Burrowing in the Antarctic anemone, *Halcampoides* sp., from Signy Island, Antarctica

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Abstract

Antarctic anemones of the genus *Halcampoides* inhabit low intertidal and shallow subtidal zones. They readily burrow into soft sediments following disturbance. The process of re-burying was recorded using time-lapse video in the aquarium of the British Antarctic Survey with specimens of a species collected from the shallow sublittoral (\(<1\) m depth) at Signy Island. Penetration of the sediment takes place by a similar mechanism to that employed by burrowing anemones such as *Peachia hastata* from lower latitudes. Penetration initially is brought about by peristaltic contractions that involve only the modified base, or physa. Later, as the column becomes buried, the peristaltic contractions start in the upper part of the scapus and pass down the column before extending the physa. At this stage penetration is aided by contractions of the longitudinal muscles that draw the column down into the sediment. At 0°C the frequency of initiation of peristaltic contractions down the column, and of contractions of the longitudinal muscles are on average >1.6 and >4.0 times slower, respectively, compared with those of *Peachia hastata* from Scotland, recorded at \(\sim11\text{°}-14\text{°}C\). \(Q_{10}\) values calculated from these data are in the range 1.4–3.0, and thus provide little evidence supporting any evolutionary acclimation of the processes involved in burrowing has occurred in *Halcampoides* from the Antarctic, although the data are limited. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Antarctic; Anemone; *Halcampoides*; Disturbance; Burrowing; Peristalsis; Adaptation

1. Introduction

Polar benthic ectotherms are characterised by generally slowed ecological and physiological processes (Peck, 2000). These include growth and development rate (Clarke, 1983, 1991; Pearse et al., 1991; Peck and Robinson, 1994; Peck et al., 1997), colonisation (Barnes et al., 1996; Stanwell-Smith and Barnes, 1997) and reproductive output (Clarke, 1993). However, perhaps the most studied physiological attribute is...
metabolism. Over the last 10–20 years many investigations have found low or very low metabolic rates in Antarctic benthic species (Clarke, 1991; Chapelle et al., 1994; Johnston et al., 1991a; Luxmoore, 1984; Peck, 1989). Although a small number of studies have reported higher than expected metabolic rates (e.g. Wells, 1987) the general condition is one of no measurable compensation of metabolism for low temperature at the whole animal level (Clarke and Johnston, 1999; Peck and Conway, 2000). Recent work showing high enzyme activity levels in Antarctic fish (Somero et al., 1998) and increased numbers of mitochondria in muscles (Johnston et al., 1998) would also suggest that some elevation of metabolism must be present, albeit below measurable levels at the whole organism level (Peck, 2000). Investigations of factors raising metabolism have mainly centred around temperature and feeding, and both have been shown to elicit relatively small responses in polar species (Davenport, 1989; Peck, 1989, 1998; Johnston and Battram, 1993; Portner et al., 1999).

Direct measurements of activity in polar ectotherms are rare, and are predominantly reported for fish, where maximum sustainable speeds are within the range reported for temperate species, but burst swimming performance is reduced (Van Dijk et al., 1998; Johnston et al., 1991b). Data are scarce in invertebrates. Davenport (1989) measured ventilation rates in *Yoldia eightsi* (Couthouy), but did not compare them with rates for temperate species. Buchan et al. (1988) found heartbeat rates of around 12 min⁻¹ for the limpet *Nacella concinna* (Strebel) and 0.8 min⁻¹ for the brachiopod *Liothyrella uva* (Broderip), both at 0°C. Recently adduction frequency during swimming by Antarctic scallops *Adamussium colbecki* (Smith) has been found to be lower than for temperate species (Ansell et al., 1998), and normal locomotory speeds in the limpet *Nacella concinna* have been found to be 8–15 mm min⁻¹ (Palmer, pers. commun.). Maximum speeds were 20–60 mm min⁻¹ which compared to 26–223 mm min⁻¹ in a range of temperate limpets (Branch and Marsh, 1978).

Here we present the first data on burrowing activity in the anemone *Halcampoides* using time-lapse video. These are the first reported measures of burrowing activity in any infaunal species from Antarctica. *Halcampoides* sp. is a small species usually around 30 mm in body length. It lives at the low end of the intertidal range and upper parts of the shallow subtidal zone. At Signy Island it inhabits an area of runoff from an inlet produced by the retreat of the Orwell Glacier, and is found near the base of large stones and boulders in sediment of varying grade. Its crown of tentacles is laid close to the sediment surface, where it feeds by the capture of small particles. Salinities at this site varied from 34 ssu at high tide to <10 ssu at low tide when the locality was dominated by meltwater runoff. It occurred at densities of up to 45 m⁻², which is much lower than that recorded for the other more common burrowing Antarctic anemone *Edwardsia meridionalis* which occurs at densities of up to 2300 m⁻² at McMurdo Sound (Williams, 1981).

