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Rapid estimation of in situ growth rates of *Caridina nilotica* (Crustacea: Decapoda) in Lake Victoria: Description and pilot application of a simple, field-compatible technique

Abstract—A simple rapid approach to estimating in situ growth rates of *Caridina nilotica* (Roux), a small shrimp that plays a pivotal role in Lake Victoria's food web, is described. The approach, potentially applicable to many arthropods, is based on moulting intervals (MI) and per moult size increments (PMI) determined during brief experimental confinements. Physiological justification of its reliability as a measure of in situ rates is given. *Caridina* moults at night. Feral animals collected shortly (≤2 h) before dusk were sorted into one of five arbitrary size classes and held around 27°C overnight without food. MI, the inverse proportion of a batch moulting overnight, increased from 2 d in small shrimps (carapace length [CL] ≤1.8 mm) to >9 d in larger animals (CL ≥4.3 mm)—a value comparable to egg development time (10.3 d) at the corresponding temperature. PMI was measured from differences in CL of postecdysal shrimps (CL_{i+1}) and corresponding cast exuviae (CL_i). In absolute terms, PMI, surprisingly, was constant (0.284 ± 0.027 mm moult^{-1}) over the size range of shrimps tested, although relative growth (PMI as a percentage of CL_i) declined with size. Growth trajectories modeled with regressions fitted to the data ($MI = 1.573 \times CL^{0.999}$ and $CL_{i+1} = 0.284 + 0.977 \times CL_i$) show that *C. nilotica* grows significantly faster (by at least 20%) in L. Victoria than previously estimated (Ignatow et al.), with corresponding implications to other evaluations of lake productivity. Prospective refinements and future uses for this simple technique are outlined.

Caridina nilotica (Roux) is a small decapod shrimp (carapace length up to 7 mm and dry weight up to 50 mg; Hart 1980, 1981) that is widely distributed in African inland waters. It is a dominant macroinvertebrate in tropical L. Victoria, where it abounds in deep open offshore waters, in inshore bays, and in littoral margins (Fryer 1960; Branstrator et al. 1996; Lehman et al. 1996). Functioning primarily as a benthic detritivore (Fryer 1960), it replaced the detritivorous haplochromines of L. Victoria following their decimation by introduced Nile perch—*Lates niloticus* (Ligtvoet and Witte 1991; Goldschmidt et al. 1993). However, *C. nilotica* is additionally recognized as a pelagic component in this and other African great lakes (Lehman 1996). Recent studies indicate that it constitutes up to 20% of zooplankton standing stock in deep offshore waters of L. Victoria (Lehman et al. 1996; Ignatow et al. 1996).

Caridina nilotica plays a key role in the contemporary lake's food web. It is a dominant food item for *L. niloticus*, L. Victoria's major vertebrate predator (Ogari and Dadzie 1988; Ligtvoet and Witte 1991; Hughes 1992; Mkumbo and Ligtvoet 1992; Goldschmidt et al. 1993). And it presumably serves as a major trophic intermediary between decomposing mats of the prolific invasive water hyacinth, *Eichhornia crassipes* (Twongo 1996), and other secondary producers. Despite this functional significance, its population dynamics

and ecology in the eutrophic (Hecky 1993) waters of L. Victoria are poorly known. The only estimate of its production (Ignatow et al. 1996) relies upon growth rates determined for a population of *C. nilotica* inhabiting L. Sibaya, an oligotrophic coastal lake in South Africa (Hart 1980). No intersite validation was attempted, almost certainly owing to the well-known methodological difficulties that constrain the determination of growth and secondary production rates (Downing and Rigler 1984), difficulties that are particularly acute in tropical environments and for small continuously breeding animals, especially where cohort overlap precludes any size-frequency approach (Benke 1993) to growth estimation.

This paper describes a remarkably simple, rapid, and direct method to estimate growth rate for use in studies of secondary production. The method is potentially applicable to any arthropod with short moult intervals, can be effectively implemented under unsophisticated field conditions, and should accordingly find wide applicability as a rapid assessment tool. Parallel approaches for copepods have been used shipboard (Burkill and Kendall 1982; Peterson et al. 1991), in field incubations (Kimmerer and McKinnon 1987), and in the laboratory (Miller et al. 1984).

