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Effects of environmental stressors on blood-glucose levels in sea hares, *Aplysia dactylomela*

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Abstract. Effects of natural stressors such as tidepool strandings, air exposure, and low salinity on blood-glucose levels were investigated in the sea hare *Aplysia dactylomela* from shallow areas of Discovery Bay, Jamaica. All treatments produced large and significant elevations in blood-glucose titre, 1.5- to 2.3-fold above baseline levels of 25 to 35 μg glucose ml^{-1}. Response times were variable, with significant elevations being manifested within 30 to 120 min from initiation of the stressor. Recovery was swift, within an hour or two of restoration to pre-treatment conditions, and often involved an undershoot to levels below control values. In two experiments involving tidepool strandings and associated high body-temperatures, excessively low blood-glucose titres were followed by death of all test individuals. When sea hares were exposed to 75 and 50% seawater (100% = 33‰ S) for 1 h, maximum elevation in blood-glucose concentrations occurred 1 to 2 h from onset of exposure, coincidental with maximum dilution of the body fluids of test individuals. The responsiveness of blood-glucose titres to relatively small temperature or salinity changes, or to short-duration air exposures, suggests that monitoring this physiological parameter may be a useful and sensitive means of diagnosing a wide variety of stressors in marine gastropods.

Introduction

Although symptomatic of stress in aquatic vertebrates such as fishes (e.g. Hattingh 1976, McLeay 1977, Strange 1980, Mazeaud and Mazeaud 1981, Andersen et al. 1991) and in crustaceans (Telford 1968, 1974, Johnson and Uglow 1985, Santos and Nery 1987, Spaargaren and Haefner 1987, Taylor and Spicer 1987, Spicer et al. 1990), change in blood-glucose titre has not been used commonly to identify stress responses in marine molluscs (e.g. see Bayne 1985, Veldhuizen-Tsoerkan et al. 1991). Exceptions to this are starvation stress, known to lead to a reduction in blood-glucose levels in several marine gastropods, including sea hares and abalone (Carefoot 1991 a, Carefoot et al. 1993). Also, Ram and Young (1992) showed that electrical shocks applied to *Aplysia californica* significantly increased hemolymph-glucose levels, and preliminary indications from measurements of glucose levels in *Dolabella auricularia* (another sea hare) with perforated crops were that this type of blood contamination induced a massive rise in blood-glucose concentration (to 560 μg glucose ml^{-1} from a baseline level of 41; Carefoot unpublished data).

In the sea hares *Aplysia dactylomela* and *A. kurodai*, blood-glucose levels are known to be positively correlated with activity and food intake, and these and other factors influence the natural daily cycles of concentrations in different species (Carefoot 1991 a, b). Depending on meal size and type, feeding will cause a 2- to 3-fold increase in blood-glucose titre within 1 to 2 h of a meal, with effects diminishing to pre-prandial levels within 8 to 10 h (Carefoot 1991 a). Daily values for *A. dactylomela* (the sea hare for which most information is available) range from ~20 to 40 μg glucose ml^{-1} with two significant peaks: one at mid-day correlated with food digestion, and the other around dusk associated with bouts of locomotion, mate-seeking, and copulation (Carefoot 1991 a, b). Blood-glucose levels in different species of sea hares are similar, with values for *A. californica*, *A. juliana*, *A. kurodai*, and *A. dactylomela* ranging from 29 to 34 μg glucose ml^{-1} (Carefoot 1991 a, b, Ram and Young 1992). This interspecies similarity, plus an absence of size-effect over a broad range of body weights (Carefoot 1991 b), indicates the presence of a strong but, as yet unknown, regulatory mechanism for blood-glucose titre in sea hares. This regulatory mechanism will maintain blood glucose at a constant level over at least 5.5 d of starvation in *A. dactylomela* (at 27 °C; Carefoot 1991 a) and 17 d of starvation in *A. californica* (at 18 °C, Young 1990) before glycogen stores are exhausted.

This precise regulation prompted the question of effects of environmental stressors on blood-glucose titre in sea hares. The present study investigates the effect of several environmental stressors such as tidepool strand-

ing, air exposure, and lowered salinity on blood-glucose titres in *Aplysia dactylomela*. Throughout this paper, the terms "stress" or "stressor" are used to describe a stimulus, while the reaction of the biological system is the "stress response" (Pickering 1981).

