Two patterns of colonial water flow in an erect bilaminate bryozoan, the cheilostome *Schizotheca serratimargo* (Hincks, 1886)

Frank K. Mc Kinney

Department of Geology
Appalachian State University, Boone, N.C. 28608 USA.

Abstract : The cheilostome bryozoan *Schizotheca serratimargo* grows in the northern Adriatic Sea predominantly as adeoniform bushes, less commonly as free, eschariform sheets. Zooids occupied by functioning polypides are commonly confined to the outer 15-20 mm of branch tips. Lophophores placed centrally along branches are equi-tentacled and radially symmetrical; within the 0.5 mm band along branch margins, lophophores become progressively larger, more inequi-tentacled, laterally elongated, and supported on longer introverts out to the branch edge. These variations in lophophore parameters are related to the colonial pattern of feeding currents, which flow towards the flat branch surfaces, through lophophores, laterally in the space between lophophores and branch surface provided by the extended introverts, and out as a continuous narrow sheet along branch margins. Marginal outflow in the only eschariform sheet seen feeding is supplemented by outflow from chimneys spaced regularly across the frond surface.

Résumé : Dans la région septentrionale de la mer Adriatique, les zoariums de *Schizotheca serratimargo* (Bryozoaires, Cheilostomes) affectent généralement une morphologie buissonnante adéoniforme ; ils se présentent moins fréquemment comme des lames eschariformes libres. Les autozoécies fonctionnelles sont ordinairement limitées aux 15-20 premiers millimètres de la face externe de l'apex des ramifications. Les lophophores situés en position axiale le long des branches zoariales sont caractérisés par leur symétrie radiaire et des tentacules de longueur identique. Les lophophores autozoéciaux de la partie marginale des branches, sur une largeur de 0,5 mm, s'accroissent progressivement ; leurs tentacules sont de longueur inégale, les plus latéraux étant plus allongés ; ceux-ci sont portés par des introverts de plus en plus allongés vers la région latérale. Ces variations des paramètres lophophoriens sont corrélées avec le type zoarial, lui-même en relation avec les courants vecteurs d'apports nutritifs. Ces courants se dirigent vers la surface des colonies en traversant les lophophores ; ils convergent vers les portions latérales du zoarium, celles comprises entre l'aire à autozoécies normales et celles à introverts développés, puis s'écoulent en un étroit flux continu vers l'extérieur, le long des régions marginales des branches. A cet écoulement vers la région latérale du zoarium, seulement rencontré dans le cas des colonies laminaires eschariformes, se surimpose un flux nutritif additionnel transitant par des orifices régulièrement espacés perforant la surface de la fronde.

INTRODUCTION

The existence of colonial water flow patterns and their interaction with colony morphology have been investigated actively since the first paper on the topic was published in 1974 (Banta *et al.,* 1974 ; Cook, 1977 ; Winston, 1978, 1979 ; Cook & Chimonides, 1980 ; Lidgard, 1981 ; Nielsen, 1981 ; Okamura, 1984, 1985, 1987 ; McKinney, 1986 a, 1986 b ; McKinney *et al.,* 1986, 1987). The only erect bilaminate colonies (i.e. those with two sheets of zooids positioned back-to-back) included in these studies are diminutive and disordered portions of *"Hippodiplosia" insculpta* (Winston, 1979 ; Nielsen, 1981).

Two forms of rigidly calcified, erect bilaminate Bryozoa incorporate most erect bilaminates. These have been termed eschariform, characterized as "Zoarium bilaminate, foliaceous; attached to the substratum either by radicles or direct adherence" (Stach, 1936, p. 62), and adeoniform, originally described as "rigid, bilamellar, lobate zoaria"" (Brown, 1952, p. 32). Adeoniform branches have a near-inviolate maximum width of 5 mm, an upper limit that has existed for the almost 500 ma historical record of the phylum (McKinney 1986 a). Moreover, each adeoniform species has characteristic and narrowly varying branch width, bifurcation angle, and branch link length (Cheetham et al., 1980, 1981; Cheetham & Hayek, 1983; Cheetham, 1986). Eschariform growth, however, is less precise, commonly generating irregularly shaped boxworks with widely varying expanses of foliaceous sheets even within a single species.

