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DESTRUCTION OF KELP POPULATIONS
BY *LACUNA VINCTA* (MONTAGU)

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ABSTRACT

A localized population expansion of *Lacuna vincta* (Montagu) has caused a marked depletion of kelp populations near Newcastle Island, New Hampshire. As many as 277 snails per *Laminaria* plant were observed. The stipes and blades of *Laminaria* plants become riddled with holes (up to 12 holes/25 cm²) from *L. vincta*; eventually only residual holdfasts and stipes remain. A grazing rate of 0.326 cm² of *Laminaria saccharina* blades/snail/day was recorded in the laboratory. Respiration studies indicate that *L. vincta* is an osmoconforming species with a salinity optimum of about 25‰. It is suggested that the population increase of *L. vincta* may have been initiated after a period of extensive rainfall, - i.e. reduced salinities. *Lacuna vincta* may be a major grazer of seaweeds in a variety of locations.

While conducting subtidal studies of the benthic marine algae of New Hampshire we have observed extensive grazing of *Laminaria* populations by the prosobranch gastropod, *Lacuna vincta* (Montagu). The gastropod is a small (1.0-1.5 mm wide and 1.0-1.8 mm long) littorinid snail (Fig. 1) that is often found in limited numbers on kelps and other seaweeds along the northeast coast of North America (Miner, 1950). During 1972 we have observed a "population explosion" of *L. vincta* at Newcastle Island, New Hampshire (43° 04' 05" Latitude and 70° 42' 45" Longitude), and a marked depletion of *in situ* kelp beds. Subsequently we have seen continued destruction of kelp populations at Newcastle Island, as well as at adjoining open coastal and estuarine sites in Southern Maine and New Hampshire.

In June, 1972, we examined 64 randomly collected specimens of *Laminaria saccharina* and *L. digitata* within a 1000 m² area at Newcastle Island at 3 to 6 m below mean low water. All of the plants exhibited severe damage, for their fronds and stipes were riddled with round or ellipsoidal holes that were

3-10 mm in diameter (Fig. 2 and 3). As many as 12 holes per 25 cm² were found on many blades. The majority of the holes penetrated through the entire plant(s). In most cases the blades were more heavily grazed than other portions of the plants. The intercalary meristem, or the transitional zone between the blade and stipe, was rarely damaged. At sites with heavy grazing only residual holdfasts and stipes of *Laminaria* were present.

During July, 1972 we found as many as 277

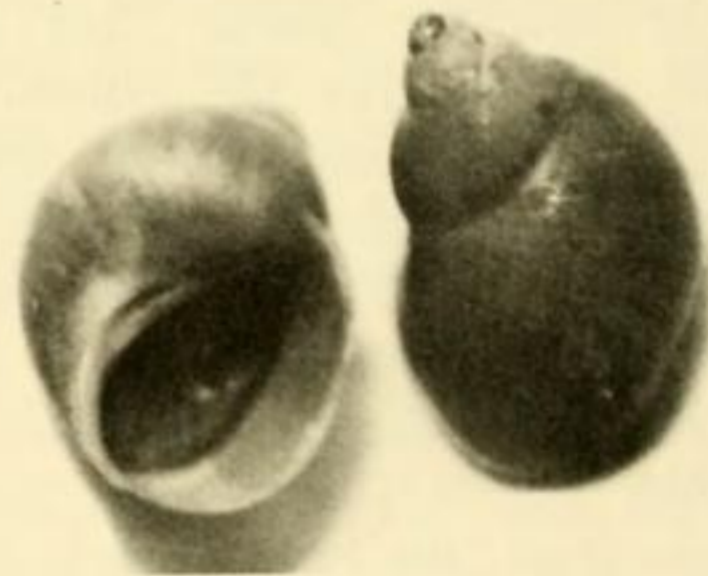


FIG. 1. Two New Hampshire specimens of *Lacuna vincta* (Montagu), 30 X.

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snails per *Laminaria saccharina* plant at Newcastle Island - at 3 to 6 m below mean low water. In the early part of the summer few snails were found on the understory vegetation beneath the kelp canopy. However, as the summer progressed a variety of economically important species such as *Chondrus crispus*, *Gigartina stellata* and *Rhodomenia palmata* (Mathieson, 1969) also showed extensive grazing by *Lacuna vincta*.