Materials and methods

Aplysia dactylomela were collected from shallow areas of Discovery Bay, Jamaica, near the Discovery Bay Marine Laboratory of the University of West Indies. Water temperature ranged from 26 to 28 °C. The habitat was characterized by sometimes considerable spatial and temporal salinity fluctuations caused by freshwater percolation through the coral-rock substrate. Salinity fluctuations of 8‰ were not uncommon in inshore regions and, in small embayments near the laboratory, temporary haloclines of 10 to 15 cm depth with surface salinities <16‰ S often formed. Tidal fluctuation was small, usually <1 m even on spring tides. Sea hares frequented shallow waters in search of the most abundant growths of seaweeds as foods, often right at the sea surface; thus, it was not uncommon for them to be air-exposed or occasionally stranded in tidepools during low-tide periods (also common in other geographical areas inhabited by *A. dactylomela*; Carefoot 1987), and subjected to large and often rapid salinity change.

Four experiments were done, each involving one or more treatments and a control, with $N=5$ for each group. Small sample sizes have been appropriate for studies on *Aplysia dactylomela* involving blood-glucose monitoring, mainly because the relatively precise regulation of the glucose titre leads to small within-treatment variances (Carefoot 1991 a, b). Blood-glucose values obtained from repetitive samples of individuals over time were analysed by repeated-measures analysis of variance (R-MANOVA) (coupled with Newman–Keuls multiple comparisons tests: N–K MCT). In all experiments with *A. dactylomela*, the sea hares were fed normally up to the day of an experiment, but were not fed over the 24 h duration of an experiment. Individuals ranged in size from 420 to 600 g live weight, with balanced weight ranges being selected for control and treatment groups in each experiment.

The first experiment measured the effect of tidepool-stranding on blood-glucose levels. The "tidepool" was a natural fissure at high-water mark which, when plugged with paper towelling, created a pool of ~3 litre volume and 10 cm depth. The pool was filled and drained three times to bring its start temperature to the same as that of the sea. Five test individuals were placed in the pool at 10.00 hrs on a bright sunny day. Five control individuals were suspended in an open-mesh container in the sea at the same depth (5 to 10 cm) as those in the tidepool. After 5 h, to mimic the incoming tide, test individuals were placed in a container identical to that of the controls and suspended in the sea. Blood was sampled hourly from 10.00 to 18.00 hrs, and then again the following day at 10.00 hrs. The methods of blood sampling and glucose analysis were the same as those described earlier (Carefoot 1991 a). In this and other experiments, the sea hares were out of water for no more than 15 s during blood-samplings. All blood samples (200 µl vol), were immediately placed on ice and then frozen within 10 min for later glucose analysis. Sea and tidepool temperatures were recorded at each blood-sampling.

The tidepool treatment resulted in all test individuals dying between Times 8 and 24 h. Since it was presumably either rise of temperature or lack of oxygen (or both) which caused death, a second tidepool experiment was conducted. This was identical to the first, save that the tidepool was aerated throughout the 5 h duration of the experiment using an aquarium bubbler. Aeration removed hypoxia as a factor in the treatment and allowed the effect of temperature to be examined alone.

The third experiment with *Aplysia dactylomela* tested effects of air exposure on blood-glucose levels in both field and laboratory individuals. Five sea hares were positioned at a high intertidal level such that the receding tide left them air- and sun-exposed at ≃10.00 hrs. Simultaneously, five control individuals were placed in an open-mesh container in the sea at about 0.5 m depth, and five individuals were air-exposed in the laboratory (in an attempt to remove UV radiation and other effects of sunlight as factors in the treatment). The mantle-cavity temperature of one experimental individual from each treatment was recorded over the 1.5 h duration of air exposure, using thermistor leads. Field seawater temperatures were recorded every 30 min for 5 h, and then again at 24 h. After 1.5 h of air exposure, when both sets of experimental sea hares were exhibiting symptoms of respiratory distress (gill extension and foot-musculature tightening), they were placed in mesh containers and immersed in the sea together with the controls. Blood samples were taken at Times 0 (10.00 hrs), 0.5, 1.5, 3, 4.5 and 7.5 h and, finally, at Time 24 h.