Taylor (1979) and McKinney (1986 a) predicted that erect bifoliate bryozoans expel filtered water along the keel-shaped edge where the two zooidal orifice-bearing surfaces meet. This was reported for "Hippodiplosia" insculpta by Nielsen (1981), who suggested that confinement of the outflow of filtered water to the marginal keel puts a hydrodynamic limit on width of the species because of increased resistance to flow as the colony size increases.

The purpose of this paper is to describe the interaction of colonial flow patterns and colony morphology in Schizotheca serratimargo as a test of the predictions that a) filtered water is vented only from branch margins in adeoniform species (Taylor, 1979; McKinney, 1986 a) & b) bifoliate surfaces appreciably greater than 5 mm in width supplement marginal outflow of filtered water by outflow at local, regularly spaced spots (chimneys) across the colony surface (McKinney 1986 a).

MATERIALS AND METHODS

Living colonies of the ascophoran cheilostome Schizotheca serratimargo (Hincks 1886) were collected by divers from rock (gravel to boulder and rock ledge) bottoms in the vicinity of Rovinj, Yugoslavia (9 September 1987 and 20 June 1988, west side and northwest tip of San Giovanni Island, ~20 meters depth; 14 September 1987 and 7 June 1988, west side of Banjole Island, 5-20 meters depth; 10 June 1988, within Lim Channel, about 3 km from mouth, 20 m depth; 23 June 1988, west side of Santa Maria Island, ⩽20 m depth). Colonies were kept live in running seawater for one to nine days until completion of study in the Ruder Boškovič Center for Marine Research, Rovinj. Specimens were examined, and measurements of morphology and colony-generated currents were made, with a Wild M8 dissecting microscope. Colonies were examined in still water in 200 and 400 cc bowls. A small number of 12 µm neutral bouyancy beads were added to clarify current patterns and for determination of current velocity. The only food available in the water was that present in the unfiltered water. This water, derived

from 5 m deep offshore of Rovinj, should have had approximately the same types of food particles available to the colonies in their natural habitat. Incurrent velocities were measured by timing the travel of beads and other particles from 400 μm above to tops of lophophores; velocities of outflow were measured similarly but for travel from tentacle tips to 1 600 μm away. Travel was timed by a watch stoppable at increments of 0.05 second.
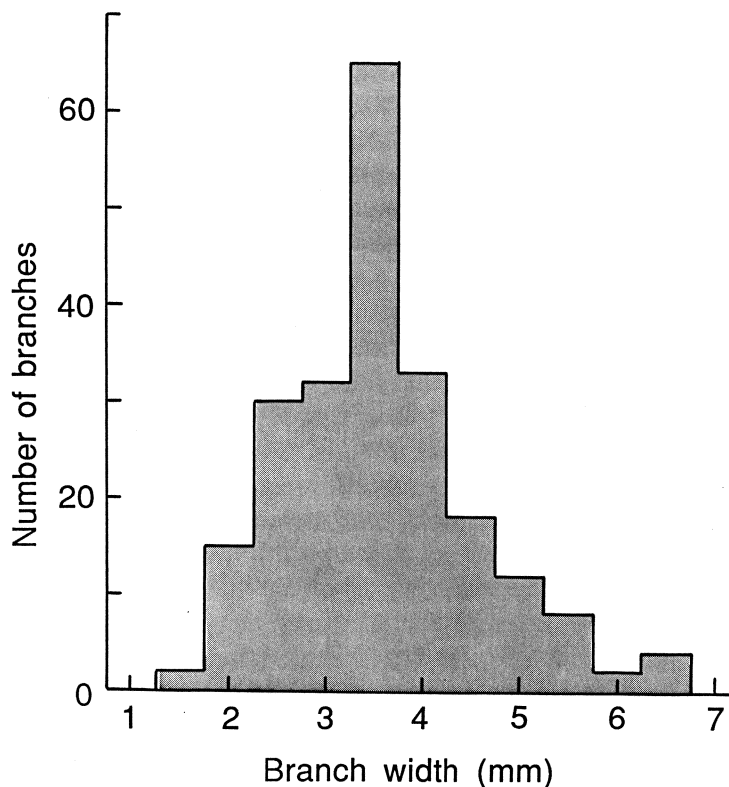

