Workshop: "Biology of Ampullariidae"

Minireview

Pomacea canaliculata (Gastropoda: Ampullariidae): Life-history Traits and their Plasticity

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Freshwater snails belonging to the Ampullariidae family show noteworthy anatomical, physiological and ecological characteristics (Berthold, 1991), which have captivated scientific interest since long ago. However, few field studies have focussed on apple snail population dynamics (Burky, 1974; Lum Kong and Kenny, 1989). International concern about the Argentinean apple snail *Pomacea canaliculata* (Lamarck, 1822) rose enormously when it became established as a serious rice pest in Asia. The biology, impact and management of apple snails as agricultural pests and biological control agents has been extensively reviewed by Cowie (in press).

The aim of this paper is to analyze the information on *P. canaliculata* life history and to review the effect of different factors on growth, survivorship and reproduction of this remarkably plastic snail. Unfortunately, most information generated in Asia since its establishment in the '80s is fragmentary. The sparse data comes mostly from short-term studies focussed on particular life-history traits, which are also difficult to compare, owing to very diverse or vaguely described environmental conditions. In addition, the identity of the snail species studied is doubtful or unknown in many cases (Cazzaniga, this issue of BIOCELL; Cowie, in press).

Laboratory studies on growth, survivorship and reproduction, specially those comprising an entire lifetime, albeit not directly extrapolable to natural populations, provide an useful base to seek a better biological comprehension of *P. canaliculata*. Many factors potentially influence life-history traits of *P. canaliculata*, but the published information allows us to discuss only the proximal effects of some of them at the organismic level.

Growth, Survivorship and Reproduction, and their Dependence on Temperature

P. canaliculata distribution is basically tropical and subtropical, including the Amazonas and La Plata basins (Ihering, 1919); the southernmost record for the species –the southernmost apple snail in the world– is Paso de las Piedras reservoir (38° 24'S), south of the Buenos Aires province, Argentina (Martín *et al.*, 2001). Mean annual air temperature ranges from 25° to 14°C,
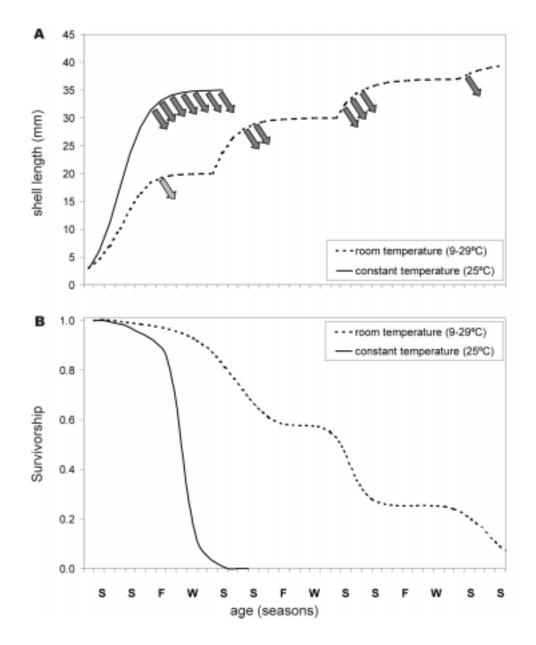
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with almost null seasonal thermal amplitudes at low latitudes and up to 18°C in southern Buenos Aires province.

Even without considering harmful or lethal effects (Cowie, in press), temperature has a striking influence on most aspects of *P. canaliculata* biology. In most of its natural geographical range growth is continuous but growth rates are highly dependent on temperature. In temperate climates seasonality imposes winter resting periods during which growth ceases almost completely (Fig. 1A, Estebenet and Cazzaniga, 1992) and crawling and feeding is null. In small streams they remain motionless under boulders or entangled in submersed plants, with their cephalopodium partially withdrawn, but quickly becoming active when taken out of water (pers. obs.). Some authors reported that *P. canaliculata* overwinters buried, surviving either in submersed substrata (Hylton-Scott, 1958; Bachmann, 1960; Martín, 1984) or in drained soil (Oya *et al*., 1987; Tanaka *et al*., 1999) but it is not known if this behavior is as easily interrupted. Growth is resumed when water temperature rises in spring (Fig. 1A; Estebenet and Cazzaniga, 1992), but this response depends of snail size: post-resting growth rates recorded for big sized snails (Estebenet and Cazzaniga, 1998; Albrecht *et al.*, 1999) are very much lower than for small ones (Tanaka *et al*., 1999).

