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Environmental influence on activity levels and behavioural allocation in the polychaete *Nereis virens* (Sars)

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Abstract

Influence of environmental factors such as temperature, food, and photoperiod on activity levels and behavioural allocation of *Nereis virens* was examined using laboratory experimental essays. Animals were subjected to 4 temperatures (1, 6, 13, and 18 °C), two food concentrations (low and abundant), and two photoperiod regimes (6 and 12 h of daylight) for 10-day periods. A general linear model was used to evaluate how these three factors and their possible interactions affected relative activity levels. Furthermore, a log-ratio redundancy analysis was used to examine the relationship between behavioural allocation and environmental factors. Activity levels increased with temperature and food abundance. Extreme cold induced quiescence, yet the polychaetes retained their ability to react to food stimuli, especially at higher food abundances. Food abundance explained the greatest amount of variation in behavioural allocation. However, its effect varied with temperature. Feeding predominated under low food conditions, whereas storage (accumulation of organic matter in their burrows) predominated under abundant food conditions, especially at higher temperatures. Animals seemed to anticipate food shortage, which is often synchronised by temperature in a natural environment. The potential for carbon sequestration resulting from food storage is therefore present and may be controlled by these same exogenous factors that usually characterise seasonal variations.

Keywords: Activity level; Behavioural allocation; Food abundance; Hoarding; *Nereis virens*; Photoperiod; Quiescence; Temperature

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1. Introduction

Polychaete behaviour has been widely studied, from their feeding habits (Hylleberg, 1975; Olivier et al., 1993) to their learning abilities (Evans, 1966a,b), diel activity cycle (Last and Olive, 1999), and spawning behaviour (Beckmann et al., 1995; Williams et al., 1997). Evans (1971) underlined the importance of these and other behavioural signals in the survival of many polychaete species. Since then, efforts have been made to better understand the relationship between polychaete behaviour, metabolism, and environment, as many behavioural patterns are controlled or influenced by environmental cues. Three of the most commonly studied environmental cues are temperature, photoperiod, and food abundance.

Temperature has been shown to affect life history attributes (Fong, 1991; Olive et al., 1997), resource allocation (Neuhoff, 1979; Qiu and Qian, 1998; Olive et al., 1998), feeding habits (Yokoyama, 1988; Lambert et al., 1992), and ventilation (Kristensen, 1983b) in polychaetes. For example, low temperatures inhibit feeding in *Paraprionospio* sp. (Yokoyama, 1988) and foraging in *Nereis diversicolor* (Lambert et al., 1992), whereas ventilation and respiration are modulated by temperature in *Nereis virens*, *N. succinea*, and *N. diversicolor* (Kristensen, 1983a). Because temperature regulates the metabolic processes underlying behaviour in ectotherms (Newell and Branch, 1980), it is not surprising that this environmental cue is so important.

Temperature is often considered in combination with salinity or photoperiod. The latter is deemed responsible for resource allocation, maturation, and reproduction of many polychaete species, particularly nereids (Olive et al., 1997; Rees and Olive, 1999; Last and Olive, 1999). Some behavioural processes may therefore follow a seasonal cycle synchronised by exogenous factors. While photoperiod is mostly related to seasonal variations in day length, it has also been shown that some polychaetes have a diel activity rhythm, such as *N. virens* which has nightly activity peaks (Miron et al., 1992a; Last and Olive, 1999).

While it is known that temperature and photoperiod each affect behaviour, the combined effects of temperature, photoperiod, and food abundance or their possible interactions on polychaetes remain largely unexplored. Yet, food abundance influences metabolic processes such as growth (Scaps et al., 1993; Nielsen et al., 1995) and reproduction (Linton and Taghon, 2000a,b). Moreover, feeding behaviour may be naturally regulated by food availability and abundance in intertidal organisms. For example, *N. diversicolor* is known to actively feed at high tide (Esselink and Zwarts, 1989; Masson et al., 1995) when food is abundant and, most importantly, available (Roman and Daiber, 1989). This paper examines the influence of temperature, photoperiod, and food abundance on the behavioural allocation patterns and activity levels of *N. virens*.

Among polychaetes inhabiting the shores of the St. Lawrence River, *N. virens* is a common species in the boreo-atlantic *Macoma balthica* community (Desrosiers and Brêthes, 1984). It plays an important role in this community as it regulates infaunal benthic populations (Commito and Shrader, 1985; Ambrose, 1986) and represents food for many shore birds and benthic fish (Michaud and Ferron, 1990; Vaillancourt, 1982). Although adults of this omnivorous species are predators, juveniles feed mostly on organic matter (Desrosiers et al., 1994). However, food is exported from the shores and into the subtidal zone by ebb tides and imported by flood tides (Roman and Daiber, 1989). Therefore, food is available for only short periods every day, especially since *N. virens* are more active at night (Miron et al., 1992a). Hence, *N. virens* may avoid temporary food shortage by accumulating organic matter in their burrows (Olivier et al., 1995).

Although the accumulation of organic matter in sediments may result in sequestered organic carbon, this storage behaviour remains largely unexamined. Therefore, it is essential to understand the underlying processes that modulate this behaviour pattern, before assessing its impact on carbon sequestration. More specifically, objectives were to examine the relationship between storage frequency and other behaviours, as well as the link between temperature, photoperiod, and food abundance on behavioural allocation with respect to storage. Because this behaviour is part of a response pattern to food stimuli, all behaviours will be investigated as such.