Unlike these former approaches, however, the technique described here requires absolutely no maintenance of the test animals wherein incubations of even a single day could alter natural conditions (diel food changes) and behaviors such as diel vertical migration that influence metabolism and physiology. It measures only the responses of animals that are at or beyond the physiological threshold point of no return, predetermined in and by the natural environment. Various assumptions underlying the approach are evaluated using *C. nilotica* as a model organism, and resulting estimates of in situ growth rates are reported for an inshore littoral population of *C. nilotica* in Lake Victoria. The simplicity of the approach will hopefully encourage further studies on *C. nilotica* and secondary production of crustaceans generally.

Methods—Underlying principles: Crustacean growth is the well-known outcome of two features: moult interval (MI), and per moult size increment (PMI), or growth factor (GF). Both features generally vary through life, resulting in ontogenetic changes in relative growth rate (Kurata 1962; Mauchline 1976, 1977; Hartnoll 1982); both are variously influenced by the ambient environment (Hartnoll 1982).

Crustacean MI is regulated through the neuroendocrine controlled moult cycle (Barrington 1963; Highnam and Hill 1977), with various underlying environmental settings—particularly temperature and day length (Skinner 1985). Influences of tidal, circadian, lunar, and other cycles of longer periodicity are also known. In the progressive moult cycle sequence, animals reach a particular physiological threshold, the point of no return (PNR), after which they become due to moult, and cannot halt this process, regardless of nutritive status (Gore 1985).

Within underlying structural and architectural constraints, PMI is determined by the energy and material reserves (Klekowski and Duncan 1975) derived from the ambient environment. Their satisfactory acquisition leads to a critical reserve saturation point, preceding PNR (Gore 1985). Natural fluctuations in resource availability within the environment preceding moult effectively modify growth potential by influencing the 'scope for growth' (Warren and Davis 1967; Elliott 1994).

Based on these fundamentals, a simple two-pronged approach was applied to determine development and growth rates of *Caridina*. First, the incidence of moulting in batches of freshly collected shrimps of comparable size was assessed over a short time period (overnight). Second, changes in size of shrimps moulting during a corresponding time interval were measured. Provided artificial confinement is kept as short as possible (within practical limits), the size increment shown at moult by freshly collected animals is predetermined entirely by the nutritional and other conditions experienced in situ, and the resulting growth metrics are expected to reflect those applicable to animals under natural conditions, regardless of experimental disturbance. For this reason, however, the approach is practically feasible only for species moulting at relatively short intervals. Measurements of both MI and PMI over a full size range of animals are needed to provide a comprehensive growth profile.

The resulting estimates of MI and PMI allow for reliable and accurate size-dependent estimates of in situ growth rates, which can be scaled up to the population level, using independent stock assessment data (abundance and size structure). Despite long appreciation of the underlying principles (Kurata 1962; Mauchline 1976, 1977; Bliss 1985; Gore 1985), and their articulation by Hartnoll (1982), the present study represents a novel practical application of this understanding to measure in situ growth rates. No further consideration is given here to the stock assessment issues.

The existence of any markedly synchronous moulting imposed for instance by seasonal, lunar, or tidal periodicity, or by intracohort growth concordance obviously negates this approach. Precautionary assessments of this potential problem are readily undertaken, however, and relevant evaluations in respect of *Caridina* are reported below.

Practical procedures: Shrimps were collected in a dip-net (0.5-mm mesh aperture) in the late afternoon (generally between 1630 h and 1830 h) from floating vegetation (mostly *Eichhornia crassipes*) banked on L. Victoria's shoreline at Jinja pier (00°25.0′N, 33°12.5′E). Using a simple ranking procedure, specimens were immediately sorted by eye into one of five nominal size categories (very small, small, medium, large, very large), to generate batches of between 50 small and 300 large individuals of roughly comparable size on each occasion. Egg-carrying females were excluded.