FIGURE 1. Growth (**A**) and survivorship curves (**B**) of *P. canaliculata* cohorts reared under different temperature regimes (arrows: spawning).
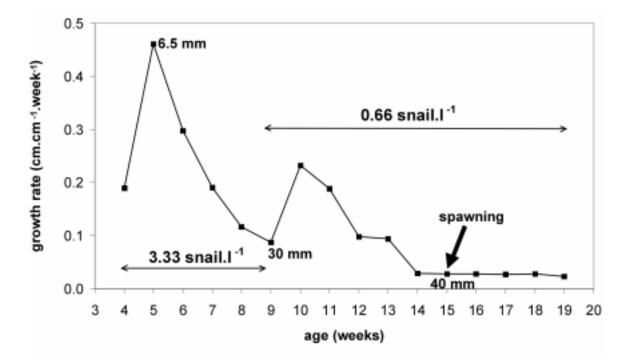
Most authors agree that a minimum size of *ca.* 25 mm is necessary for females to reproduce (Martín, 1986; Estebenet and Cazzaniga, 1992; Tanaka *et al.*, 1999), age at first oviposition being hence highly dependent on growth rate. Cohorts reared under permanent illumination, a condition promoting very fast growth (see below), attain maturity at 40 mm in only 107 days, the earliest recorded age for laboratory populations (Fig. 2; Estebenet and Martín, 2000). These results suggest that maturity depends not only on size but that a minimum development time is also required, though a direct effect of lack of photoperiod cannot be totally discarded.

Under uniform temperature conditions growth in length is continuous and constant till maturity (Fig. 1A), decreasing quickly down to zero afterwards (Estebenet and Cazzaniga, 1992, 1998). Such a decline is not due solely to mating and post-mating costs (sperm, eggs, spawning, etc.) since virgin, isolated snails also showed this decrease (Estebenet and Cazzaniga, 1998).

Egg-laying period extends from early spring to early fall in temperate climates (Hylton-Scott, 1958; Bachmann, 1960); snails born in fall must go through the winter to initiate growth and reach maturity, but those born in spring probably reach maturity during the same

reproductive season (Fig. 1A). Under suboptimal conditions (e.g. food scarcity or low temperatures) two or more cold seasons must be passed before reaching maturity (Estebenet and Cazzaniga, 1992).

Reproduction is continuous in tropical areas (Fig. 1A) and the duration of the reproductive period decreases with latitude to a minimum of six months in the southern limit of its natural distribution (Martín *et al.*, 2001). The temperature and not the photoperiod may be the critical factor causing the seasonal onset of copulatory and spawning activities in *P. canaliculata* in temperate regions (Albrecht *et al.*, 1999); reproductive intensity is positively related to the temperature increase in respect of winter levels, but absolute threshold temperatures for reproduction are not known.

Estebenet and Cazzaniga (1992) suggested that *P. canaliculata* is iteroparous (more than one reproductive period during lifespan) in temperate climate and semelparous (only one reproductive period) under more "tropical" conditions (Fig. 1B). Intrinsic mortality seems to be very low (from 0 to 20%) during the pre-reproductive or inter-reproductive periods (Estebenet and Cazzaniga, 1992, 1998), survivorship curves generally conforming to one or more Type I curves according to the temperature regime. Maximal longevity recorded

FIGURE 2. Specific growth rates of a cohort of *P. canaliculata* and the effect of an increase in water volume per snail (figures in mm are mean shell lengths).

under laboratory conditions was 49.5 months at room temperatures and 13.5 months under constant temperature of 25ºC, 72.5% of the snails surviving to this age under naturally fluctuating temperatures (Estebenet and Cazzaniga, 1992). Under high constant temperatures growth rates are higher, age at maturity and longevity are lower and reproduction is continuous, all life cycle events tending to concentrate in a shorter lifespan (Fig. 1A, B).

In spite of its overwhelming influence on most aspects of the biology of *P. canaliculata*, an hydrological discontinuity, not temperature, is probably the main factor impeding the spread of apple snails further South in Buenos Aires province (Martín *et al.*, 2001).

Reproduction and Sexually Dimorphic Life-History Traits

P. canaliculata are gonochoristic snails (Hylton-Scott, 1958; Andrews, 1964; Berthold, 1991) but the possibility that they change sex, showing protandric hermaphroditism, has been suggested (Keawjam and Upatham, 1990) but this was never reported for natural or laboratory populations of *P. canaliculata*. They show secondary sexual dimorphism in shell size, shape and weight (Cazzaniga, 1990; Estebenet, 1998).