The fourth experiment with *Aplysia dactylomela* tested effects of 1 h exposure to salinities of 75 and 50% of normal laboratory seawater (33‰ S on the day of the experiment, measured by refractometer). Three groups of five individuals each were placed in 10 cm-deep plastic trays of 10 litres volume in the laboratory. Test salinities were 24.7‰ (=75%) and 16.5‰ (=50%) for two of the groups (experimental) and 33‰ (=100%) for the third group (control). The low-salinity waters were obtained by diluting laboratory seawater with non-chlorinated freshwater. Three 20-litre carboys positioned above the trays allowed continuous delivery of seawater of appropriate salinity to the trays at a rate of ~1 litre min^{-1}. After 1 h, all trays were flushed completely with 100% laboratory seawater, and 100% seawater was substituted for the test-salinity waters in the carboys. Blood samples were taken for glucose analysis at Time 0 h (10.00 hrs), every 30 min until Time 2 h, and then at Times 4, 8, and 24 h. Sea hares in the dilute salinities immediately gained water through osmotic influx, thus leading to dilution of the blood and therefore to potentially erroneous values for blood-sugar levels. Therefore, the sea hares were weighed immediately after each blood sampling to obtain a measure of the extent of dilution. This allowed a correction factor to be applied to apparent blood-glucose titres for dilution effect using an estimate of total blood-volume obtained from another study (50% of total live weight; Carefoot 1991 a).

Results

Tidepool

Effects of simulated tidepool-stranding on blood-glucose levels in *Aplysia dactylomela* are shown in Fig. 1. Highly significant treatment effects were evident 3 to 5 h from the start of the experiment ($F_{1,80}=15.5$, $p=0.004$; R-MANOVA), with blood-glucose titres more than doubling from 36 to 80 µg ml^{-1} at Time 5 h. Although elevated temperature (increase from 25.8 to 32.5 °C over 4 h) or decreased oxygen availability in the tidepool were probably the main stressful agents, other contributing factors could have been enhanced UV exposure, and increases in ammonia and CO_2 levels. By Time 3 h individuals were displaying typical symptoms of respiratory distress: parapodial flapping and extended gills. After their return to the sea following 5 h tidepool treatment, glucose titres dropped to 6–8 µg ml^{-1} over the next 3 h. By Time 24 h, all experimental individuals were dead and all had zero blood-glucose concentrations. Highly significant time effects were evident ($F_{9,80}=22.3$ $p<0.001$; R-MANOVA). Experimental individuals differed from controls at Time Periods 3 to 5 h and 7 to 8 (the 24 h data were not included in the analysis; $p<0.05$, N–K MCT). Control values fluctuated non-significantly between 27

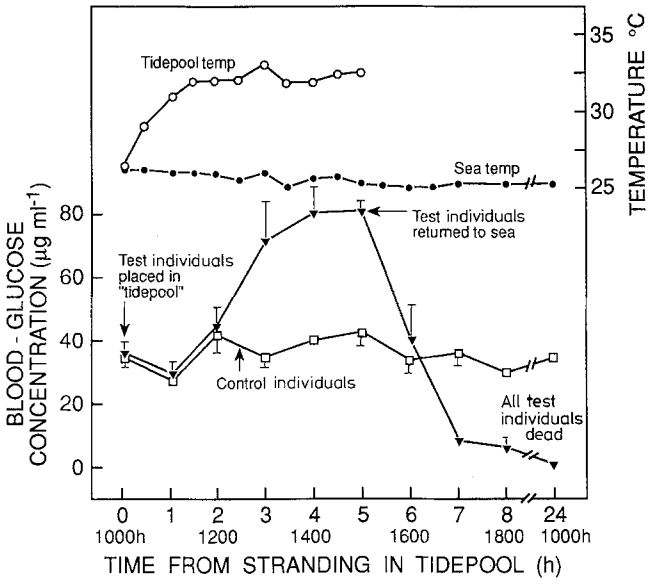

Fig. 1. *Aplysia dactylomela.* Effect of 5 h simulated tidepool stranding on blood-glucose levels. Control individuals were kept in a mesh basket in the sea; after 5 h, tidepool individuals were similarly placed in a mesh basket in the sea. Data points are means of $N=5$, with standard errors; where error bars are not shown, they are contained within the dimensions of the data point. Tidepool and sea temperatures are also shown.