Fig. 1 - Histogram of widths of branches in *Schizotheca serratimargo* N = 221; mean = 3.56 mm; standard deviation = 0.98 mm; mode = median = 3.5 mm.

RESULTS

The colonies of *Schizotheca serratimargo* collected from the Adriatic Sea in the vicinity of Rovinj were up to 21 cm in diameter and predominantly adeoniform, with branch width averaging 3.56 mm (see Pl. I, Fig. A & C, Fig. 1). Only one of these colonies had a broad, eschariform frond (see Pl. 1, Fig. B). Distal surfaces of the branches were occupied by polypide-containing autozooids, with large vicarious avicularia ranged along the branch margins (see Pl. I, Fig. D & Pl. II, Fig. A).
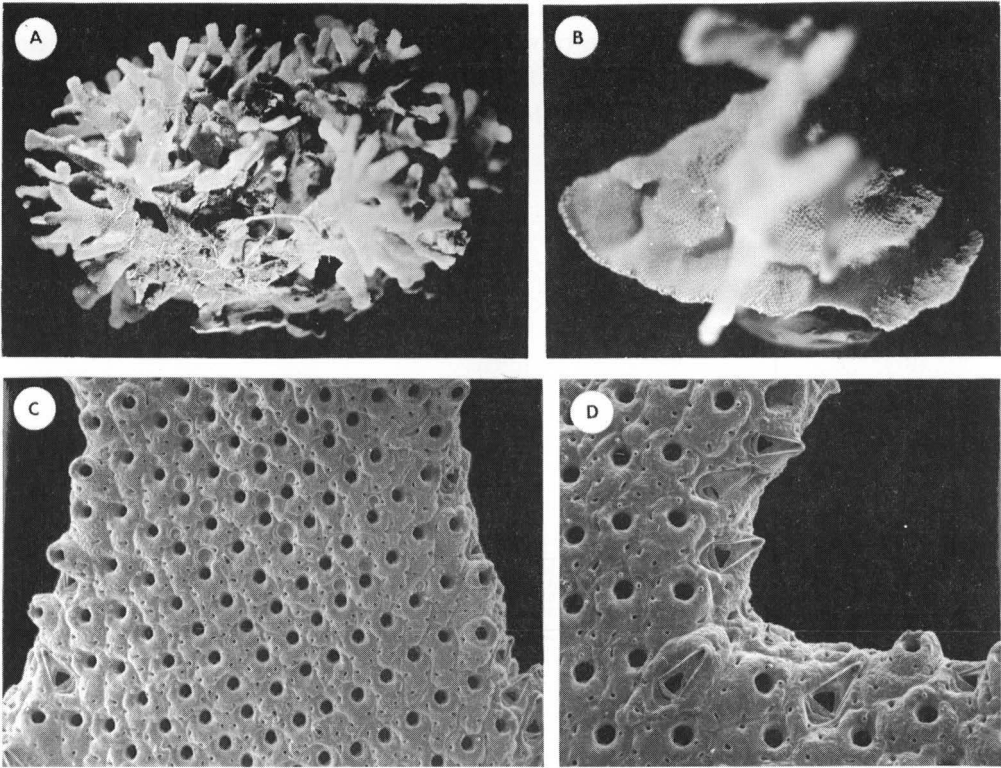
PLATE I - *Schizotheca serratimargo* (Hincks). A, light photograph of adeoniform colony with fouling
organisms (especially the annelid *Filograna*) on older portions of colony, x 1. B, light pho-
tograph of colony with adeoniform and eschariform portions, x 2. C, SEM micrograph of
branch portion, showing regular disposition of zooidal orifices, x 22. D, SEM micrograph
showing several large vicarious avicularia intercalated along branch margin, X31.