Size-sorted batches were held in separate wide-mouth plastic containers of lake water and transferred to a nearby laboratory—a shady, well-insulated room with several wall skylights but no artificial lighting, exposed to reasonably natural solar and lunar cycles and thermal fluctuations. Experimental temperatures mostly ranged between 26 and 28°C (*see Fig. 1*), with illumination maximally around 0.05 μmol Quanta m^{-2} s^{-1}. No food was provided.

Around 0800 h the following morning, the number of moults was tallied in relation to the number of shrimps isolated in each batch. A total of >5,000 shrimps was tested during the study. Mean size of individuals within a batch

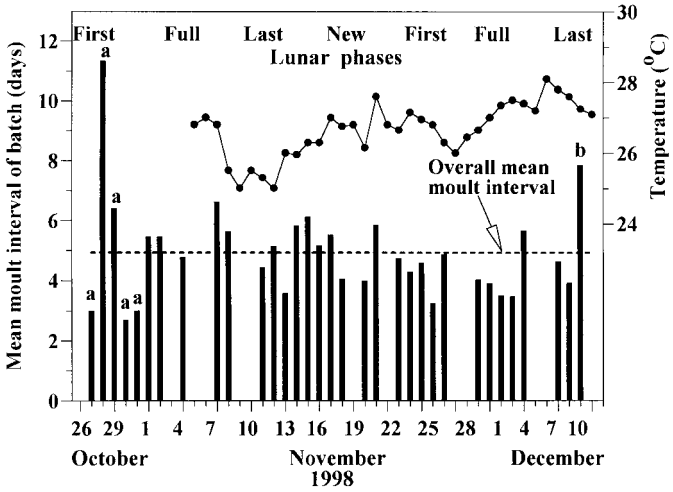

Fig. 1. Mean moulting interval of consecutive batches of freshly collected *C. nilotica* of mixed body size in relation to lunar periodicity and experimental temperature fluctuations during the study period. Marked outliers are attributable to batches of few animals ($n \leq 50$) (a) in some pilot experiments or (b) batches dominated by large individuals.

was estimated from the carapace lengths (CL) of cast moults, measured to ca. 0.1 mm under a dissecting microscope, using a finely graduated precision ruler (as no micrometer eyepiece was available).

Moult interval (MI, in days) was simply calculated as the reciprocal of the proportion of the batch moulting overnight, regardless of the precise experimental duration. The basis for this per diem rounding is discussed in the Results section on moulting synchrony. The values of MI and CL are within-batch mean estimates from a total of more than 800 moults.

Size was measured as CL rather than total length (TL), since cast moults were frequently broken and/or separated at the cephalothoracic-abdominal junction, and also in view of the inconsistent angle of flexure of this junction both in intact moults and preserved animals. As previous studies of *C. nilotica* in L. Victoria used measures of TL, interconversions were made where necessary using the expression $CL = 0.387\ TL^{0.931}$ (Ignatow et al. 1996). However, body dry weight was estimated directly as $W = 0.05CL^{3.595}$ (Hart 1980) to avoid a two-stage conversion from the TL-mass regression available for shrimps in L. Victoria (Lehman et al. 1996).

Single shrimps, or small groups ($n \leq 5$) of clearly size-distinguishable individuals, were held overnight to determine per moult size increments (PMI), measured as the difference in CL of postmoult shrimps (CL_{i+1}), and the premoult size determined from the corresponding exuvium (CL_i) . The resulting Hiatt growth diagram plotted with these values is accordingly a hybrid version of the customary consistent pairing of specimen or exuvial values (Hiatt 1948; Mauchline 1976). Consideration of the impact of this modification is reserved for the Discussion. Growth factor (GF) or relative growth (PMI as a percentage of CL_i), the recommended index for comparative growth measurements (Hartnoll 1982) was calculated as the difference between preecdysal and postecdysal size (as CL or estimated dry weight).

Table 1. Regression relationships describing growth features of *Caridina nilotica* in Lake Victoria. Corresponding figures are identified by number.