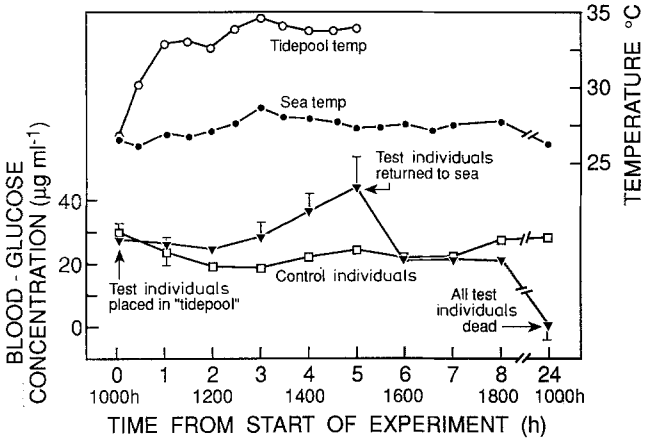

Fig. 2. *Aplysia dactylomela.* Effect of 5 h simulated tidepool stranding on blood-glucose levels when tidepool was aerated with a bubbler system. Further details as in Fig. 1

and 42 µg glucose ml^{-1} ($p>0.05$, N–K MCT) indicating here, as in the experiments to follow, that the effects of handling, short-duration air exposure, and needle prick and blood withdrawal associated with repetitive sampling were not reflected in significant elevation in blood-glucose titre.

Fig. 2 shows comparative data for *Aplysia dactylomela* in an aerated tidepool. Temperature elevation in the tidepool was similar to that in the first experiment (6.5 °C), but blood-glucose elevations were substantially less (increase from 28 to 44 µg ml^{-1} over 5 h; $F_{1,80}=8.0$ $p=0.02$, R-MANOVA). The sea hares displayed less respiratory distress (evidenced by fewer parapodial flappings and gill extensions) in this experiment than in the

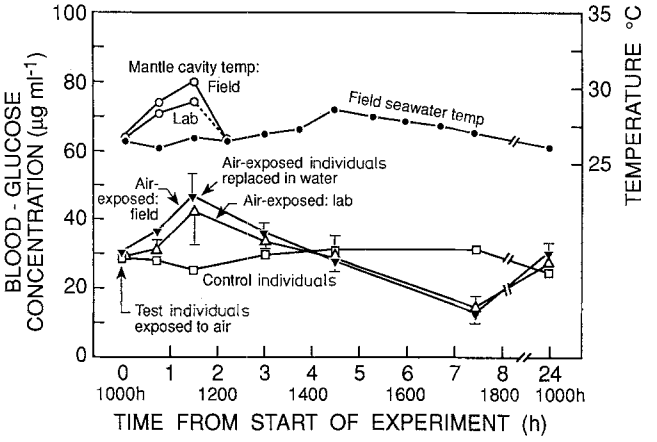

Fig. 3. *Aplysia dactylomela.* Effect of air exposure on blood-glucose levels. Controls were kept in a mesh basket in the sea; after 1.5 h, air-exposed individuals were placed in containers in the sea. Data points and error bars as in Fig. 1. Mantle-cavity and sea temperatures are shown

first experiment. However, despite the comparatively lower elevation in mean blood-glucose concentration here compared with the first experiment, by 24 h four out of five test individuals were dead (the 1 live individual had a titre of 26 µg ml^{-1}, the 4 dead ones of 0 µg ml^{-1}; however, the fifth sea hare died at Time 30 h). Experimental sea hares differed from control individuals only at Time 5 h ($p<0.05$, N–K MCT; 24 h data were excluded from analysis). Control values fluctuated non-significantly between 18 and 30 µg glucose ml^{-1} ($p>0.05$, N–K MCT).

Air

Fig. 3 shows the effects of 1.5 h air exposure on blood-glucose levels in *Aplysia dactylomela.* Treatment values were significantly higher than control values over the first 3 h of the experiment ($F_{2,60}=3.34$, $p=0.04$, R-MANOVA), but not when measured over the whole experiment ($F_{2,84}=1.05$, $p=0.38$, R-MANOVA). The initial rise in titre diminished quickly on re-immersion of the test individuals, leading to an undershoot a few hours after their return to seawater. However, by Time 24 h, blood-glucose levels in the experimental sea hares had returned to normal, and all subsequently survived. Responses might have been more intense had the period of air exposure been longer; however, after 1.5 h in air, all test individuals, especially those in the field, had dry skin on the exposed surfaces and were exhibiting extreme signs of distress – manifested in exposed gills, contracted foot musculature, and protruding penises. Mantle-cavity temperatures were only slightly higher in field individuals (30.5 °C) than in laboratory individuals (29.0 °C) over the treatment period (Fig. 3).

