4%, $n = 3$ independent samples).

Hart (1980b) reported intermolt durations (days) of *Caridina nilotica* as a function of animal size, sex and temperature (his table 2). We used Hart's data for nonbreeding females at 23.4°C, which is within 1°C of in situ temperatures in Lake Victoria, to determine a schedule of ages at which molting occurs. We divided predicted molt masses (μg) by intermolt duration (days) to establish rates associated with molt production (Table 1).

Results

We developed our production model from published data and equations for pre-reproductive *Caridina* acclimated at 24°C. Table 1 reports our estimates for age, weight, respiration rate, growth rate, and rates of egestion, molting, and ingestion for *Caridina* of specified length. According to Hart (1980b), first reproduction of females usually does not occur in *Caridina* having total lengths less than 19 mm. Hart's observation coincides with empirical data from Lake Victoria. Offshore populations were composed almost entirely of juveniles (Lehman et al., 1996); only 279 ovigerous females were found among 28073 animals less than 19 mm length measured from offshore waters (unpublished data).

Assimilation efficiencies were determined using the following equation:

$$\text{AE} = (G + R + M)/(G + R + E + M), \quad (13)$$

Table 1. Numerical estimates for mass and metabolic rate functions applied to *Caridina* in Lake Victoria. L = length (mm), W = dry mass (μg), C = carbon mass (μg), Age (days), R = respiration (μg C d^{-1}), G = growth (μg C d^{-1}), Molt = carbon mass of molt (μg C), M = carbon accumulation for molting (μg C d^{-1}), E = egestion rate (μg C d^{-1}), AE = assimilation efficiency

L	Age	W	C	G	R	E	Molt	M	AE
2	0	11.6	5.2	1.4	0.6	2.7	0	0.2	0.46
2.67	3.5	27.8	12.3	2.8	1.3	6.4	0.8	0.2	0.40
3	5.1	39.5	17.5	3.6	1.7	9.1	0	0.5	0.39
3.38	7.0	56.6	25.1	4.7	2.3	13.1	1.6	0.5	0.36
4	9.9	94.2	41.8	6.8	3.5	21.7	0	0.8	0.34
4.13	10.5	104	46.1	7.3	3.8	23.9	3.0	0.8	0.33
4.89	14.0	173	76.7	10.4	5.7	39.8	4.9	1.4	0.31
5	14.5	185	82.1	10.8	6.1	42.6	0	2.0	0.31
5.78	18.1	286	127	14.5	8.7	66.0	8.2	2.0	0.28
6	19.1	320	142	15.6	9.6	73.9	0	3.1	0.28
6.67	22.2	441	196	19.1	12.5	102	12.6	3.1	0.25
7	23.7	511	227	20.9	14.1	118	0	4.5	0.25
7.55	26.3	642	285	24.1	17.0	148	18.3	4.5	0.24
8	28.5	764	340	26.7	19.7	176	0	5.6	0.23
8.56	31.1	938	416	30.1	23.3	216	26.8	5.6	0.21
9	33.3	1091	485	32.7	26.5	252	0	7.6	0.21
9.54	36.0	1301	578	36.0	30.6	300	37.2	7.6	0.20
10	38.5	1500	666	38.7	34.5	346	0	10.1	0.19
10.48	40.9	1728	768	41.6	38.8	399	49.4	10.1	0.19
11	43.8	2000	889	44.6	43.8	461	0	11.7	0.18
11.51	46.5	2294	1019	47.7	49.1	529	65.5	11.7	0.17
12	49.4	2602	1156	50.4	54.5	600	0	14.9	0.17
12.48	52.1	2929	1301	53.1	60.1	676	83.7	14.9	0.16
13	55.4	3313	1472	55.8	66.6	764	0	18.5	0.16
13.39	57.6	3623	1609	58.0	71.7	836	103	18.5	0.15
14	61.7	4145	1841	60.7	80.2	956	0	15.6	0.14
14.75	66.5	4852	2155	64.3	91.4	1119	139	15.6	0.13
15	68.5	5105	2268	65.1	95.3	1177	0	19.8	0.13
15.98	75.3	6181	2745	69.1	111.7	1426	177	19.8	0.12
16	75.8	6204	2756	68.8	112.0	1431	0	16.7	0.12
17	83.6	7451	3310	71.8	130.4	1719	0	16.7	0.11
17.78	89.8	8532	3790	74.2	146.0	1968	244	16.7	0.11
18	92.2	8855	3934	74.1	150.5	2043	0	21.4	0.11
19	101.5	10427	4632	75.5	172.4	2405	0	21.4	0.10
19.34	104.4	11001	4886	76.3	180.2	2537	314	21.4	0.10

