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Regeneration of lost siphon tissues in the tellinacean bivalve *Nuttallia olivacea*

Takeshi Tomiyama *, Kinuko Ito

Graduate School of Agricultural Science, Tohoku University, Aoba-ku, Sendai 981-8555, Japan

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Abstract

The inhalant siphon of the tellinacean bivalve *Nuttallia olivacea* is an important prey item for juvenile stone flounder *Platichthys bicoloratus* in estuaries in Japan. We examined quantitative siphon regeneration of *N. olivacea* in rearing experiments of siphon-removed bivalves (> 30 mm shell length) both in the laboratory and in their natural habitat. Under laboratory conditions, siphon-removed bivalves regenerated lost tissues quantitatively at 15 and 25 °C 1 mo after siphon removal, although regeneration was incomplete. A 3-mo caging experiment in the field showed that great regeneration occurred in siphon-removed bivalves. However, the siphon weight of removed bivalves was significantly smaller than that of non-amputated bivalves, suggesting the incomplete regeneration. In a 1-mo caging experiment, bivalves that had approximately 15% of their siphons amputated were selected at some intervals to illustrate the quantitative regeneration process. Estimated daily siphon production was remarkably high only a few days after amputation. It decreased greatly thereafter, but regeneration was not completed within 30 d. These results indicate that bivalves regenerate siphons rapidly just after losing siphon tissues and then regeneration is slowed down before it is completed.

Keywords: Caging experiment; *Nuttallia olivacea*; Quantitative regeneration; Tellinacean bivalve

1. Introduction

Predation on tissues of benthic invertebrates, such as bivalve siphons, polychaete palps and brittlestar arms, is common in marine environments (de Vlas, 1979; Woodin, 1982; Bowmer and Keegan, 1983; Zajac, 1985, Duineveld and Van Noort, 1986; Lindsay and Woodin, 1992, 1995; Pape-Lindstrom et al., 1997); it is sublethal because these tissues are regenerable in most cases (e.g. Pekkarinen, 1984; Zajac, 1985; Stancyk et al., 1994). Such animals' continual tissue loss and regeneration usually serve an important function in food webs by providing a renewable food source for predators.

Tellinacean bivalves possess long siphons to bury themselves deeply. The tip of siphons is often cropped by juvenile flatfishes and crustaceans in tidal flats and shallow coastal waters (Edwards and Steele, 1968; de Vlas, 1979; Peterson and Quammen, 1982; Poxton et al., 1983; Ansell and Gibson, 1990; Bonsdorff et al., 1995). The siphon regeneration process is an essential aspect of bivalve siphon productivity. Past studies have specifically addressed the duration to completion of bivalve's siphon regeneration or the extent to which they can regenerate during a period of time. Trevallion (1971) estimated that *Tellina tenuis* regenerate siphons at 0.3 mg wk^{-1} in dry weight; Hodgson (1982a) estimated the siphon regeneration capability of

* Corresponding author. Present address: Fukushima Prefectural Fisheries Experimental Station, Onahama, Iwaki 970-0316, Japan. Tel.: +81 246 54 3153; fax: +81 246 54 9099.

E-mail address: tomiyama_takeshi_01@pref.fukushima.jp (T. Tomiyama).

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Scrobicularia plana and *Donax serra* at 20% wk^{-1} of initial siphon weight. Furthermore, de Vlas (1985) calculated the daily change in siphon weight through an in vitro siphon-amputation experiment using *Macoma balthica*. However, the regeneration rate of the siphon increased when siphons were amputated repeatedly (de Vlas, 1981, 1985). This finding indicates that the regeneration rate is variable. It is important to reveal why bivalves change the regeneration rate, and what factors, other than the number of cropping incidents, affect the regeneration rates and amounts.