In paired snails copulation occurs with higher frequency (2.9 copulation.wk^{-1}) than spawning (1.4 spawn.wk^{-1}, Albrecht *et al.,* 1996), though some females can spawn up to 3.7 times by week on average during their whole life (unpublished data). Copulation and spawning are very time-consuming activities: intercourses last 10-20 hours and males fast during them (Bachmann, 1960; Andrews, 1964; Albrecht *et al.,* 1996), while egg-laying takes up to five hours (pers. obs.). Egg-masses are aerial, pink and conspicuous, and are deposited well above the water-line, imposing an additional cost to females. Nocturnal oviposition behavior (Schnorbach, 1995; Albrecht *et al.,* 1996) probably lowers predation and desiccation risks. Recorded lifespan fecundities in laboratory range from 1,316 to 10,869 eggs per female (mean: 4,506), distributed in 8 to 57 egg masses (Martín and Estebenet, 2002; unpublished data). Females can store sperm for 140 days, laying up to 3,000 viable eggs along this period (Estebenet and Cazzaniga, 1993; Estebenet and Pizani, 1999); Albrecht *et al.* (1996) reported that winter resting females spawned fertilized eggs without intervening copulation when activated by an artificial temperature increase.

All the studied cohorts showed sexually dimorphic growth patterns: females grew invariably to be larger

than males (Estebenet and Cazzaniga, 1998; Tanaka *et al.*, 1999; Martín and Estebenet, 2002), in most cases owing to slightly higher growth rates and not to more extended growth periods. Biomass differences are more noteworthy, taking into account that females are heavier than males of the same total length (Estebenet, 1998).

Substantial variation in size dimorphism expression, probably genetic in origin, was observed (Estebenet and Martín, 2000). Different stock origin combined with different rearing conditions (light regime, see below) lead to an important variation in size and age at which dimorphism is expressed. For example, growth rates differences could appear long before attaining sexual maturity (at 10-15 mm, Estebenet and Martín, 2000), or after it (at 30 mm, Estebenet and Cazzaniga, 1998); on the other hand, in a laboratory trial both sexes reached the same size at the beginning of reproductive activity, but male growth ceased thereafter, while females grew during their whole lifetime. Sex related differences in growth rates showed considerable variation even among different egg-masses of the same population (Estebenet and Cazzaniga, 1998).

In several laboratory trials males of *P. canaliculata* showed slightly higher survivorship rates than females (Estebenet and Cazzaniga, 1998; Martín and Estebenet, 2002). The larger size attained by females in some natural populations (Martín, 1984; Estebenet and Cazzaniga, 1998) probably is not due to differential survivorship but to higher female growth rate.

In inter-population comparisons female survivorship seems to be negatively related to genetically fixed levels of reproductive effort (measured as weight or volume of eggs by week), and noteworthy, male survivorship showed the same inter-population pattern (Martín and Estebenet, 2002). Female growth is negatively related to spawning frequency (Albrecht *et al.*, 1999). Mate search and the long non-feeding periods associated with copulation seem responsible of male stunting at least in one population (Estebenet and Cazzaniga, 1998). These findings suggest that competition between somatic and reproductive allocation occurs and presumably this would also affect survivorship. However, high egg-laying frequency or high egg production not necessarily corresponds with high mating frequency (Estebenet and Cazzaniga, 1993; Albrecht *et al.*, 1996; Estebenet and Pizani, 1999).

P. canaliculata shows size assortative mating: in laboratory trials males prefer big females as mates but females don't show any size preference (Estebenet and Pizani, 1999). Female size is positively related to fecundity (Estebenet and Cazzaniga, 1992, 1993) and also

to egg size (unpublished data), so by choosing a big female males probably increase the number and quality of offspring obtained from each of the expensive intercourses. In contrast, irrespective of male size, sperm transferred after one insemination allows females to spawn repeatedly (unpublished data). Genetic studies on laboratory stocks by Fujio and von Brand (1990) suggest that hatchlings from each egg-mass are full-siblings, a result compatible with findings of higher inter- than intra-spawn variability in field-collected egg-masses (Cazzaniga and Estebenet, 1988; Estebenet and Cazzaniga, 1998) but incongruent with the higher frequency of copulation as compared to spawning observed by Albrecht *et al*., (1996); perhaps either the sperm of each new copulation replaces all the one stored previously or old ejaculates impede the utilization of the fresh one for fertilization.

Food and Feeding and their Effects on Growth and Fecundity

P. canaliculata are extremely polyphagous snails, feeding on vegetal, detrital and animal matter, and they also show quite flexible methods of food acquisition (Cazzaniga amd Estebenet, 1984; Cowie, in press). In contrast with most freshwater snails, they are primarily macrophytophagous, preferring floating or submersed plants over emergent ones (Bachmann, 1960; Bonetto and Tassara, 1987). Hatchlings deprived of food can fast during several days relying on endogenous reserves (Cheesman, 1958; pers. obs.), probably lipoproteins absorbed from the perivitelline fluid (Heras *et al*., 1998). Ontogenetic shifts in diet have been reported, young snails feeding on detritus and algae; they begin to attack higher plants when they reach 15 mm (Halwart, 1994; Schnorbach, 1995). However, laboratory trials showed that even hatchlings 2.5 mm long are capable of continuous feeding on lettuce and submersed macrophytes when other food sources are absent, and that food preference do not change with age (Estebenet, 1995; Estebenet and Cazzaniga, 1992, 1998).