Proximally, approximately 15-20 mm from branch tips, autozooids were heavily
calcified, with abundant adventitious avicularia (see Pl. II, Fig. B & C). Typically,
polypides were present in autozooids only to a depth within colonies of 15-20 mm
from branch tips; proximal to this, branch surfaces were heavily fouled by green
and red algae, other Bryozoa, hydrozoans, sedentary annelids, ascidians, and
sponges (see Pl. I, Fig. A & Pl. II, Fig. D). Green algae and occasional spirorbid
annelids (Pl. II, Fig. B) were the first fouling organisms to invade, and some zooids
continued to contain functioning polypides in this region.

Larger colonies tended to have a smaller proportion of the available surface area
occupied by polypide-containing zooids because of the increase in the fouled,
polypide-barren proximal portion of the colony as it grows. However, even large
colonies had a substantial proportion of their surface area occupied by polypides
(see Fig. 2).

Approximate % area with polypides

100

80

60

40

0.1   0.5   1   5   10

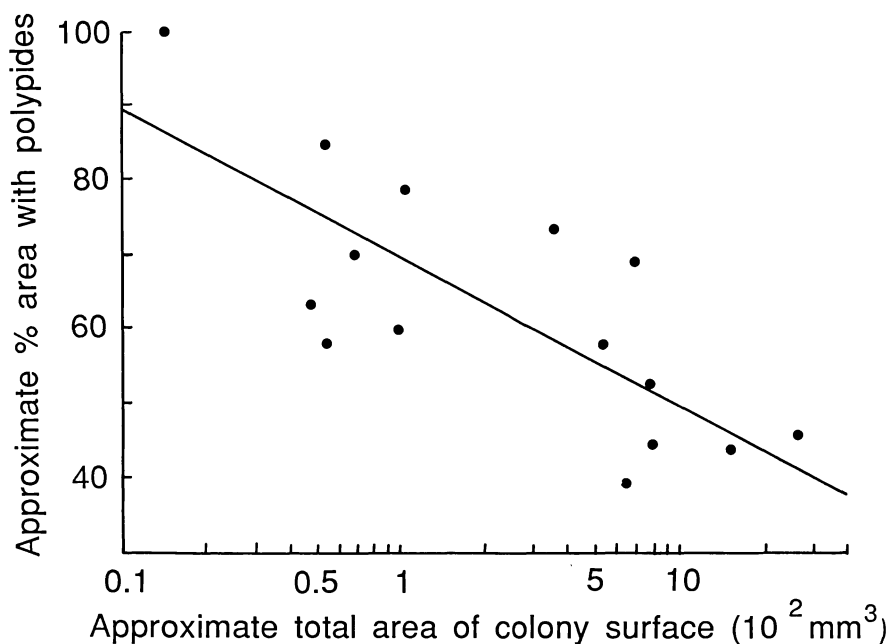Approximate total area of colony surface (10^2 mm^3)

Fig. 2 - Semilogarithmic plot of approximate area of total colony surface area against the approximate percentage of the total area that is occupied by feeding zooids in colonies of *Schizotheca serratimargo*. Y = 69.36 - 19.83 logX; coefficient of correlation (r) = -0.791.

When feeding, the adeoniform colonies protruded lophophores from all zooids in the nonfouled distal portions of branches. This produced a continuous mat of slightly overlapped, funnel-shaped tentacle bells across the two flat surfaces of the branches (see Pl. III). Number of tentacles per lophophore averaged 14.0 and ranged from 12-15 (standard deviation = 0.32, N = 51). There is no gradient in tentacle number from margin to center of branches; 49 of the 51 zooids whose tentacle number was recorded had 14 tentacles.