Kain (1971) and R. Waaland (personal communication to A.M.) also report abundant populations of *L. vincta* on seaweeds in Norway and Washington, U.S.A., respectively. Thus, *Lacuna* may be a major grazer of seaweeds in a variety of locations. Kain and Svendsen (1969) record extensive grazing by the gastropod *Patina pellucida* on *Laminaria hyperborea* in western Norway and Great Britain; they state that *P. pellucida* may cause considerable loss of plants due to weakening of the holdfast or damage to the frond or stipe. In Great Britain they observed that the animals initially settled on the frond and then migrated to the holdfast, where they created large cavities. Preliminary

observations indicate that *L. vincta* may show a similar pattern of attachment and migration on New England kelps. According to Kain (1971) O. Vahl (unpublished data) has found considerably higher densities of *L. vincta* than *P. pellucida* on *Laminaria hyperborea* populations in Norway, and the holes it makes are much deeper than those of *P. pellucida*.

Preliminary culture experiments were conducted in August and September, 1972, in order to determine grazing rates of *L. vincta* on *Laminaria saccharina*. A small section of frond (25 cm²) was placed in a crystallizing dish with 200 ml of filtered sea water (30 ‰) and 10 snails. The dishes were incubated at 300-400 foot-candles and at 10°C in a Sherer-Gillete Incubator. After 5 days the fronds were remeasured and the consumption of plant material was determined. An average grazing rate of 0.326 cm²/snail/day was recorded. It should be emphasized that this is an approximation and further studies should be conducted to determine the effects of differential temperatures, salinities and plant materials on grazing.

Respiration rates of *L. vincta* at 10°C and in three different salinities (20, 25, and 30 ‰) were measured in a Gilson Differential Respirometer (Model GRP-14), according to the methods outlined by Mathieson and Burns (1971). The temperature was maintained at about 0.1 C; it was the same as the ambient temperature when the snails were collected. Two flasks containing ten snails per flask were run at each of the test salinities. The respiration rates for the three salinities were recorded simultaneously in the same instrument. Figure 4 illustrates the results of the