2. Material and methods

*Halcampoides* sp. (relaxed column diameter range = 3–9 mm) were collected by hand at extreme low water level of spring tides. The species used was up to a maximum of 70 mm long, with a crown of 12 tentacles and was living tightly grouped around the base of
small rocks. About 30 individuals were returned to the United Kingdom in aquaria aboard the RV Bransfield and transferred to the aquarium at British Antarctic Survey, Cambridge. The seawater temperature at Signy at the time of collection was \(\sim 0.5^\circ\text{C}\), and the anemones were kept at \(\sim 0^\circ\text{C}\) on board ship and subsequently in the aquarium. They were transported back to the UK in sediment from their site of collection, and were maintained in a tank with the same sediment. Specimens were not directly fed but were regularly observed producing tentacle movements indicative of feeding, and it was assumed they were taking microinvertebrates and meiofauna. After collection in Antarctica over 95% of the collected anemones reburied within 24 h. On transfer to a new tank in the United Kingdom again over 95% reburied within 24 h. Only those anemones which had burrowed into the sand in the aquarium tanks were used when recording activity. The *Halcampoides*, once buried in the sediment, remained with the disk and tentacles level with the sand surface, with the column contained in a mucus-lined tube within the sand. After use in experiments specimens were returned to the holding aquarium system. Mortalities over the following year were less than 5% and specimens removed from sediment reburied within 24 h after this time. All specimens remaining after 1 year were still thriving in the holding aquarium 2 years after burrowing experiments, and a sample of ten removed from sediment reburied within 24 h. For video recording experiments anemones were placed in a tank containing medium to fine sand (grain size 0.2–0.3 mm), and recordings made within 1 month of their arrival in UK.

Recordings of burrowing behaviour were made by means of time-lapse video. Animals were removed from the aquarium holding tank and placed on the surface of sand in a glass-sided aquarium tank with aerated seawater at \(0^\circ\text{C}\). A Vista NCD370 CCD video camera was mounted alongside the tank and recordings were made continuously using a Panasonic AG6124HB 24 h time-lapse video recorder in 24-h mode. Generally, a number of *Halcampoides* (maximum six) were placed in the field of view of the video camera and allowed to burrow unimpeded by any restraint, but for more detailed observations the camera was moved closer to record the movements of a single *Halcampoides* only. All the individuals used burrowed readily, although with some variation in success.

Analysis of the resulting video recordings was carried out using an analysis video recorder (JVCBR-S610E) that allowed tape replay at variable speeds as well as freeze frame. In particular, measurements were made of the frequency of (a) the peristaltic movements in the physa, and later in the column and (b) the retractions of the longitudinal muscles of the column. Recordings of all the anemones used were examined to define the processes involved in burrowing, but only those recordings that showed the movements involved most clearly were analysed quantitatively. For these, the maximum and minimum widths of the column during the passage of a peristaltic wave were also measured from the video recordings as an indication of the size of the anemone involved.

3. Results

3.1. The mechanism of burrowing

At the start of burrowing, the body of the anemone becomes curved downward so that
the base of the column, the physa, presses directly down onto the sediment (Fig. 1). The physa is everted and expanded and a series of peristaltic contractions starting in the lower part of the column passes down the physa which, as a result, gradually penetrates the sediment. As penetration proceeds, the peristaltic contractions affect a progressively greater length of the column, until each new peristaltic wave eventually starts in the upper region of the scapus. Initially only one wave of peristaltic contraction is apparent

![Figure 1](image_url)

Fig. 1. Frames from time-lapse video of *Halcampoides* sp. burrowing into sand. (A) Initial phase of burrowing with a single peristaltic contraction (arrow) visible on the expanded physa (p); (B and C) later stages in which the physa and part of the column have penetrated the sediment and a collar of sand (s) passes up the anemone probably by means of ciliary action; (C) a single peristaltic contraction (arrow) is visible on the column; (D) later stage with the column almost buried and a single peristaltic contraction visible on the column.
on the column at any time; later new contractions are initiated as a previous wave travels down the column. Maximum contraction of the circular muscles during peristalsis results in the diameter of the column being reduced to \( \sim 50\% \) of the relaxed diameter (Table 1).