Salinity

Effects of low salinity on blood-glucose levels in *Aplysia dactylomela* were highly significant (Fig. 4; $F_{2,96}=66.5$,

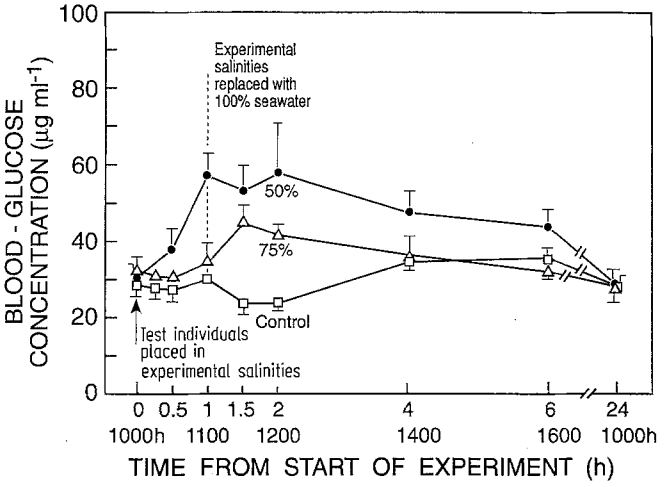

Fig. 4. *Aplysia dactylomela.* Effect of hyposmotic salinities on blood-glucose concentrations. After 1 h, test salinities were replaced with 100% seawater (=33‰ S). Data points and errors bars as in Fig. 1. Values for 50 and 75% curves have been corrected for dilution of body fluids through osmotic influx which, for both groups, resulted in body-weight gains of 12% at Time 0.5 h, 22% at 1 h, 9% at 1.5 h, 5% at 2 h, and 0% at 4 h. Corrections are based on assumptions of 50% blood volume of total body weight, as measured previously in the same species (Carefoot 1991 a), and dilution effects only on the blood. On these bases, then, a blood-glucose reading at Time 1 h for an individual in either 50 or 75% seawater, which weighed 500 live g at Time 0 and 610 g at Time 1 h, would be corrected by a multiplication factor of 1.44

$p<0.001$, R-MANOVA), with maximum increases occurring 1 to 2 h after the start of treatment. This corresponded with maximum dilution of the blood which occurred in both experimental salinities at Time 1 h and was reflected in a 22% increase in mean body weight in each treatment group (0.5 h after return to 100% seawater, both treatment groups had dropped to 9% over starting body weights; after a further 2.5 h, body weights of all experimental groups had returned to normal). Body-weight gain was similar for sea hares in both test salinities, suggesting the presence of some osmoregulatory activity or resistance (e.g. body musculature or skin elasticity preventing further swelling) to prevent greater dilution in the lowest salinity treatment. The higher mean blood-glucose level displayed by the 50%-test individuals (52 to 57 µg ml^{-1}) suggests, however, that their response was energetically more costly than that of the 75% individuals (42 to 45 µg ml^{-1}). The 50%-test group deviated significantly from controls at Times 1 to 2 h and from the 75%-test group at Time 1 h, while the 75%-test group differed significantly from controls only at Time 1.5 h ($p<0.05$, N–K MCT). Control individuals displayed non-significant fluctuations in blood-glucose concentrations around values of 24 to 35 µg ml^{-1} ($p>0.05$, N–K MCT). Body weights of controls exhibited essentially 0% change from Time 0 h to Time 6 h, but were 6% lighter at Time 24 h, possibly due to faecal loss, since the salinity of the laboratory seawater was the same on both days. By Time 2 h, both test groups were 5% heavier than they had been at the start of the experiment, and by Time 24 h their weights were 4 to 6% lighter than at the start, similar to the control group. Experimental treatments were terminated after 1 h, when individuals in the test salinities exhibited symptoms of gill protrusion, excessive parapodial flapping, and tightening of the foot musculature, suggestive of severe distress. However, all sea hares survived the treatments.