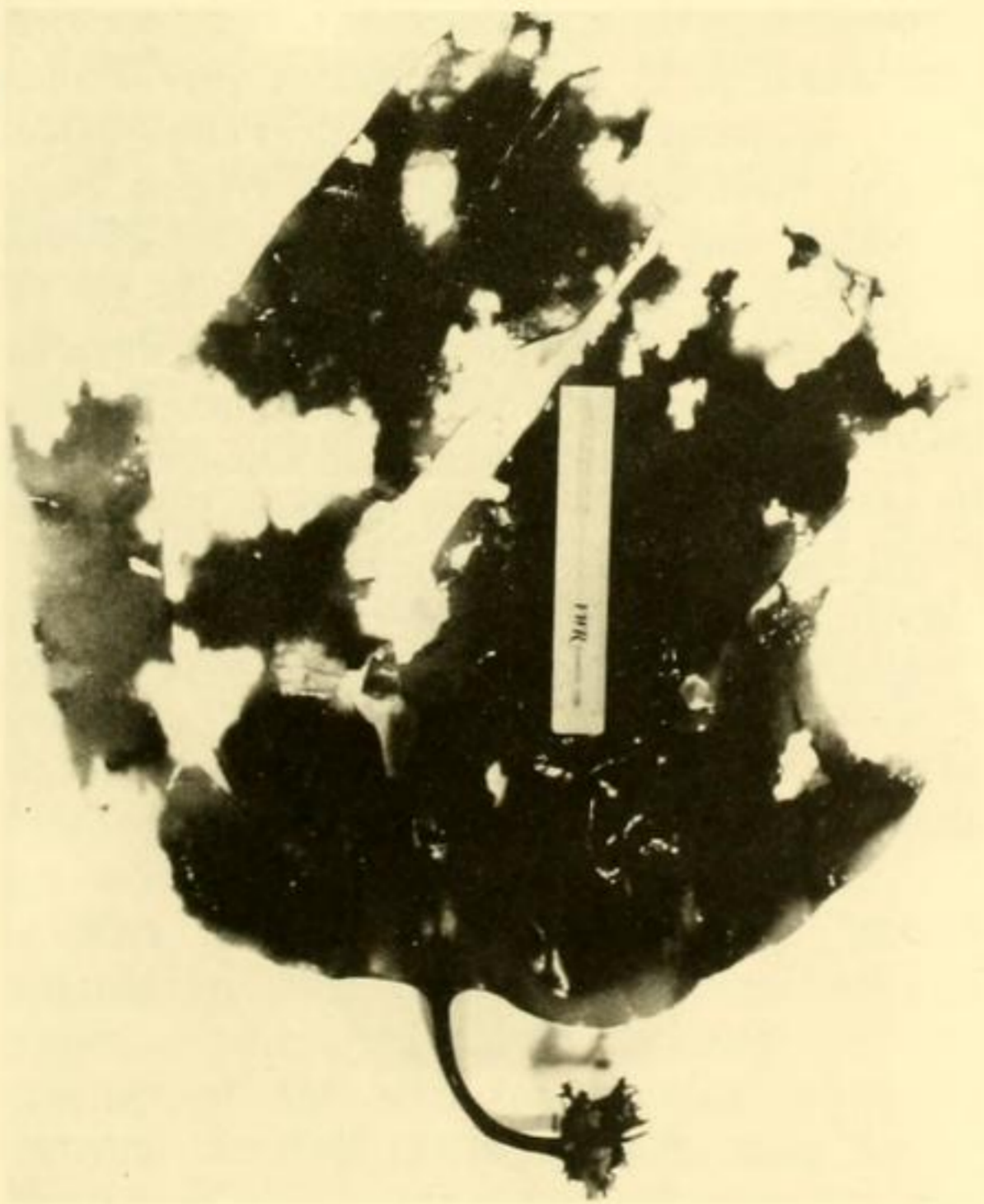


FIG. 2. A *Laminaria saccharina* plant showing severe damage from *L. vincta*.

