CHANGES IN GAPE FREQUENCY, SIPHON ACTIVITY AND THERMAL RESPONSE IN THE FRESHWATER BIVALVES *ANODONTA CYGNEA* AND *MARGARITIFERA FALCATA*

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ABSTRACT

Physiologically-driven rhythms in bivalve molluscs are predicted to vary as a function of metabolic rate and temperature, in contrast to genetically predisposed biological clocks. These rhythms can be evaluated using long-term video monitoring techniques under controlled conditions in laboratory aquaria. The bivalves *Anodonta cygnea* and *Margaritifera falcata* were used to evaluate the effect of temperature on rhythms in gape and the formation of siphons at the mantle edge. Frequency and duration of shell closure vary with temperature in both species, but with different responses. Mean duration of intervals of valve closure decreases as temperature rises in both species, and is consistent with physiological limitation by increased biological oxygen demand. For *A. cygnea*, cumulative gape duration peaks at 25°C, with less time spent closed than at any other temperature, but increasing temperatures correspond to an increase in gape frequency with a strong increase observed at 31°C. In contrast, frequency of adduction and valve closure peak at 25°C in *M. falcata*, and continuous gaping is observed above 29.5°C. This physiological stress is consistent with evidence from sclerochronologically-calibrated stable isotope studies of shells, where growth breaks in many marine taxa coincide with maximum temperatures above 31°C as derived for $\delta^{18}O_{carbonate}$. The results of this study suggest that these growth breaks may be due to physiological limitations in oxygen uptake and metabolic activity, rather than being a direct consequence of elevated temperature alone.

INTRODUCTION

Biological rhythms have been documented in bivalve molluscs for decades, and their timing and significance remains a topic of great interest. Early studies of circadian rhythms (24-h insolation cycles matching the period of Earth's rotation) emphasized entrainment of activity by daily light variations (e.g. Pannella & MacClintock, 1968; Rhoads & Pannella, 1970). In many marine species, however, circalunidian cycles (rhythms synchronized with the lunar daily period of 24.8 h) often play a dominant role (e.g. Evans, 1972, 1975; Pannella, 1976; Richardson, 1988; Palmer, 1995). Both endogenous (e.g. Beentjes & Williams, 1985; Abell, Amegashitsi, & Ochumba, 1995) and environmentally entrained rhythms have been observed, and some bivalves have been demonstrated to switch between circalunidian and circadian rhythms when transferred to controlled conditions (Kim *et al*., 2003). In the case of circalunidian clocks, two separate clocks appear to operate, coupled in antiphase with periods of ca. 12.4 h under normal conditions but decoupling in the laboratory (Palmer & Williams, 1986). In contrast to circadian and circalunidian rhythms, however, the influence of environmental factors on periodicities at ultradian (subdaily, infradian, intra-daily) time-scales with durations shorter than 24 h have yet to be fully evaluated.

Studies at this resolution, including measurements of gape periodicity, feeding and heart rates, are generally invasive in nature. They frequently require that the studied organism be affixed with one or more sensors and often wired to recording equipment, and are only suitable for relatively passive organisms that move infrequently. Many bivalve molluscs are ideal for such studies, and their biorhythms have been evaluated by techniques as diverses as actographs (Akberali, 1978; Kontreczky *et al*., 1997), electrodes (Englund, Heino & Melas, 1994), inductive proximity sensors (Miller & Payne, 1999), magnetic relays (Garcia-March *et al*., 2008) or electromagnetic coils and infrared optocouplers (Curtis, Williamson & Depledge, 2000). Particularly invasive studies have even required that sensors be inserted into the mantle cavity through holes drilled through the shell (e.g. Trueman & Lowe, 1971; Gordon & Carriker, 1978). However, while these techniques provide data regarding shell gape or cardiac activity, they provide no insight on siphonal activity. Beyond the problems inherent in affixing sensors, complications arise when experimental animals are studied without provision for food (e.g. Kontreczky *et al*., 1997; Moura *et al*., 2000; Curtis *et al*., 2000). In order to minimize the experimental impact of observation, modern workers are increasingly pursuing non-invasive video monitoring techniques both in short-term field deployments and in longer term laboratory studies (e.g. Thorin, Bourdages & Vincent, 1998; Thorin, 2000; Newell, Wildish & MacDonald, 2001; Riisgård, Kittner & Seerup, 2003; Rodland *et al*., 2006). While limitations remain for either setting, video techniques provide an avenue to control for potential experimental effects in more invasive studies.

One major difficulty in understanding the periodicity of behaviour, growth and activity lies in discriminating

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