Moult interval (days) as a function of premoult carapace length (mm)—Fig. 2.

$$MI = 1.573 \cdot CL^{0.999} \quad (r^2 = 0.473;\ df = 1, 47;\ P < 0.001) \quad (1a)$$

$$MI = -0.627 + 1.853 \cdot CL \quad (r^2 = 0.420;\ df = 1, 47;\ P < 0.001) \quad (1b)$$

Post-moult carapace length (CL_{i+1}, mm) as a function of premoult size (CL_i, mm)—Fig. 4.

$$CL_{i+1} = 0.284 + 0.977 \cdot CL_i \quad (r^2 = 0.992;\ df = 1, 100;\ P \ll 0.001) \quad (2a)$$

$$CL_{i+1} = 1.186 \cdot CL_i^{0.911} \quad (r^2 = 0.990;\ df = 1, 100;\ P \ll 0.001) \quad (2b)$$

Per moult increment (PMI, %) in relation to premoult size, expressed in terms of carapace length (CL_i, mm) or predicted weight (W, mg)—Fig. 4.

$$PMI = 28.560 \cdot CL_i^{-1.349} \quad (r^2 = 0.537;\ df = 1, 100;\ P < 0.001) \quad (3)$$

$$PMI = 129.703 \cdot W^{-1.472} \quad (r^2 = 0.540;\ df = 1, 100;\ P < 0.001) \quad (4)$$

An indirect estimate of egg development time (D_e) was obtained for one batch of freshly collected egg-carrying shrimps by regressing number of unhatched clutches as a function of time since isolation (*see* Hart 1980).

In keeping with familiar growth allometry (Peters 1983), power curve regressions were fitted and used to model growth where possible, unless other equations gave significantly better fits (*see Table 1*).

Results—Moulting rate: Moult synchrony: In several trial batches (involving ~750 shrimps) inspected roughly every 12 h over 1.5 to 3 d, moulting was restricted almost exclusively (>99%) to hours of darkness. In view of this strong nocturnal synchrony, subsequent experiments were restricted to single overnight laboratory confinements (as described in the Methods section).

In keeping with the short MI values shown by this shrimp, no lunar periodicity was discernible in mean moulting incidence in 33 consecutive batches of animals of mixed body size held overnight (Fig. 1). Seemingly disparate batch mean MI values are attributable to small sample sizes, or body size biases (*see Fig. 1 legend*).

Indications of weak moulting pulses at intervals of around 3 to 5 d were apparent in some batches of shrimps of comparable size cultured on different diets in separate experiments (not shown here), cautioning that some degree of intracohort moulting synchronization may exist. However, whereas it is logical to anticipate such synchrony in separate discrete cohorts experiencing identical growth conditions, its weak manifestation in randomly collected samples of mixed body size drawn from the continuously breeding feral stock

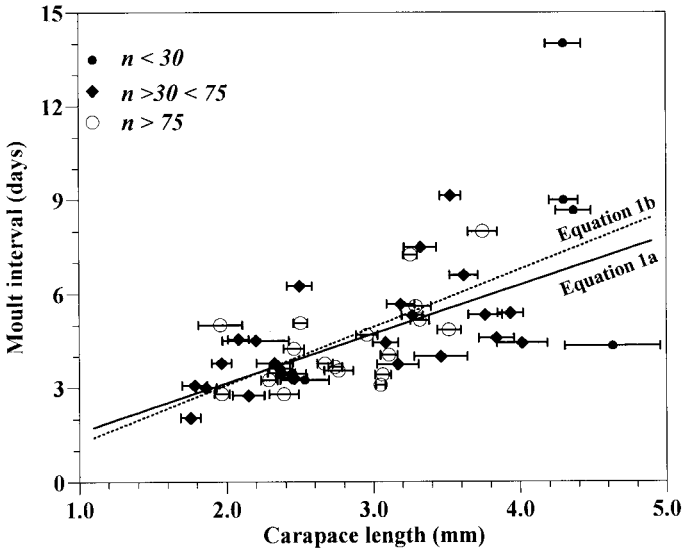

Fig. 2. Moult interval of *C. nilotica* as a function of shrimp size. Values plotted are batch means (±SE) of carapace length determined from exuviae ($n > 800$) recovered from overnight holdings of 55 separate batches of shrimps ($n > 5\ 000$) differentiated by sample size.