where all variables are in rates of carbon (μg C d^{-1}). Assimilation efficiencies of *Caridina* were found to range from less than 50% to as low as 10%, and mean calculated assimilation efficiency during juvenile development, 2 mm to 19 mm, was 19%. These low assimilation efficiencies were calculated from data for Hart's experimental animals maintained on a diet of detritus, thus indicating that most of the detritus is not readily digestible to these organisms.

In situ secondary production

We computed the biomass (mg C m^{-2}), net production (NP: growth + molt production, mg C m^{-2} d^{-1}) total gross production (GP: growth + molts + respiration, mg C m^{-2} d^{-1}) and ingestion rate (I_{tot}: growth + molts + respiration + egestion) for offshore *Caridina* populations in Lake Victoria from our model estimates (Table 1) combined with empirical determinations of

abundance and size distributions (Lehman et al., 1996). *Caridina* lengths were measured to the nearest 1 mm (midpoint of eyes to base of telson) and relative frequencies by size class were used to weight the rate functions for the population. The total population rate of respiration (R_{tot}, mg C m^{-2} d^{-1}), for example, was calculated as:

$$R_{tot} = N \cdot \Sigma(f_i R_i) \quad (14)$$

where f_i is relative frequency of size class i and R_i is the respiration rate for individuals in size class i. N is total population abundance (individuals m^{-2}). Population estimates of growth, molting, egestion, and ingestion were calculated, as well.

The total net production (NP) of the population was calculated by

$$NP = G_{tot} + M_{tot} \quad (15)$$

where G_{tot} is the total growth rate, and M_{tot} is the total molting rate. The total gross production (GP) of the population was calculated by

$$GP = G_{tot} + R_{tot} + M_{tot} \quad (16)$$

where R is the total respiration rate. The total ingestion or consumption rate of the population was calculated by the equation:

$$I_{tot} = G_{tot} + E_{tot} + R_{tot} + M_{tot}. \quad (17)$$

Table 2 shows representative calculations for Lake Victoria data, and Figure 1 summarizes biomass and production rates from 1992 to 1994 based on empirical abundances and size frequency distributions, combined with the model equations given here. We found the average NP of *Caridina* for the years studied to be 11.4 (SE = 3.6, n = 19) mg C m^{-2} d^{-1}, the average GP = 20.1 (SE = 6.4, n = 19), and the average I_{tot} = 112.2 (SE = 35.9, n = 19) mg C m^{-2} d^{-1}.

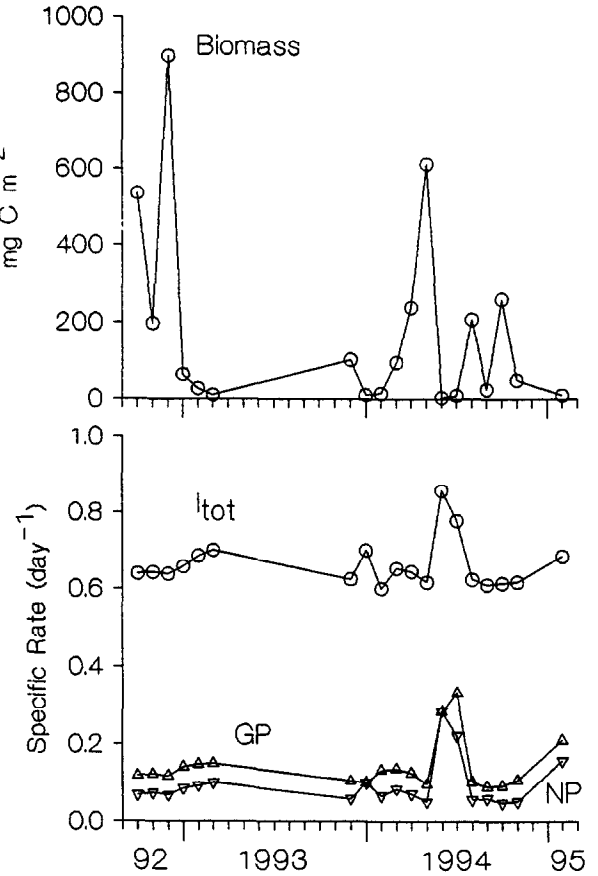

Figure 1. Biomass (mg C m^{-2}) and ratios of secondary production or total ingestion rate (NP, GP, I_{tot}: mg C m^{-2} d^{-1}) to biomass by *Caridina* at an offshore reference station in Lake Victoria south of Bugaia Island, Uganda (Station BG: 0°3.16′S, 33°16.59′E; depth = 62 m).