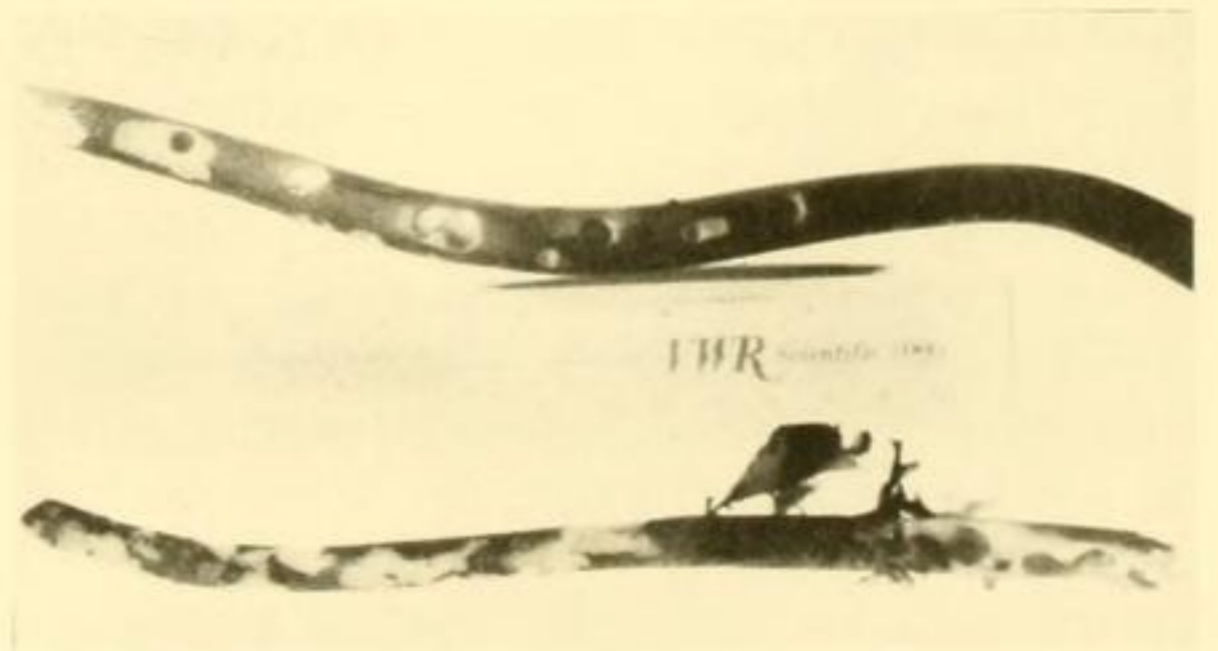


FIG. 3. A stipe of *Laminaria saccharina* riddled by *L. vincta*.