P. canaliculata snails actively locate (through distant chemoreception) and select those freshwater macrophytes that promote faster growth when the snails are reared on monospecific diets, growth rates depending partially on the ingested macrophyte biomass (Estebenet, 1995). Under restricted feeding conditions growth of post-resting mature snails was almost null while the reproductive effort of females was significantly lower than those under *ad libitum* feeding (Albrecht *et al.,* 1999).

Lacanilao (1990) fed *P. canaliculata* with leaves of terrestrial and aquatic plants (alone or combined), detecting an effect on number and size of egg-masses, but it is not possible to discriminate from her results if it was due to differences either in quality or in palatability. Palatability can override quality in certain cases: e.g., *Elodea canadensis* was so unpalatable to *P. canaliculata* that snails famed and died (Estebenet, 1995) although this aquatic plant is consumed by other ampullariids (Seaman and Portfield, 1964; Cedeño-Leon and Thomas, 1982). On the other hand, the same diet can differentially affect growth and reproduction (Lacanilao, 1990), suggesting that both processes have different nutritional requirements.

Three different stocks reared under constant light (Estebenet and Martín, 2000; Martín and Estebenet, 2002) showed growth rates, from hatching to maturity, notably higher than those observed in a previous study with similar rearing conditions, but under natural photoperiod (Estebenet and Cazzaniga, 1998). As in both cases snails were fed with lettuce *ad libitum*, the most plausible explanation is a higher total daily consumption under constant light, probably due to an extension of the period of more intense feeding since *P. canaliculata* also feeds during night. Permanent illumination seems to be a breeding practice to consider in developing mass production techniques for *P. canaliculata*, despite Schnorbach´s (1995) claim about the need of a minimum dark period for oviposition. The effect of light on foraging must be considered when investigating the influence of photoperiod on growth and reproduction.

Effects of Density and Crowding on Life-History Traits

Tanaka *et al*. (1999) suggested that *P. canaliculata* population size in paddy fields may be regulated by density. With densities as low as two adult snails per square meter, growth, number of spawns and eggs per female were actually limited, probably due to low food availability. The proportion of juveniles that potentially survives the winter is negatively related to density. However, nothing is known about populations in non-managed aquatic systems.

In laboratory trials, even with food *ad libitum*, detrimental effects of density (number of snails by volume) on growth, spawning and survivorship are common (Cazzaniga and Estebenet, 1988; Lacanilao, 1988, 1990). Feeding interference between individuals may in part explain these effects (pers. obs.), but the accumulation of inhibitory substances has also significance (Lacanilao, 1988; Schnorbach, 1995).

In trials at constant density, specific growth rates decrease asymptotically with age (Fig. 2). This is partially attributable to endogenous factors, but the increase in snail concentration (snail biomass per liter) during the rearing period has also significance, since specific growth rates peak abruptly when water volume per snail is increased (Fig. 2). These results show that crowding effects on growth are reversible, even in 30 mm long, though immature, snails (Estebenet and Martín, 2000).

Crowding effects must be considered when comparing inter-study results and for designing experiments. For example, in an experiment designed to evaluate the influence of repetitive mating on oviposition, females isolated after mating in 3 l aquaria grew significantly more than females maintained with a male in 3 l aquaria, though total egg production was the same (Estebenet and Pizani, 1999). Isolated females showed hence a higher net production than coupled females, attributable to the energetic saving of copulatory costs or lower crowding effects. The effects of doubled density and those related to the repetitive mating cannot be discriminated. So, even at densities usually considered optimal for experimental rearing (Schnorbach, 1995; Estebenet and Cazzaniga, 1998) detrimental effects could appear.

Perspectives

The information reviewed in this paper not only highlights the great plasticity of *P. canaliculata* to endogenous and exogenous factors but also warns on the necessity of heeding them when developing experimental and sampling designs or making inter-study comparisons. Factors usually not considered such as illumination, genetic variation, rearing density, sexual dimorphism, sex ratio, etc. may bias results and conclusions. In addition to the artifacts produced by rearing conditions, the long-term effects of inbreeding in laboratory stocks of *P. canaliculata* (Fujio *et al.*, 1997) must be considered.

We are just beginning to understand *P. canaliculata* biology at the organismic level and descriptive and experimental field studies are badly needed. For example, in spite of its pest status and its potential use as an aquatic weed control agent, we don't know any quantitative study on trophic niches in natural habitats. The lack of data at supraorganismic levels is even greater. Population dynamics, regulating mechanisms and the snails' role in aquatic systems are all unknown. An environmentally sound solution to the problem of *P. canaliculata* as an invader requires an integrated and rational population management, that will not be achieved until the basic aspects of its ecology are investigated.

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