Feeding & Digestive Rhythms in Intertidal Bivalve Molluscs, *Anadara rhombea* (Born) & *Crassostrea madrasensis* (Preston)

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Rhythmic changes in the morphology, length, protein content and dry weight of the crystalline style and histological changes undergone by the digestive tubules in *A. rhombea* and *C. madrasensis* are reported in relation to one complete tidal cycle. In both the species, crystalline style is completely lost during low tide and is reformed during high tide. At peak of the high tide, maximum values in length, protein content and dry weight occur in the style of both *A. rhombea* and *C. madrasensis*. Digestive tubules in the two species show that intracellular digestion is also rhythmic and monophasic i.e. at a particular tidal phase almost all the tubules have a homogeneous structure. During high tide, the digestive tubules pass through digestive and absorptive phases while over the low tide regime the disintegrating and reformative phases are dominant indicating that these intertidal bivalves feed and digest rhythmically during high tides.

Feeding and digestive processes in bivalve molluscs are considered to be continuous and simultaneous1. This concept is based on the assumption that the crystalline style dissolves slowly to maintain a constant supply of enzymes for extracellular digestion in the stomach. Morton2 has first presented evidence, that feeding and digestion in the high intertidal bivalve, *Lasaea rubra* are cyclic in nature synchronising with the tidal period. The crystalline style is lost during ebb tide and reformed again during flood tide. The present communication reports the nature of feeding and digestive processes in two intertidal bivalves in relation to the tidal cycle.

**Materials and Methods**

Blood cockles *Anadara rhombea* (28-30 mm in length) and oysters *Crassostrea madrasensis* (58-61 mm in length) were collected from the mud flats of the Vellar estuary at Porto Novo, (lat. 11°29'N and long. 79°46'E) and transferred to a series of wooden quadrants that were exposed at the low tide for 3 h during each tidal cycle. The bivalves were acclimatised to these conditions for a week before the commencement of the experiments. Each species was sampled at 90 min intervals for a continuous period of 15 h. The sampling periods were determined on the basis of Indian Tide Table Part I, 1982.

**Crystalline style parameters** — Length: The crystalline style was extracted from each animal, washed in distilled water and blotted dry. The length of the style was measured to the nearest 0.1 mm. After measurement the styles were preserved in a 10% formaldehyde solution.

Dry weight: Styles of individuals from each sample were dried in a hot air oven (60°C) to constant weight. The dry weight determined to the nearest 0.1 mg.

Total protein: The protein content of the style was determined by the modified biuret method of Raymont et al3.

**Relative size of entire style and its central core** — Formaldehyde preserved styles were used. Cross sections (2-3 mm) were made with a sharp razor at the region of maximum width. The diameter of the central granular core and that of the entire style were measured micrometrically. The ratio of the granular core diameter to the total style diameter was calculated.

**Histology of digestive diverticula** — Histological changes in the digestive tubules were studied in the specimens collected at intervals of 3 h. Small portions of digestive diverticula close to the oesophagus, from 3 individuals were fixed in Gilson's fluid, embedded in paraffin wax, sectioned (8 μm) and stained with Ehrlich haematoxylin and eosin.

**Results**

During peak of high tide maximum style length, protein content and dry weight were recorded for *A. rhombea* and *C. madrasensis* (Fig. 1). During the first half of the low tide these values progress-
Fig. 1 – Rhythmic changes involving complete dissolution and reformation of the style in *C. madrasensis* and *A. rhombea* during a tidal cycle (Values are mean ± SE of 5 styles)
Rhythmic changes in the style morphology were also observed in relation to the tidal cycle for both species. During high tide, the style was firm and rod-like with a pointed head capped with a mixture of mud and food particles. Food and sand particles were found on the style body also. The style lost its firmness and became flaccid during the first half of the low tide. The mud cap was absent. At the late low tide, the style dissolved completely. The ratio of the diameter of central core to the total style diameter was minimal (0.22 ± 0.02 in A. rhombea and 0.15 ± 0.03 in C. madrasensis) during peak high tide but continued to increase at low tide (0.33 ± 0.03 in A. rhombea and 0.35 ± 0.02 in C. madrasensis).