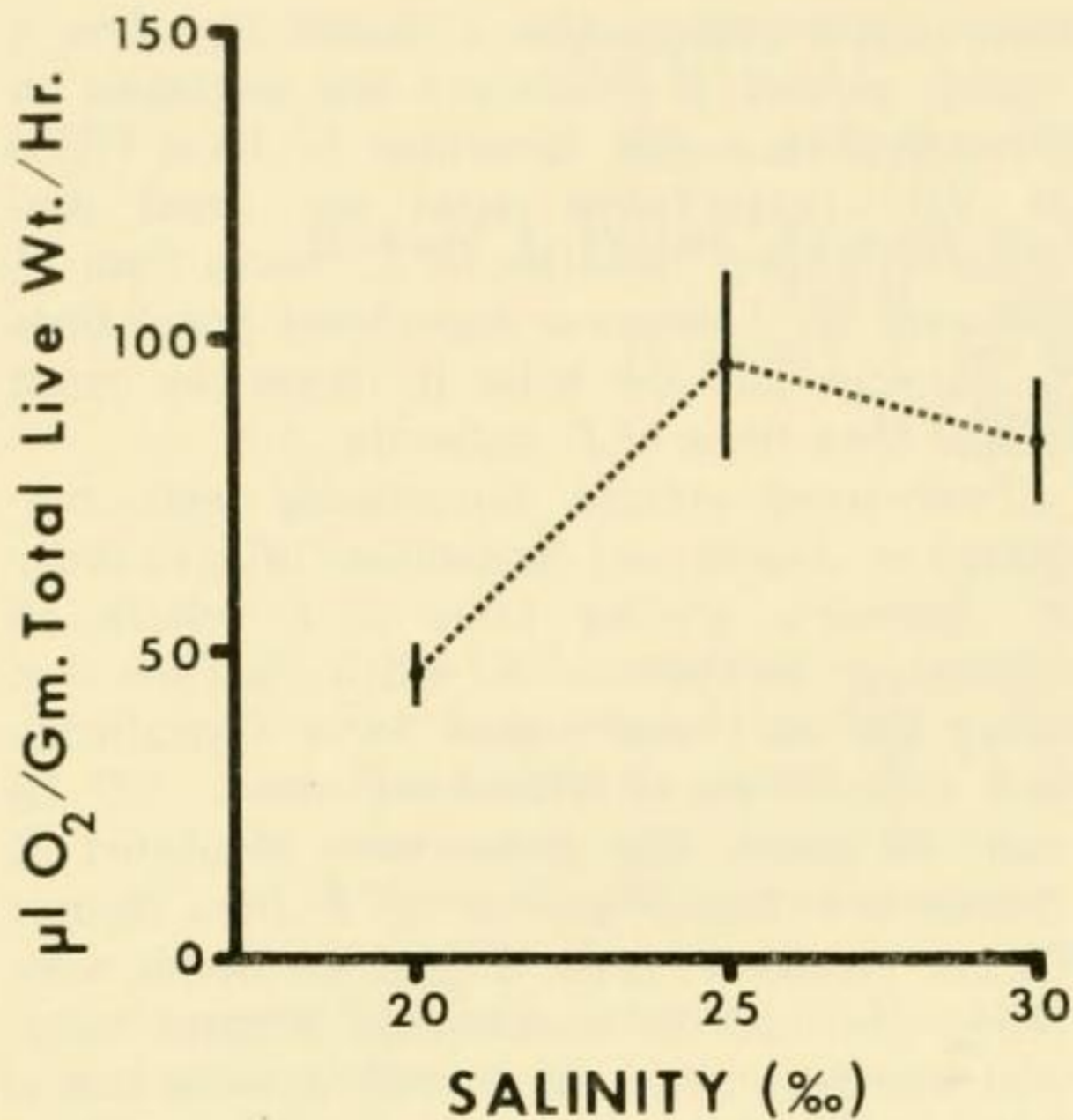


FIG. 4. Respiration of *L. vincta* at 10C and in three different salinities.