During the initial stages of burrowing, gentle penetration of the sediment is achieved by the probing action of the tip of the physa alone brought about by the peristaltic contractions. This is aided by the movement of sediment for a short distance up the side of the column, presumably caused by ciliary action and involving some secretion of mucus. At later stages, when penetration is sufficient for the physa to form an anchorage in the sediment by dilation (physal anchor: Ansell and Trueman, 1968), penetration is also aided by periodic contraction of the longitudinal muscles of the column, which assists in drawing the column down into the sediment. Expansion of the column to form a ‘column anchor’ (Ansell and Trueman, 1968) then aids further penetration of the physa. These movements are repeated over a long period, in some \textit{Halocamoides} for > 24 h.

3.2. Frequency of peristalsis and retraction

The frequency at which new waves of peristaltic contraction are initiated was measured by timing the intervals between equivalent phases of peristalsis in that part of the column that remained above the sediment surface. The first peristaltic waves, which affected only the physa, were initiated at intervals of 4.1–5.6 min (Table 1). As penetration proceeded and more of the column became involved, the period between the initiation of peristaltic waves decreased so that, during the main period of penetration, new waves were initiated in the column at between 2.8 and 4.0 min intervals (Table 1). At all stages, the rate of progression of the peristaltic wave down the column was so slow as to be barely perceptible without the benefit of time-lapse video recording and fast replay. Major contraction of the longitudinal muscles (retraction) began when some one third of the column was buried and these then occurred at somewhat irregular intervals, interspersed with waves of peristalsis. The intervals between retractions ranged from 15.8 to 34.3 min (Table 1). The mean numbers of peristaltic waves that occurred between retractions ranged from 5.7 to 9.8. Both the interval between initiation of consecutive peristaltic waves and the interval between retractions increased in larger anemones (Fig. 2). The time taken to reach complete burial was variable (Table 1). There was a trend for increasing time to complete burial with increasing anemone size (Fig. 3), but the relationship was marginally non significant. Errors may have been increased by variability in tendency to burrow, and individual \textit{Halocamoides} frequently re-emerged partially before completing burial. Animals reemerging were excluded from the analysis. The angle of entry into the sediment may also affect burial time; two individuals that burrowed obliquely showed the shortest time for complete burial.

4. Discussion

In most respects the mechanism of burrowing in \textit{Halocamoides} sp. resembles closely that of the only other burrowing anemone, \textit{Peachia hastata} Gosse, for which the process
Table 1
Summary of data for burrowing characteristics of *Halcampoides* sp. and comparison with the temperate burrowing species *Peachia hastata* (Ansell and Trueman 1968) and, for peristalsis intervals with the temperate epifaunal species *Metridium senile* (Batham and Pantin, 1950a, 1950b, 1953)*

<table>
<thead>
<tr>
<th>Animal sp.</th>
<th>Animal Width (mm)</th>
<th>Peristalsis interval (min)</th>
<th>Retraction interval (min)</th>
<th>Peristaltic waves/retraction</th>
<th>Time to complete burial (min)</th>
</tr>
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<tr>
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<td>Relaxed</td>
<td>Contracted</td>
<td>Physa</td>
<td>Column</td>
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<td>2</td>
<td>6.3</td>
<td>2.7</td>
<td>4.4 (0.6)</td>
<td>3.0 (0.5)</td>
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<td></td>
<td>3</td>
<td>7.6</td>
<td>3.6</td>
<td>5.0 (0.5)</td>
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<tr>
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<td>4</td>
<td>6.4</td>
<td>3.7</td>
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<td></td>
<td>5</td>
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<td>4.7 (0.6)</td>
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<td>B</td>
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<td>n = 10</td>
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<td>n = 10</td>
<td>n = 10</td>
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</table>