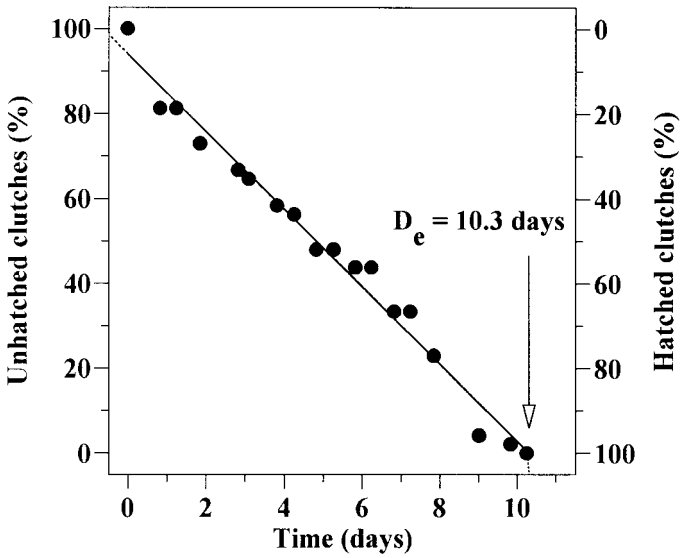

Fig. 3. Regression estimate ($Y = 94.009–2.121 \times X$; $r^2 = 0.982$; $df = 1, 17$; $P < 0.001$) of egg development time (D_e) of *C. nilotica* at a median temperature of 27.5°C determined from the hatching progress of clutches in a random sample ($n = 75$) of ovigerous females.

of *C. nilotica* can only be regarded as capricious. Moult synchronicity issues are accordingly not considered to invalidate the approach in this species population (*see further in Discussion*).

Moulting frequency: Moult interval clearly increased with shrimp size, but considerable variability was evident (Fig. 2). Much of this scatter is attributable to intrabatch variability associated with the use of batch mean values of CL and MI. Some differentiation of intrabatch sample size and corresponding CL variation is reflected on Fig. 2 to indicate the likely reliability of individual points.

MI increased (Fig. 2) from around 2 d for the smallest shrimps tested (mean CL ±1.8 mm) to around 9 (maximally 14) d for large females (mean CL ± 4.6 mm), effectively in a linear manner (Eqs. 1a and 1b in Table 1). The smallest egg-bearing female collected in this study was 3.6 mm in CL. Above this size most MI values tended to diverge, either exceeding 7 d or remaining below 5 d (Fig. 2). The resulting weak bimodality perhaps reflects sexual dimorphism. Virtually all shrimps above 4.0 mm CL were adult females, in which MI becomes tied to egg development times in egg-carrying individuals. Upper MI values observed were mostly around 9 d (Fig. 2), in line with the egg duration estimate of 10.3 d obtained at 27°C in this study (Fig. 3). This apparent match between MI in nonovigerous females and D_e suggests that MI may adaptively scale directly with temperature-dependent egg development times. But significant interpopulation differences in D_e may also exist, since the predicted value of 15.1 d at 27.5°C for the Sibaya population (Hart 1980) greatly exceeds the single estimate obtained in this study. Lower MI values (<5 d) evident (Fig. 2) in the higher CL range (3.4–4.0 mm) conceivably reflect batches dominated by males, a possibility that could be evaluated in the future using presence or absence of the distinctive appendix masculina process on the second pleopod to sex exuviae.

Per moult growth increment: Observed per moult size increments in relation to shrimp size are illustrated in modified Hiatt growth diagram format in Fig. 4. Corresponding descriptive equations are given in Table 1. Absolute per moult increments were effectively constant (at 0.284 ± 0.027 mm moult^{-1}: Eq. 2a) over the entire size range of shrimps (1.2 to 4.9 mm CL) tested in the present study.