experiment. The lowest respiration rates were found at 20 ‰ and the highest was recorded at 25 ‰. The results suggest that *L. vincta* is an osmoconforming species with a salinity optimum of about 25 ‰.

In conclusion the extensive grazing of seaweeds at Newcastle Island, New Hampshire, appears to be directly associated with a localized population expansion of *L. vincta*. Our laboratory studies confirm the field observations that *L. vincta* was the causative organism. It should be emphasized that previous seasonal investigations at Newcastle Island (Mathieson, *et al.*, in press) have never shown extensive seaweed grazing by *L. vincta*. It is suggested that the population increase of *Lacuna* may have been associated with a spring season

(1972) with abnormally high rainfall, and thus periods of reduced salinities. Our respiration studies confirm the tolerance of *L. vincta* to low salinity regimes recorded prior to the period of severe grazing. It is apparent that further studies of gastropod/algal grazing should be conducted in the New England area.

ACKNOWLEDGEMENTS

We would like to thank Dr. R. D. Turner, Museum of Comparative Zoology, Harvard University and Dr. R. T. Abbott, Delaware Museum of Natural History, for confirming the identification of *Lacuna vincta* and encouraging our study of its grazing on seaweeds.

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ROLE OF THE INCURRENT SIPHONAL VALVE IN THE SURF CLAM,
SPISULA SOLIDISSIMA (MACTRIDAE)

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ABSTRACT

Observations of the behavior of the surf clam, Spisula solidissima have indicated that debris such as sand may be entrapped in the incurrent siphon cavity temporarily before being expelled by a jet of water from the mantle cavity. The morphology and responses of the incurrent siphonal valve are well suited for mediation of a possible sand storage behavior. The incurrent siphonal valve is positioned across the opening between the incurrent siphon cavity and the mantle cavity, hence can, when extended, separate the two cavities. Extension (closing) of the valve occurs in response to mild tactile stimulation of the siphons. Contraction (opening) of the valve only occurs in response to strong tactile stimulation. The responses of the incurrent siphonal valve and the adductor muscles (which cause the jet of water) are co-ordinated in such a way that during the cleaning reflex the valve is open when shell valve adduction occurs thus allowing free passage of water out of the mantle cavity.

While studying the neural control of siphon withdrawal in the surf clam, *Spisula solidissima* (Dillwyn), it was necessary to examine siphonal behavior in detail, (Prior, 1972).

The siphons of *Spisula* respond in a progressively more complex fashion as the intensity of tactile stimulation of the siphonal tentacles (papillae) is increased. In response to touching a single siphonal tentacle with a glass stylus the siphon apertures close (a local reflex mediated by peripherally located neurons). As the intensity of tactile stimulation is increased (touching several tentacles or the inner wall of the incurrent siphon) the siphon musculature responds with progressively greater contractions until finally, the siphon retractor muscles respond, withdrawing the siphons into the mantle cavity.

Often in response to gentle tactile stimulation, such as touching several tentacles, siphon closure is rapidly followed by contraction of the adductor muscles, which by drawing the shell valves together, cause the expulsion of a jet of water out the incurrent siphon (the excurrent siphon remains closed). This "Cleaning reflex" occurs regularly and

serves to eliminate feces and debris, such as sand, drawn in through the incurrent siphon.

