An energetics model of an aquatic predator and its application to life-history optima

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Summary. A bioenergetics simulation model of the growth and life history of the aquatic predator *Nephelopsis obscura* Verrill was developed and validated using both experimentation and sensitivity analysis. Sensitivity analysis demonstrated that the model's internal feedbacks resulted in stability similar to homeostatic biological mechanisms. The experimental validation showed the model very accurately predicts growth at 10°C and 15°C but is slightly biased at 20°C. Simulation output was also consistent with the observed data on *Nephelopsis* from the site from which the simulation input data were obtained and indicated that *Nephelopsis* growth is more sensitive to prey variation among years than to temperature variation. Although built using data from a population at one extreme of the spectrum observed in life history and growth, the model was able to emulate the growth of *Nephelopsis* throughout its range. Thus, the variability in size and life history observed in the field can be explained as the result of a plastic phenotype responding to different habitat conditions.

Key words: *Nephelopsis* – Leeches – Life history – Model

*Nephelopsis obscura* Verrill (Erpobdellidae) is a predatory leech widely distributed in freshwater habitats in temperate regions of North America (Davies 1973; Sawyer 1972; Klemm 1982). Over its geographic range it shows considerable variation in body size, being up to 2,000 mg in Minnesota ponds (Peterson 1983), about 1,400 mg in ponds in the Rocky Mountain foothills of Alberta (unpublished work), but rarely exceeding 700 mg in the prairie ponds of Alberta (Davies and Everett 1977). In the prairies of Alberta *Nephelopsis* is semelparous, breeding at age one year (Davies and Everett 1977) but has the potential to be iteroparous (Baird et al. 1986) whereas in Minnesota it delays its age of first reproduction to two years (Peterson 1982, 1983). These differences in maximum body size and life history could either be the result of phenotypic plasticity reflecting environmental differences, or the result of genotypic differences across its range.

It is difficult to predict the optimum life history of *Nephelopsis* strictly from first principles since it depends critically upon schedules of mortality and natality, which are in turn dependent upon environmental conditions. Individuals that delay reproduction until age two years would be larger than those that breed at age one year, and expected to produce more offspring and thereby may have higher fitness. Alternatively, the compound interest effect of breeding at age one year, and the extra mortality risk experienced during the period of delay to age two years, may offset the advantage of delaying reproduction. Baird et al. (1986) showed that post reproductive survivorship of *Nephelopsis* increases with body size and that individuals that survive reproduction re-enter breeding condition. Thus, individuals that delay reproduction may gain the added advantage of increasing probability of breeding more than once (becoming iteroparous) swinging the balance in favour of delayed reproduction. Baird et al. (1986) also showed that increased feeding in the weeks following cocoon production increases post-reproductive survival suggesting that in habitats with high prey availability, individuals that breed at age one year would be larger and have a greater probability of surviving to breed a second time. It is not certain whether *Nephelopsis* would maximize its fitness by breeding at age one year or two years; whether becoming iteroparous provides significant fitness gains; or whether food availability will change the position of the optimum.

The objectives of this study were to explore these alternatives through the development of a computerized simulation model of the growth and life history of *Nephelopsis* in a population at one of the extremes of the range variation. If manipulating environmental parameters in the model causes it to emulate the growth and life history of *Nephelopsis* throughout its range, then the phenotypic plasticity hypothesis would be supported. Alternatively if the model can not explain the variation over the entire range, genotypic difference would be suggested.

The *Nephelopsis* population upon which the model was based was from Stephenson's Pond, a small (2.2 ha), shallow (<2.5 m) eutrophic prairie pond near Calgary, Alberta (114°16'W, 51°9'N), which has been described by Rasmussen (1983). The main prey of *Nephelopsis* in Stephenson's Pond are *Daphnia* (for small leeches) and chironomids and oligochaetes (for larger leeches). Breeding occurs in late spring with cocoon deposition by each hermaphrodite individual lasting approximately 4 wks.

The design criteria for the simulation were: 1. it should be reductionist in its design (Paloheimo et al. 1982) so that its structure is a mechanistic representation of how growth.