This study is intended to examine quantitative regeneration of lost siphon tissues under laboratory and field conditions and to confirm flexibility in regeneration. We used the tellinacean bivalve *Nuttallia olivacea*, which is predominant in estuarine tidal sandy areas in Japan, as a model organism. This species buries itself to a depth of approximately 15 cm and extends its siphon to the sediment surface. Their inhalant siphons are one of the most important prey items in the diet for juvenile stone flounder *Platichthys bicoloratus* (Tomiyama et al., 2005). Juvenile stone flounder utilize estuaries as important nursery grounds (Malloy et al., 1996; Yamashita et al., 2000, 2003) and exert high predation pressure on *N. olivacea* siphons from April to May when juveniles are abundant (Sasaki et al., 2002; Tomiyama et al., 2004, 2005). Therefore, regeneration process of *N. olivacea* siphons should be determined to evaluate the food productivity for juvenile stone flounder.

We conducted three experiments. Initially, we carried out a laboratory experiment in which siphon-amputated bivalves were reared for 1 mo at three different temperatures to evaluate the interaction of temperature with siphon regeneration. We also carried out two field caging experiments in natural conditions. In a field experiment, siphon-amputated bivalves were deployed into their natural habitat and collected after 3 mo to examine the extent to which they regenerated their siphons. In the other field experiment, we collected siphon-amputated bivalves at some intervals to evaluate temporal changes in the rate of siphon regeneration. These experiments also examined soft tissue weights to test whether or not siphon loss impacts somatic tissues, as is observed in other species (Hodgson, 1982a; Kamermans and Huitema, 1994; Bonsdorff et al., 1995).

2. Materials and methods

2.1. Bivalve collection

Bivalve collections and field experiments were carried out at an estuarine tidal sandy area located approximately 1.5 km up-river from the mouth of the Natori River in northern Japan (38° 11′ N, 140° 57′ E) where *N. olivacea* is common but juvenile stone flounder are not abundant; it was at the same location as station B in Sasaki et al. (2002). The maximum tidal range is approximately 1.5 m. Annual water temperature ranges from 5 to 27 °C there. Salinity shows tidal fluctuations between 1 and 30 PSU. The substratum is fine sand, with a silt–clay content < 1% (Ito et al., 2001). This site is appropriate for field experiments on siphon regeneration because predation pressure on siphons is relatively low (Sasaki et al., 2002).

Bivalves for the laboratory and field experiments were collected with spades in November 1999 and in May and June 2000, respectively. When preparing the experiments, bivalves whose siphons lacked tentacles were excluded from the experiments. *N. olivacea* grows up to 50 mm shell length (SL). To minimize effects of size variation and growth of bivalves, large bivalves > 30 mm SL were chosen.

2.2. Laboratory experiment

All 105 bivalves were brought to the laboratory and placed in three aerated aquaria of 44 × 28 × 30 cm (length × width × height) with a 10-cm layer of sand covered by 10 cm of 20 PSU water. To allow complete recovery of their siphons, the bivalves were reared at a laboratory temperature of approximately 5–10 °C and fed diatoms once or twice a day. After 2 mo, all bivalves were transferred to two aquaria of 30 × 15 cm (diameter × height) with a 5 cm layer of brackish water for siphon-amputation. The naturally extended inhalant siphons of 51 bivalves were removed to the greatest possible extent with tweezers. These 51 'Removed' bivalves and 31 'Control' individuals (intact siphons) were contained individually in numbered 1-L beakers with a 5 cm layer of sand covered by 5 cm of 20 PSU water, but one Removed individual failed to burrow and was omitted from the experiment. Other bivalves buried themselves within 4 d (mostly within 1 h) after placement in the beakers. The remaining 23 bivalves were analyzed to determine the intact siphon weight at the beginning of the experiment.

Bivalves were divided into three groups; each consisting of approximately 17 Removed bivalves and 10 Control individuals as replicates. They were transferred to three experimental rooms with respective controlled temperatures of 5, 15 and 25 °C, determined from the range of annual temperatures in the field. Water in each beaker was exchanged twice a week. Bivalves were fed 5 ml of the diatom *Cylindrotheca closterium* (1,000,000 cells ml^{-1}, approximately 0.001 mg ml^{-1} in chl. *a*) three times per day; the diatoms had been