In one of the very few reports on observations of *Spisula* in their natural habitat, Jacobson (1972) describes the siphonal behavior of young individuals in a sandy intertidal zone. During the interwave periods the clams kept their siphons open. But in response to each sand laden wave, the siphons were observed to close rapidly. The siphons remained closed until the sand settled and was no longer being roiled about. Jacobson further noted that at somewhat regular intervals a small jet of water, laden with sand grains, was ejected from the incurrent siphon (the cleaning reflex). Jacobson points out that this cleaning reflex is of adaptive value in that it minimizes the build up of sand in the mantle cavity. Furthermore, he suggests that sand is probably stored briefly in the incurrent siphon before being expelled, as a further means of preventing accumulation in the mantle cavity.

The present report describes the anatomy and general responses of a muscular flap of tissue (incurrent siphonal valve) in *Spisula* that is positioned across the opening of the incurrent

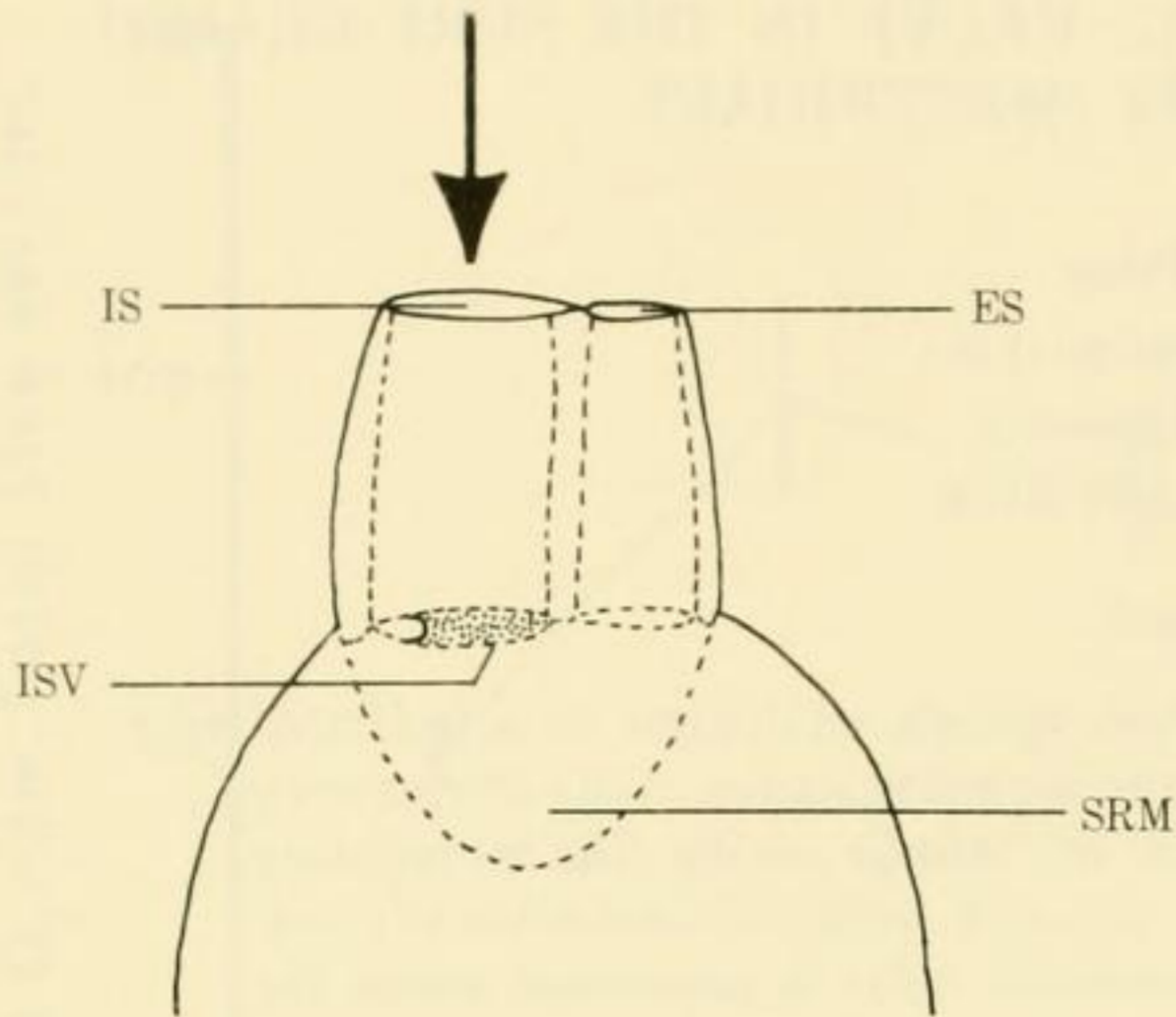


FIG. 1. A schematic of the posterior end of a clam with the incurrent siphon (IS) and excurrent siphon (ES) in an extended position. One of the siphon retractor muscles (SRM), which adhere to the inner surface of the shell valves, is indicated. The incurrent siphonal valve (ISV; stippled) is shown partially extended across the opening between the siphon cavity and the mantle cavity. The incurrent siphonal valve is attached to the lateral walls of the incurrent siphon and to the septum between the incurrent and excurrent siphons.

siphon leading to the mantle cavity (a detailed report of the electrophysiological properties of the muscle fibers will appear separately; Prior, 1974). This valve is attached to the base of the muscular wall separating the two siphonal cavities and to the lateral walls of the incurrent siphon cavity (Fig. 1). The valve protrudes across (partially occluding) the inner incurrent siphon opening. The incurrent siphonal valve is composed of two bundles of smooth muscle fibers and a diffuse array of muscle fibers sandwiched between two layers of epithelium (Fig. 2).

The activity of the incurrent siphonal valve was examined by removing from the animal the entire siphonal apparatus (mantle musculature, siphon retractor muscles and intact visceral ganglion) to a wax dish of cold (10° C) sea water. With this sort of arrangement the tentacles and inner walls of the siphons could be