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is believed to occur (Kerr 1971a) rather than a statistical fit to observed growth data; 2. to aid experimental validation the parameters of the model should be easily measured under either field or laboratory conditions; 3. it should be as simple as possible since complexity increases the difficulty of obtaining accurate measures, but, realism must not be sacrificed for the sake of simplicity. For these reasons, the model was based upon the energy balance equation (Ricker 1971):

$$P = (I - F) - U - R = E_a I - U - R = A - U - R \quad (1)$$

where $P$ is energy production (growth and reproductive products released), $I$ is the total energy content of the food ingested, $F$ is the energy content of feces, $U$ is the energy value in excretory products, $RT$ is energy expended as metabolism, $E_a$ is absorption efficiency, and $A$ is energy absorbed across the gut wall. This equation (reviewed by Calow 1981), integrates the major physiological processes considered to be the important components of growth (Bayne et al. 1976) and has formed the basis of growth models for fish (Makorova and Zaika 1971; Kerr 1971a, 1971b; Solomon and Bradfield 1972; Ware 1975; Elliott 1976; Kitchell, Stewart and Weininger 1977; Ware 1978; Kitchell and Breck 1980; Stewart et al. 1983) and invertebrates (Bayne et al. 1976, 1981; Palheimo et al. 1982). It also permits feedbacks (Hubbell 1971) among the different components of growth, as well as feedbacks between environmental variables and the growth components, allowing homeostatic mechanisms to be expressed. Few models of invertebrate growth include empirically measured feedbacks among growth components and environmental variables (Calow 1981), but see Bayne et al. (1976).

Methods

Growth and reproduction

The model simulated weekly (= one model cycle) growth and reproductive energy expenditures of an individual under various environmental conditions of temperature and food availability. In each cycle (t) equations (below) estimated energy expended in reproduction ($Rep_t$) and the thems of Eq. (1) as functions of the body size ($B_t$) and environmental conditions. Equation (1) was then solved and the next week's body size ($B_{t+1}$) was calculated as

$$B_{t+1} = B_t + P_t - Rep_t \quad (2)$$

The time resolution of one week was chosen since potential non-linearities in the model should be minimal at this scale and computational overheads not excessive when simulating a number of years growth.

Feedbacks were included in the model by introducing terms from the right-hand sides of Eq. (1) and (2) into equations estimating other terms of these equations. For instance, in each cycle respiration rate ($R_t$) in Eq. (1) was a function of ingestion ($I_t$) and reproduction ($Rep_t$). Beyond these empirically measured feedbacks the model was unconstrained and reacted solely to the environmental conditions input throughout a data file (but see ingestion).

Life histories

Life histories were varied by constraining only the maximum age an individual could attain and the age at first reproduction. The probabilities of surviving each week ($p_t$) were simulated as functions of age, body size and environmental conditions and the likelihood of attaining any age $t$ calculated as:

$$l_t = II p_t \quad (3)$$

Reproductive output at age $t(m_t)$ was calculated as a function of body size and temperature.

Collections and acclimation

Nephelopsis were collected as needed from Stephenson's Pond and acclimated to laboratory temperatures and food regimes for at least 2 wks. Laboratory diets were ad libitum Tubifex Tubifex (Linn), since these prey were commercially available all year. When feeding experiments were performed Nephelopsis were acclimated on the experimental prey.

Ingestion ($I_t$)

Weekly prey ingestion rates were modelled using the functional feeding response equation

$$I_d = -6.825 + 0.511 T + 4.053 D_d \quad (4)$$

for small Nephelopsis feeding on Daphnia and

$$I_c = -37.373 + 1.939 T + 7.175 D_c + 0.021 B_{mg} \quad (5)$$

for larger Nephelopsis feeding on chironomids where $T$ is temperature ($^\circ$C), $D_d$ is Daphnia density (ml$^{-1}$), $D_c$ is chironomid density (cm$^{-2}$) and $B_{mg}$ is Nephelopsis wet weight (mg) (Linton 1985). Equation (4) was estimated by allowing groups of eight Nephelopsis to forage for 72 h on chironomids at densities ranging from 0.5 cm$^{-2}$ to 3 cm$^{-2}$ and at temperatures ranging from 12.5$^\circ$C to 20$^\circ$C. Numbers of prey consumed were estimated as the difference between initial and final counts. Equation (5) was estimated in a similar way, but foraging times were 6 h, and densities ranged from 0.25 ml$^{-1}$ to 8 ml$^{-1}$. A Phillipson (1964) microbomb calorimeter was used to estimate joule equivalents for Daphnia (0.041 J per individual) and chironomids (0.192 J mg$^{-1}$ wet wt). Joules ingested were estimated as the product of the number of prey captured [Eq. (4) and (5)] multiplied by their energy content. The capture rate of chironomids [Eq. (5)] was determined using Nephelopsis > 80 mg, and only one chironomid size, so selection of different prey sizes by different sized Nephelopsis could not be quantified. Occasionally when Nephelopsis were small and the average prey were very large, the calculation of ingestion resulted in estimates above the maximum rate observed in the laboratory under ad libitum food. In these cases ingestion was limited to the ad libitum rate.

Absorption efficiency ($E_a$)

Absorption efficiency was measured (Linton 1985) at 10$^\circ$C and 15$^\circ$C using Nephelopsis ranging from 90 mg to 380 mg by maintaining them individually on an ad libitum diet of T. tubifex. for one month and quantifying the energy equiva-