Discussion

The results show clearly that blood-glucose level in *Aplysia dactylomela* rises in response to a variety of stressors. During air-exposure and salinity stress, the increases were large and rapid, reaching significant elevation within 30 to 60 min. Ram and Young (1992) similarly showed quick response times for elevated blood-glucose titres in *A. californica* subjected to electrical shock. Within 30 min, titres had increased by 50 to 150% and were sustained at a high level, in some cases for >2 h. These response times are comparable to stress-induced blood-glucose elevations in crustaceans. For example, air-exposed Norwegian lobsters, *Nephrops norvegicus* (at 10 °C), show a quadrupling within 3 h (Spicer et al. 1990); anoxic prawns, *Palaemon elegans*, a doubling within 1 h (Taylor and Spicer 1987); and air-exposed (and handled) crayfish, more than a quadrupling in 2 min (Telford 1974).

Of the environmental stresses imposed here, tidepool-stranding with its associated temperature effects appeared to be most severe from the standpoint of magnitude of elevation in blood-glucose level in *Aplysia dactylomela.* Based on the apparent lessened respiratory distress of the aerated-treatment group in the second experiment and their correspondingly lower elevation in blood-glucose titre, a large component of stress may have been lack of oxygen in the first experiment. To some extent this is supported by the results of the third experiment, where short-duration air exposure led to only a moderate body-temperature increase coupled with a comparatively moderate and short-lasting blood-glucose increase and the subsequent survival of all test individuals. Obviously, it is not possibly here to ascribe precise causalities, nor was this the intent of these particular experiments; rather, what has been shown is that high blood-glucose titre in sea hares can be symptomatic of stress of a variety of kinds.

The acute blood-glucose responses shown by *Aplysia dactylomela* to low salinity are somewhat different from those recorded in low- and high-salinity acclimated shrimp, *Crangon crangon*, by Spaargaren and Haefner (1987). These authors found lowest blood-glucose titres in the shrimps in extreme salinities (6 and 36‰) and highest in intermediate salinities (12 to 26‰). They attributed the low values to increased energy demand and, thus, increased utilization of glucose by osmoregulatory tissues. This is an interesting concept because stress, at least in the short term, seems invariably to be associated with elevated blood-glucose titre, and the question of whether acclimation to stressors over the long term would lead to depressed levels is rarely addressed. An exception to this is starvation stress, which has been well studied in marine invertebrates especially with respect to

its effect on tissue metabolite levels (e.g. Emerson 1967, Stickle and Duerr 1970, Hiller-Adams and Childress 1983). In aplysiids, starvation stress leads to a depressed metabolic rate accompanied by low blood-sugar levels and to exhaustion of digestive-gland glycogen stores after only 1 to 2 wk, depending on the temperature (Young 1990, Carefoot et al. 1993). From the present data it is not possible to determine if death of *A. dactylomela* resulted from too-low blood-sugar levels or if, in dying from other causes, levels subsequently decreased to zero. This phenomenon in *A. dactylomela* of a rise in blood-glucose titre followed by an undershoot (often leading to death) in response to stress, differs from what has been seen in fish. Acutely stressed catfish, for example, exhibit a high blood-glucose titre which returns to near basal levels in the dying fish (Strange 1980).

Extensive work on fish and other aquatic animals has shown that a variety of indicators can be used to monitor stress, including biochemical, physiological and morphological responses, performance capability, and other variables (Pickering 1981, Bayne 1985, Adams 1990). The methods of assessing stress themselves vary with respect to (1) sensitivity to stress, (2) ease of measurement, (3) biological variability of the measurement, (4) differentiation of acute and chronic effects, and (5) relevance to higher levels of organization (Heath 1990). The last point is pertinent to the present work since, in the absence of information on glucose flux in gastropods, it is impossible to set the stress-induced glucose-enhancement data in an overall metabolic frame of reference. Nonetheless, the present work has shown that stress manifestation as indicated by changes in the blood-glucose titre in sea hares is relatively quick, yet originates from a stable and predictable baseline level, and that the method of measurement is easily applied. It may therefore be a useful and sensitive diagnostic means to identify a wide variety of stressors in these and other marine molluscs.

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