*P. hastata* from Ansell and Trueman (1968) (A) Fig. 3, initial stages of burrowing; (B) Fig. 4A–C, initial and end stages of burrowing. *M. senile* (A) from Batham and Pantin (1950a) Fig. 7, contractions of circular muscles; (B) from Batham and Pantin (1950b) Fig. 1, spontaneous activity of column (average for 10 contractions); (C) from Batham and Pantin (1950b) Fig. 2, peristalsis initiated following parietal muscle contraction; (D) from Batham and Pantin (1953) Fig. 10, spontaneous activity recorded from pedal area of experimental preparation (average for 12 contractions). Intervals are given as means and (standard deviations).
Fig. 2. Intervals between the initiation of (A) contractions of the longitudinal muscles (retraction interval, RI) for different sized Halcampoides sp. (RI = 2.01 ± 3.37 column width; $r^2 = 0.50$, $F = 7.95$, $P = 0.030$, $n = 8$) and (B) new waves of peristaltic contraction (peristaltic contraction interval, PCI = 1.53 ± 0.24 column width; $r^2 = 0.69$, $F = 19.08$, $P = 0.003$, $n = 8$).
Fig. 3. Time to complete burial for different sized Halcampoides sp. Burial time (BT) tends to increase with size. The best fit to the data was a logarithmic relationship ($\ln BT = 3.11 + 1.56 \ln \text{column width}; r^2 = 0.39, F = 5.02, P = 0.055, n = 9$).

has been closely observed and recorded (Ansell and Trueman, 1968). As in Peachia, burrowing in Halcampoides sp. comprises four stages: (1) probing downwards by the base of the column, with initial penetration into the sediment being obtained by successive eversions of the physa; (2) when part of the column is buried, dilation of the physa forms an anchor which allows the animal to pull itself down into the sediment by contraction of the longitudinal muscles; (3) elongation, accompanied by eversion of the physa on relaxation of the longitudinal muscles, achieving further penetration; and (4) repetition of the second and third stages until burial is complete. As in Peachia, penetration is aided by the successive application of a ‘column anchor’ and the ‘physal anchor’ (Ansell and Trueman, 1968) with the former partly dependent for its strength on adhesive properties of the ectoderm of the scapus and/or mucus secretion, and the latter on hydrostatic pressure.

Burrowing in Halcampoides sp. at 0°C takes place very slowly and the peristaltic movements involved are particularly slow. In their classical work on movement of the anemone Metridium senile over its rock substratum, Batham and Pantin (1950a,b, 1953) comment on the extreme slowness of peristaltic contraction although they give little quantitative data. Their published figures suggest intervals between the initiation of new peristaltic waves in the column, associated with movement but not with burrowing, of 2.8–14.7 min under natural and experimental conditions, i.e. of the same order as those recorded here for Halcampoides (Table 1) although at a higher temperature.

In the initial stages of burrowing, the mechanism in Halcampoides sp. appears to differ slightly from that of Peachia hastata in that, in the former, the peristaltic wave
affects only the inflated physa, while in the latter the peristaltic wave affects most of the column as well as the physa. Where the two species differ most markedly, however, is in the frequency of initiation of peristaltic contractions, and of retractions during burrowing. Although Ansell and Trueman (1968) provided little quantitative data, from their figures it can be seen that, during the early stages of burrowing, peristaltic contractions follow at \( \sim 1.6 \) min intervals (their Figs. 3 and 4) with this interval extending to 3–3.5 min towards the end of burrowing (their Fig. 4). Retractions follow each other at 5–6 min intervals initially, extending to \( \sim 9.5 \) min intervals near the cessation of burrowing. Comparable intervals for the slightly smaller *Halcampoides* range, for peristaltic contractions, from 4.1 to 5.6 min initially to 2.8–4.0 min later in burrowing and, for retractions, from 15.8 to 34.3 min (Table 1). Ansell and Trueman (1968) did not state the temperature at which these observations were made, but their study was made during early summer when seawater temperatures in shallow water at Loch Ewe, western Scotland, would be within the range 11–14°C, compared with 0°C at which the present observations were made. The differences in rates equate to \( Q_{10} \) values of \( \sim 1.4–2.4 \) for peristalsis and 3.0 for the retraction cycle although some allowance should be made for the size difference between the two species. If evolutionary compensation of temperature had occurred here \( Q_{10} \) values would be expected to be predominantly below 2. There is, therefore, little support in this data that an evolutionary acclimation of the processes involved has occurred in *Halcampoides*. There is too little data, however, for a definitive assessment to be made and better comparative data for temperate and tropical species are needed for this. For *Peachia hastata*, Ansell and Trueman (1968) state that, for one individual, burrowing was completed in 1.25 h. An equivalent time is difficult to define for *Halcampoides* sp. since peristaltic movements continued in some cases for \( > 24 \) h. Although the components of the process, therefore, took place at a roughly comparable rate in the two species allowing for the difference in temperature, the overall period taken to complete burrowing was greatly extended in *Halcampoides* sp. This may reflect the nature of the substratum, or may indicate that this particular mechanism of burrowing is less efficient when performed at slower rates.

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**References**