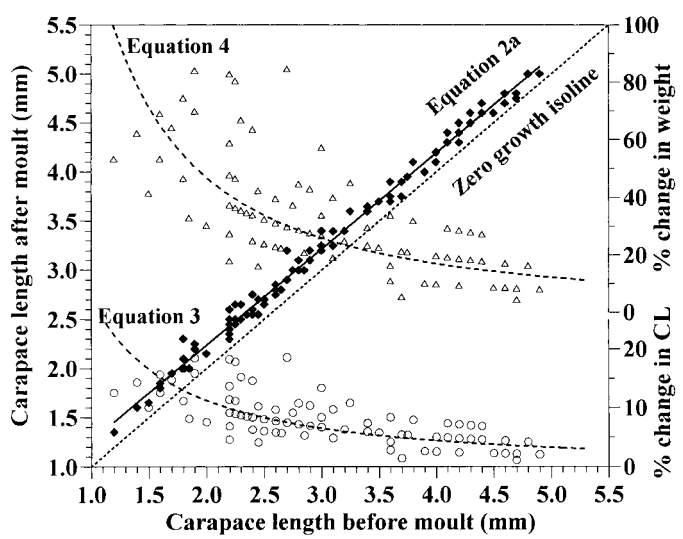

Fig. 4. Hiatt growth plot of per moult size increments of *C. nilotica* in relation to carapace length (mm CL, Eq. 2a) and corresponding relative GF values expressed in terms of CL (Eq. 3) or predicted dry weight (Eq. 4).

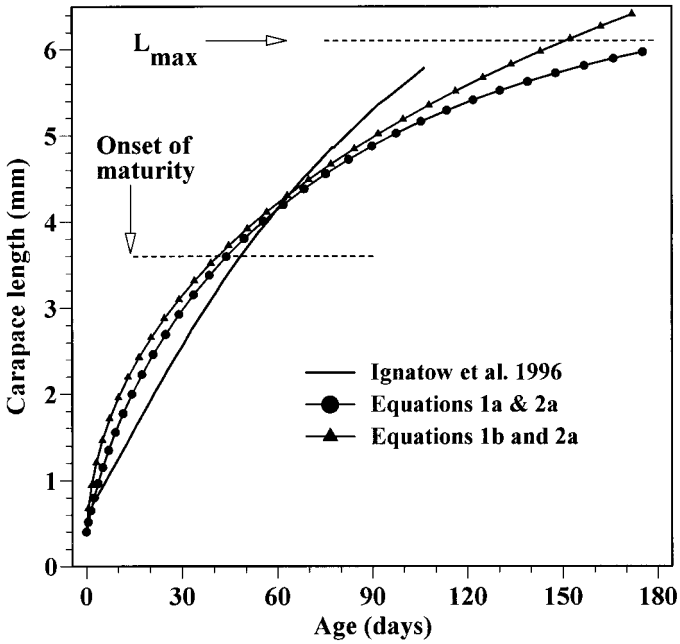

Fig. 5. Growth trajectory (CL in relation to estimated age) of *C. nilotica* from L. Victoria simulated using Eqs. 1 and 2 derived in this study (*see Table 1*), in comparison to that modeled by Ignatow et al. (1996). *See text for explanations and cautionary comments.*

Conversely, GF declined clearly and quite sharply with increasing shrimp size and hence age (Fig. 4) from around 20 to <2% in terms of CL (Eq. 3) and from 80 to <20% in terms of estimated biomass (Eq. 4).

Growth simulation: Based on the present data, the growth trajectory of *C. nilotica* in L. Victoria can be simulated from a CL above 1.75 mm. Back-extrapolation of the fitted equations (Table 1) to 0.4 mm, the nominal starting size based on the measured range of hatchling shrimps from L. Victoria (CL = 0.35 to 0.45 mm, n = 50), provides a first approximation of early growth, although empirical confirmation is required.

Equations 1 and 2 predict a surprisingly rapid growth of *C. nilotica* in L. Victoria (Fig. 5), with concomitant implications to its productivity. Females reach mature size within roughly 5 weeks of hatching, suggesting a potential generation time of as little as 7 weeks, whereas the apparent asymptotic size of around 6.1 mm CL (Ignatow et al. 1996) is reached in less than 6 months, implying longevity of much less than a year.