Discussion

Mugidde (1993) compared the seasonality of present and past daily integral productivity of phytoplankton in offshore Lake Victoria. She found the average productivity to be 13.9 g O_2 m^{-2} d^{-1}, which is 5213 (i.e., 13900·12/32) mg C m^{-2} d^{-1}. Mugidde's modern measurements are about double those reported by Talling (1965). Comparison of our estimates of total population rates of ingestion (I_{tot}) by *Caridina* with Mugidde's estimates for primary production gives evidence that if *Caridina* acts exclusively as a detritus feeder, it consumes a small fraction (2.2%) of annual lake primary production, and assimilates only about one-fifth of that. On the other hand, if the shrimp ever act as facultative zooplanktivores in offshore regions, our estimates for ingestion rates by *Caridina* could translate into a substantial predation effect on zooplankton prey.

Conversely, net production by *Caridina* appears to represent a significant potential forage resource for planktivorous fish in Lake Victoria. Our average figure of 11.4 mg C m^{-2} d^{-1} for net production is substantially larger than historical and recent estimated fishery yields. Ligtvoet and Witte (1991) report that total annual fishery yields for Lake Victoria have ranged from roughly 100,000 to 400,000 tons per year. These estimates represent 4 to 16 mg fish wet weight m^{-2} d^{-1} averaged over the entire lake. Assuming that C-content

Table 2. Representative calculations for offshore Lake Victoria *Caridina* sampled 27 October 1992 at 0930 h from 60 m to surface. Column sums are weighted by relative frequencies of each size class (f_i) and totals per m^2 are calculated from the measured areal abundance of *Caridina* (1474 individuals m^{-2}). $\Sigma f_i \cdot X_i$ is the frequency-weighted summation for each column

L (mm)	f_i	C_i (μg C)	G_i (μg C d^{-1})	R_i (μg C d^{-1})	E_i (μg C d^{-1})	M_i (μg C d^{-1})
2	0.005	5.2	1.4	0.6	2.7	0.2
3	0.016	17.5	3.6	1.7	9.1	0.5
4	0.033	41.8	6.8	3.5	21.7	0.8
5	0.096	82.1	10.8	6.1	42.6	2.0
6	0.146	142	15.6	9.6	73.9	3.1
7	0.112	227	20.9	14.1	118	4.5
8	0.225	340	26.7	19.7	176	5.6
9	0.101	485	32.7	26.5	252	7.6
10	0.050	666	38.7	34.5	346	10.1
11	0.022	889	44.6	43.8	461	11.7
12	0.096	1156	50.4	54.5	600	14.9
13	0.022	1472	55.8	66.6	764	18.5
14	0.039	1841	60.7	80.2	956	15.6
15	0.016	2268	65.1	95.3	1177	19.8
16	0.011	2756	68.8	112.0	1431	16.7
17	0	3310	71.8	130.4	1719	16.7
18	0	3934	74.1	150.5	2043	21.4
19	0	4632	75.5	172.4	2405	21.4
$\Sigma f_i \cdot X_i$		516	28.4	26.1	267.7	6.9
	N Indiv m^{-2}	C_{tot} mg C m^{-2}	G_{tot} mg C $m^{-2}d^{-1}$	R_{tot} mg C $m^{-2}d^{-1}$	E_{tot} mg C $m^{-2}d^{-1}$	M_{tot} mg C $m^{-2}d^{-1}$
	1474	760	41.8	38.4	394.6	10.2

$NP = G_{tot} + M_{tot} = 52.0$ mg C m^{-2} d^{-1}

$GP = G_{tot} + M_{tot} + R_{tot} = 90.4$ mg C m^{-2} d^{-1}

$I_{tot} = G_{tot} + M_{tot} + R_{tot} + E_{tot} = 485$ mg C m^{-2} d^{-1}

is about 5% of wet weight, these fish yields correspond to 0.2 to 0.8 mg C m^{-2} d^{-1}, more than 10-fold less than the average daily rate of *Caridina* production. In other words, the net biomass production by *Caridina* may be more than 10 times greater than the present fishery yield of the lake, which makes the shrimp quantitatively significant as a forage resource.