Rhythmic changes in histology of digestive tubules—Cross sections of digestive tubules revealed that the structure of the tubules underwent rhythmic histological changes in accordance with the feeding and digestive rhythms set by the tidal oscillations. The digestive tubules were monophasic in nature i.e. at a particular time of the tidal cycle almost all the tubules had a homogenous histological structure. Four distinct phases viz. formative, absorptive, digestive and disintegration were recognised. The observed changes were almost identical in both A. rhombea and C. madrasensis.

Early high tide: Digestive tubule consisted of 2 types of cells, larger and abundant digestive cells and clusters of deeply staining basiphil cells. During early high tide the tubules assumed a characteristic structure. The lumen of the tubules is 'H' shaped in the case of A. rhombea and in C. madrasensis it is mostly star shaped. The basiphil cells stained dark blue with haematoxylin and eosin and were located in 4 small groups in A. rhombea and 5 in C. madrasensis and developed cilia at their free ends. A number of small vacuoles were found in the digestive cells. At this time the digestive tubule were in the absorptive phase.

Peak high tide: Digestive cells enlarged resulting in a decrease in the size of tubule lumen. Food materials were readily observed in the vacuoles of digestive cells. In many cells, small vacuoles fused to form larger ones called fragmentation spherules since they fragment and release their contents into the stomach4.

Early low tide: The disintegration process initiated during the peak high tide continued further. The fragmentation spherules, pinched off from the distal end of the digestive cells, were found in the lumina of the tubules. As a result the length of the digestive cells was greatly reduced. Consequently the size of the tubule lumen increased greatly. Small clusters of basiphil cells were found, but their orientation towards the lumen of the tubule was lost. The disintegration process in the digestive tubules seemed to have reached to culmination approximately 4.5 h after the low tide. In this stage the digestive cells were reduced in length as well as in number. Only a few nuclei were found in each cross section. The basiphil cells could not be distinguished from digestive cells.

Early high tide II: The structure of the tubule was essentially similar to that described in the early high tide of the previous tidal cycle indicating the cyclic nature of the events.

Discussion
The changes observed in the style parameters of A. rhombea and C. madrasensis during a complete tidal cycle indicate that there is tidal rhythmicity of secretion and loss of crystalline style. Since crystalline style is considered to be the organ of feeding and extracellular digestion5, rhythmic changes in the structure of the style possibly imposes a rhythmicity in the feeding and extracellular digestion. Similar observations have been made from many species of oysters6-12 but it is demonstrated here for the first time in the arsid bivalve, A. rhombea.

In his new theory of feeding and digestion in the Lamellibranchia, Morton7 proposed that style is secreted at one time and dissolved at another. From the present observation it is evident that the style secretion is periodic but its dissolution is continuous. Hameed13 has reported that in vitro dissolution of style in A. rhombea and C. madrasensis is proportional to the pH of the medium within the pH range 4.5 to 8 and the maximum dissolution takes place at pH 8. Further, the optimum pH (8) for the style dissolution of A. rhombea and C. madrasensis approximately corresponds to the pH of high tide water13 of the vellar estuary and hence the style is likely to dissolve faster during high tide and promote the extra cellular digestion. Similar style dissolution during high tide has been suggested by Mathers12,14 in Pecten and Ostrea. The visual observation of style dissolution during high tide is probably concealed since dissolution of style is profitably compensated by secretion of style matrix. It is therefore, suggested that style dissolution is more a physical process and takes place continuously but at different rates throughout the tidal cycle, while style secretion is a physiological but rhythmic process.
The intracellular digestive rhythms recorded in *A. rhombea* and *C. madrasensis* are monophasic in nature i.e. at a particular time of the tidal cycle almost all digestive tubules have a homogenous histological structure. Monophasic digestive cycles correlated with tidal rhythm have been reported for many intertidal bivalves\(^{15-18}\). However, Robinson and Langton\(^{19}\) have found no variation in style length or differences in synchrony in the digestive tubules in the subtidal population of *Mercenaria mercenaria* thus implying that the animal feeds and digests continuously. In *A. rhombea* and *C. madrasensis*, the feeding and digestive processes are rhythmic and the rhythms are directly regulated by the tidal cycle. It is suggested\(^{6,19,20}\) that these rhythms are controlled by the availability of food rather than tidal cycle *per se*. It also seems to be true in the present study since the intertidal bivalves have to feed necessarily on the food materials brought by the high tide water and close their valves tightly when they are exposed in the low tide.

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**References**