Discussion—Technique evaluation: assessment, prospective refinements and further applications: Unlike previous uses of cast-off moults as a growth marker for small copepods (Twombly and Burns 1996), larger crustaceans like *Caridina* (Hart 1980), *Gammarus* (Sutcliffe pers. comm.), and various euphausids (Ikeda et al. 1985; Iguchi and Ikeda 1995), the present technique avoids most uncertainties of laboratory estimates. It improves on field incubations of size- or stage-based cohorts (Burkill and Kendall 1982; Kimmerer and McKinnon 1987; Peterson et al. 1991) in avoiding the need for delicate, laborious, and potentially injurious sorting of animals and their subsequent maintenance in confined conditions for one or several days during which unnatural changes in water quality and/or nutrition and activity constraints (on vertical migration, for instance) potentially confound results.

In contrast, the approach used here is clearly rapid and simple and should logically yield growth rate estimates realistically applicable to feral animals. Disturbances of experimental animals associated with their capture, sorting, and overnight starvation should not affect the responses measured, for the physiological reasons outlined above. The only possible caveat recognized in its application to *Caridina* relates to the observed circadian synchrony imposed by nighttime moulting, which violates any assumption of strictly random moulting. However, this has virtually no effect on predicted growth trajectories. If each MI value predicted by Eq. 1a is adjusted up or down to the nearest whole day to reflect exclusively nocturnal moulting, the maximum size of 6.1 mm CL (Ignatow et al. 1996) is reached at an identical age to the corresponding sum of unadjusted values (162 versus 162.4 d). Nocturnal moulting is clearly a protective adaptation, widely observed in other crustaceans (Hartnoll 1982; Miller et al. 1984; Gore 1985; Iguchi and Ikeda 1995). Rather than compromising the approach, this intrinsic growth feature of *Caridina* offers real practical benefits in its implementation, at least in this species, as outlined under Methods.

Per moult increment (or growth factor) is traditionally based on the difference in premoult and postmoult sizes, determined either for intact specimens or exuviae (Hartnoll 1982, and references therein). The present is a hybrid approach, using both specimen and exuvial sizes. Resulting estimates of growth may accordingly be conservative, at least to the extent that any postmoult expansion of the exoskeleton is disregarded. Hartnoll (1982) considered that intermoult growth in crustaceans could normally be ignored in practice. Especially in an animal like *C. nilotica* with a rapid moult cycle and thin, light exoskeleton, postmoult expansion of new exoskeleton is likely to be correspondingly rapid. Any error introduced by this hybrid approach will accordingly be limited, and as it is expected to scale almost uniformly with shrimp size, it will accordingly be superfluous in the context of within-species comparisons.

In principle, the method appears valid for all arthropods, pending comparable validation of moult synchronicity, etc. In practice, though, its use will likely be limited to organisms of small or intermediate size that moult at relatively short intervals (diecdysis intermoult—Highnam and Hill 1977) and that can be freshly collected and held (under laboratory, lakeshore or riverside, or shipboard conditions) in relatively large numbers. Its greatest utility obviously relates to continuously reproducing species that present the otherwise virtually intractable problem of noncohort populations (Benke 1993). Accordingly, it offers good prospects for application in tropical or warm-water environments and appears particularly suitable for *Caridina*.

Several conceptual objectives of secondary production research outlined by Downing (1984) involve the use of growth responses and production estimates as a measure or

index of environmental suitability. Accomplishment of these listed objectives is thwarted most often by constraints of practical measurement. The direct simplicity and rapidity of the present approach opens prospects for its use in comparative investigations of spatial and/or temporal variation in growth rate within or between ecosystems. In L. Victoria, for instance, comparisons between deep-water pelagic, offshore and nearshore benthic, and inshore littoral populations of *Caridina* associated with different hydrophytes could be accomplished rapidly (certainly for selected size classes of shrimps) to provide insights into the nutritional status of differing elements of the aquatic landscape. In this way, the method could provide the better spatial coverage of *Caridina* in L. Victoria, a clear need identified by Ignatow et al. (1996).

The present results derive from an unplanned and essentially opportunistic pilot study, relying on materials locally available at Jinja. The utility and accuracy of the approach could, however, be improved considerably by reducing size variability of animals within test batches to ensure greater consistency in MI estimates. The use of graded sieves of carefully selected mesh size, positioned vertically in a horizontal trough along which live shrimps could be encouraged to move quickly (into shade, for instance) is a prospective solution, provided *Caridina*'s long antennae do not practically hinder its cross-screen movements.