Our estimates for *Caridina* production are based on a time series of measurements from a single deep reference station in the Ugandan waters of offshore Lake Victoria, where the primary production measurements were conducted. More precise comparisons with lakewide fishery production should await complete spatial surveys for *Caridina*, with estimates for biomass and secondary production.

The rate functions from our model, presented in Table 2, provide the information needed to calculate biomass and secondary production by *Caridina* populations from abundance and size frequency data. The rates are applicable to tropical water temperatures of ca. 23 to 24 °C and can provide a means to convert survey data on standing crop biomass into production and ingestion rates. We believe that the model-derived numerical results presented here provide a convenient algorithm for assessment of production dynamics of an ecologically important freshwater crustacean.

Acknowledgements

We thank Donna Lehman, Arni Litt, and the staff of the Uganda Fisheries Research Institute, Jinja, Uganda, for laboratory and logistical assistance. Prof. R. C. Hart kindly provided some of his original data for analysis, and made helpful comments about the manuscript. This research was supported by U.S. National Science Foundation grant DEB-9318035, and by a grant from the NOAA National Undersea Research Program.

References

Begg, G. W., 1973. The feeding habits of the whitewinged Black Tern on Lake Kariba. Ostrich 44: 149–153.

Downing, J. A. & F. H. Rigler, 1984. A manual for the assessment of secondary productivity in fresh waters. Blackwell.

Fryer, G., 1960. The feeding mechanism of some atyid prawns of the genus *Caridina*. Trans. Roy. Soc. Edin. 64: 217–244.

Hart, R. C., 1980a. Oxygen consumption in *Caridina nilotica* (Decapoda: Atyidae) in relation to temperature and size. Freshwat. Biol. 10: 215–222.

Hart, R. C., 1980b. Embryonic duration, and post-embryonic growth rates of the tropical freshwater shrimp *Caridina nilotica* (Decapoda: Atyidae) under laboratory and experimental field conditions. Freshwat. Biol. 10: 297–315.

Hart, R. C., 1981. Population dynamics and production of the tropical freshwater shrimp *Caridina nilotica* (Decapoda: Atyidae) in the littoral of Lake Sibaya. Freshwat. Biol. 11: 531–547.

Hart, R. C. & B. R. Allanson, 1981. Energy requirements of the tropical freshwater shrimp *Caridina nilotica* (Decapoda: Atyidae). Verh. Int. Ver. Limnol. 21: 1597–1602.

Hughes, N. F., 1992. Nile perch, *Lates niloticus*, predation on the freshwater prawn, *Caridina nilotica* in the Nyanza Gulf, Lake Victoria, East Africa. Envir. Biol. Fish. 33: 307–309.

Lehman, J. T., G. B. Mbahinzireki & L. M. Ndawula, 1996. *Caridina nilotica* in Lake Victoria: abundance, biomass, and diel vertical migration. Hydrobiologia 317: 177–182.

Ligtvoet, W. & F. Witte, 1991. Perturbation through predator introduction: effects on the wood web and fish yields in Lake Victoria (East Africa). In O. Ravera (ed.), Perturbation and recovery of terrestrial and aquatic ecosystems. Elliss Horwood Ltd., Chichester: 263–268.

Mugidde, R., 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Verh. Int. Ver. Limnol. 25: 846–849.

Ogutu-Ohwayo, R., 1990. Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). J. Fish Biol. 37: 55–63.

Parsons, T. R., M. Takahashi & B. Hargrave, 1984. Biological Oceanographic Processes, 3rd edn. Pergamon Press, 330 pp.

Talling, J. F., 1965. The photosynthetic activity of phytoplankton in East African lakes. Int. Revue ges. Hydrobiol. 50: 1–32.

Worthington, E. B., 1931. Vertical movements of fresh-water macroplankton. Int. Rev. ges. Hydrobiol. 25: 394–436.