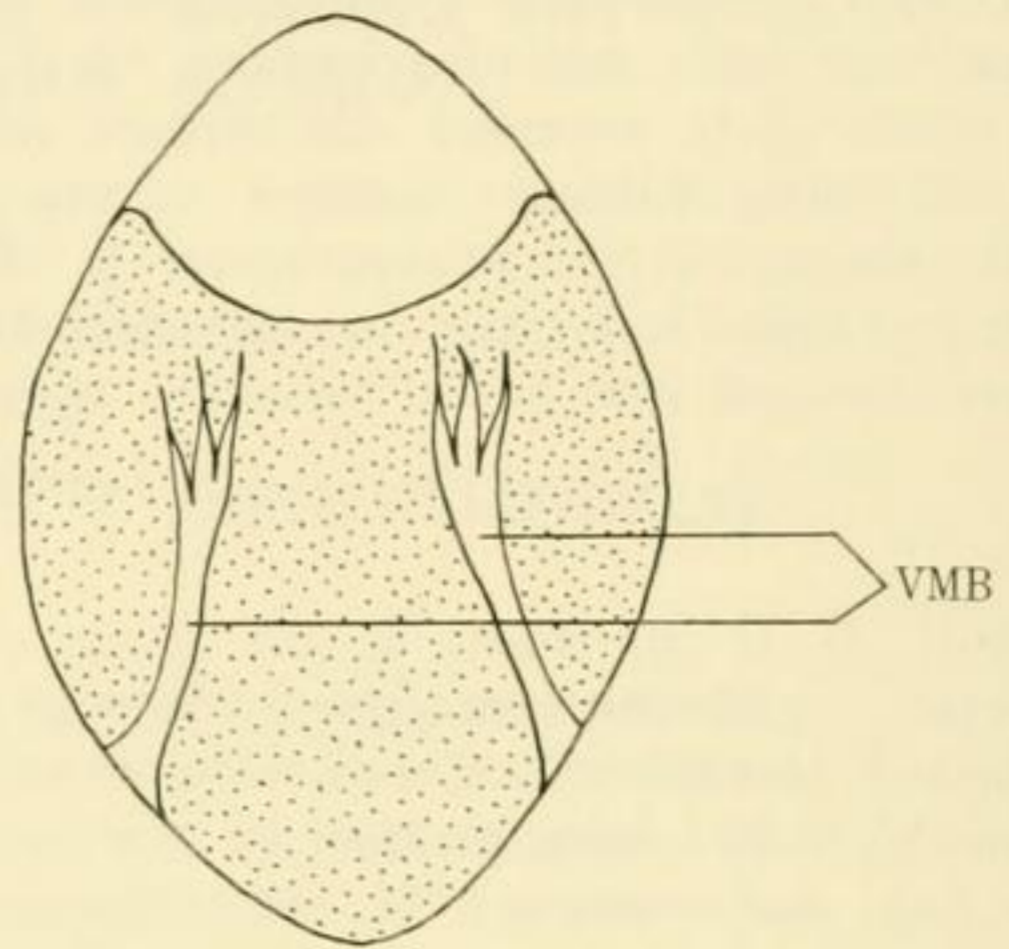


FIG. 2. This is an illustration of the incurrent siphonal valve (ISV) as seen by looking into the external opening of the incurrent siphon (see arrow in Figure 1.). The ISV (stippled area) is composed of a pair of distinct valve muscle bundles (VMB) and diffuse muscle fibers that are spread throughout the valve sandwiched between two epithelial layers.

tactily stimulated while observations were being made on the activity of the siphonal valve.

In response to gentle tactile stimulation of siphonal tentacles the dispersed muscle fibers of the valve contract, resulting in extension of the flap across the incurrent siphon cavity. This movement of the valve effectively separates the incurrent siphon cavity from the mantle cavity.

In response to stronger tactile stimulation (e.g. poking the siphon wall with a stylus) the paired muscle bundles of the valve contract in synchrony. The contraction of these muscle bundles causes withdrawal of the valve; thus opening the passage between the siphon and mantle cavities.

It is interesting to note that in the intact animal, the cleaning reflex requires contraction of the incurrent siphonal valve to allow egress of the jet of water from the mantle cavity. Equally pertinent is the fact that the neurons controlling the posterior adductor muscle (the contraction of which is involved in the expulsion of water from the mantle cavity) are activated *only* by strong tactile stimulation (Mellon, 1967; Mellon and Prior, 1970). The

activity of these motoneurons (hence the posterior adductor muscle) is inhibited by weak tactile stimulation of the siphons. Therefore, a correlation exists between the responses of the motoneurons that activate the adductor muscle (involved in the expulsion of water in the cleaning response) and the responses of the siphonal valve muscle which must be open to allow the exit of water.

The responses of the incurrent siphonal valve are in concert with the responses of the adductor muscle, both contracting in response to strong tactile stimulation.

On the basis of the foregoing observations, I suggest that the incurrent siphonal valve might temporarily entrap sand particles, thus preventing their entrance into the mantle cavity.

The siphonal valve could respond to sand grains falling on the siphons (presumably a weak tactile stimulus) by extending across the incurrent siphon cavity, entrapping the sand within the cavity. A subsequent contraction of the adductor muscles, synchronized with contraction (opening) of the siphonal valve muscle bundles, would expel a jet of water and the previously entrapped sand; the cleaning reflex.

Thus, the incurrent siphonal valve seems well suited for mediation of the "sand storage" suggested by Jacobson on the basis of behavioral observations.

A portion of this study was done at the Marine Biological Laboratory, Woods Hole, Massachusetts. This work was supported by NIH Biomedical Sciences Support Grant 5 SO5 RR07114-06 to the University of Kentucky and a Grass Foundation Fellowship in Neurophysiology.

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BOOK REVIEW

OYSTERS (TREATISE ON INVERTEBRATE PALEONTOLOGY). By H. B. Stenzel. 1971. Part N, Bivalvia, vol. 3, pp. 953-1224. 153 pls. in text. Geological Society of America, P. O. Box 1719, Boulder, Colo. 80302.

This excellent and well-illustrated systematic treatment of the subfamily Ostreina appeared three years ago but is still deserving of a review. Nearly half of the volume is a splendid treatment of the anatomy, distribution, ecology and phylogeny of the oysters. New genera and

subgenera are proposed, including *Hyotissa* for *Mytilus hyotis* Linné, and *Neopycnodonte* for *Ostrea cochlear* Poli. Our Caribbean Coon Oyster, formerly *Ostrea frons* Linné, is now in the genus *Lopha* Röding and the subfamily Lophinae. The volume contains an index and errata and revisions to the earlier two bivalve volumes 1 and 2 of Part N.

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