Site-validated features of *Caridina* growth and its production potential in L. Victoria: The consistency in absolute PMI over almost the full size range of shrimps in this population (ca. 0.4 mm at hatch to the approximate maximal size [L_∞] of 6.1 mm) is quite remarkable, if as yet unexplained. Growth increment is generally maximal at intermediate size and declines in smaller and larger individuals—the basis on which Mauchline (1976) propounded the use of a hyperbolic, rather than linear equation to describe the Hiatt line. The hyperbolic relationship fitted to the present data [$(CL_i - 1.237)(CL_{i+1} - 5.230) = -2.658$] using her method yields a very realistic estimate of asymptotic size ($L_\infty = 5.66$ mm), but otherwise predicts nonsensical negative growth in both small and large size classes. In contrast, although Eq. 1b (the Walford line, Ricker 1979) describes the observed growth adequately, it generates an absurdly high L_∞ value of 12.35 mm CL. These discrepancies remain unresolved.

The pattern of progressive reduction in GF observed in *Caridina* is commonly reported, although considerably higher values are recorded in other much larger decapods (Hartnoll 1982). Growth of *Caridina* is seemingly maximized by rapid moulting rather than high PMI—a logically adaptive response for a small, thin-shelled species.

Figure 5 compares the growth of *C. nilotica* in L. Victoria as modeled by Ignatow et al. (1996) but adjusted to account for growth from hatching to 2 mm TL, with that predicted by the present Eqs. 1 and 2. Previous growth estimates for L. Victoria shrimps smaller than 4 mm CL are clearly conservative compared to the present predictions (Fig. 5). Because shrimps smaller than 4 mm CL comprise by far the greatest bulk (±90%) of *Caridina* biomass and production potential in the offshore pelagic zone (Lehman et al. 1996), and undoubtedly also in the inshore littoral (personal observation), the present findings indicate that production of the dominant size fractions of *Caridina* may be considerably higher than anticipated by the predictive rate functions given by Ignatow et al. (1996, their table 2). For instance, using Eqs. 1a and 2a, cumulative ages to reach 6, 7, 8, and 9 mm TL (roughly 2 to 3 mm CL), the four numerically dominant size classes that comprised nearly 60% of Ignatow et al.'s model population, are reached between some 35 and 20% faster than modeled by them (Fig. 5).

Revision of the predictive rate functions provided by Ignatow et al. is inappropriate on the basis of this pilot study, especially in the absence of empirical benchmarks for growth of small shrimps (CL $\leq$ 1 mm). In this regard, estimates of early (larval) growth in *C. nilotica* in L. Victoria (this study) and L. Sibaya (Hart 1980) appear radically shorter than the time to first metamorphosis of around 14 d reported for *C. n. aruensis* from Australia (Glaister 1976). However, the present findings clearly identify the need to reassess the production rate functions proposed for a dominant organism in the L. Victoria ecosystem. It is not unreasonable that populations inhabiting the eutrophic waters of L. Victoria (Hecky 1993) should grow significantly faster than their counterparts in rather cooler, oligotrophic waters of L. Sibaya. Adjustments of even a few percentage points scale up into massive differences on a whole-lake basis. As the differences reported here appear much greater (conservatively of the order of 20% or more), radical revisions of *Caridina*'s productivity in L. Victoria may be required. Enabling methodology has been outlined here; it merely awaits further application.

Conclusions—The particular value of the approach described to secondary production research rests on two inherent features: (1) its applicability in species or situations where cohort analysis is impossible in view of cohort overlap arising from continuous or overlapping reproduction, as occurs in many tropical animals and (2) its representativeness for free-ranging individuals, exposed to entirely natural food and thermal conditions and fluctuations, and engaged in correspondingly appropriate activity levels. These variables are difficult or impossible to mimic in laboratory conditions. In addition, equipment requirements are minimal and extremely basic, opening prospects for its wide use and application. Unfortunately, though, stock density assessment, for which no panacea presently exists, remains an arduous and unreliable requirement of secondary production research.

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