Lophophores across the mid-portions of branches (>500 μm from branch margins) were radially symmetrical, equi-tentacled (see Fig. 3), and averaged 513 μm in diameter (standard deviation = 79 μm). They were borne on short (~40 μm) introverts in the middle of branches, where they extended to a total height of ~500 μm above skeletal surfaces. Increase in introvert height towards branch margins (see Fig. 4) resulted in a continuous increase in height to about 100 μm at a distance of 500 μm from branch margins. Within the outer 500 μm of branch surfaces, the introverts continued to lengthen, and in the same region lophophores progressively leaned toward the edge of the branch, had increases in maximum tentacle length and in maximum diameter normal to the margin, and became asymmetrical in tentacle length (see Fig. 3), with the longer tentacles extending towards the branch margins. The row of zooids along the edge had the greatest
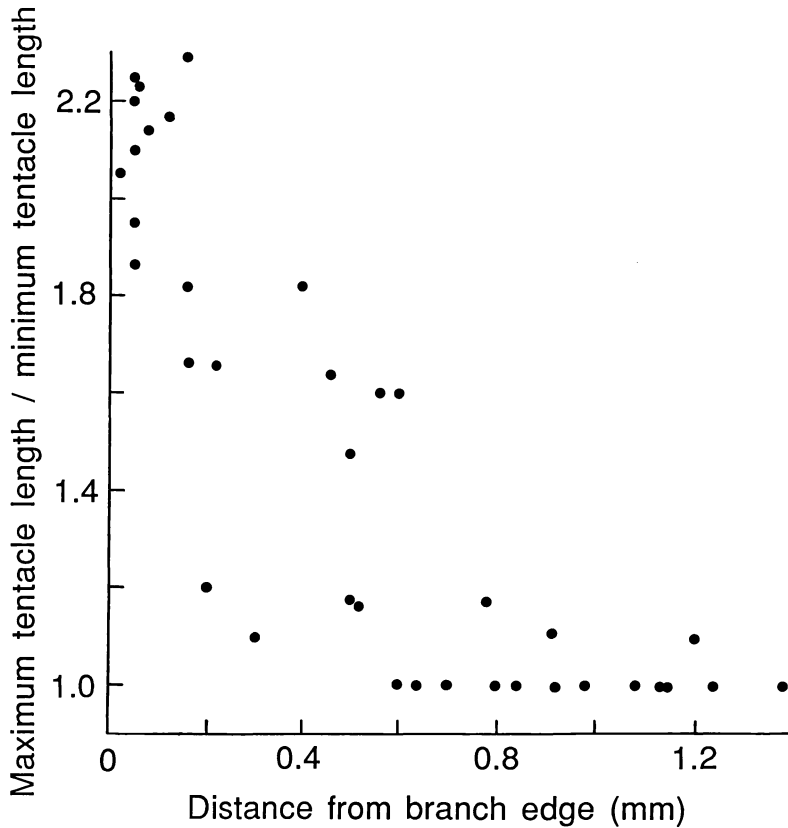
Fig. 3 - Plot of lophophore asymmetry (maximum tentacle length/minimum tentacle length) against distance from branch edge in *Schizotheca serratimargo*.

inclination, longest tentacles, and greatest asymmetry, so that their lateral tentacles extended almost parallel with the midplane of the branch for a distance of about 700 μm beyond the edge.

Morphology therefore varied both along and transverse to the branch length (i.e. growth direction). Transverse to growth direction, in addition to occurrence of large vicarious avicularia along branch margins, there is a gradient in lophophore size, shape, and orientation due to functional requirements. Along growth direction, there are two pronounced zones of ontogenetic change, one along the very margin of the branch tips where feeding zooids are added to the colony by zooidal budding, and one several millimeters proximal to branch tips where feeding zooids senesce and many adventitious avicularia are budded. The zone of feeding zooids therefore appears to be morphologically quite distinct from the more proximal senesced and fouled region, and fragments from the different regions could be mistaken for different taxa if seen out of context of entire colonies.
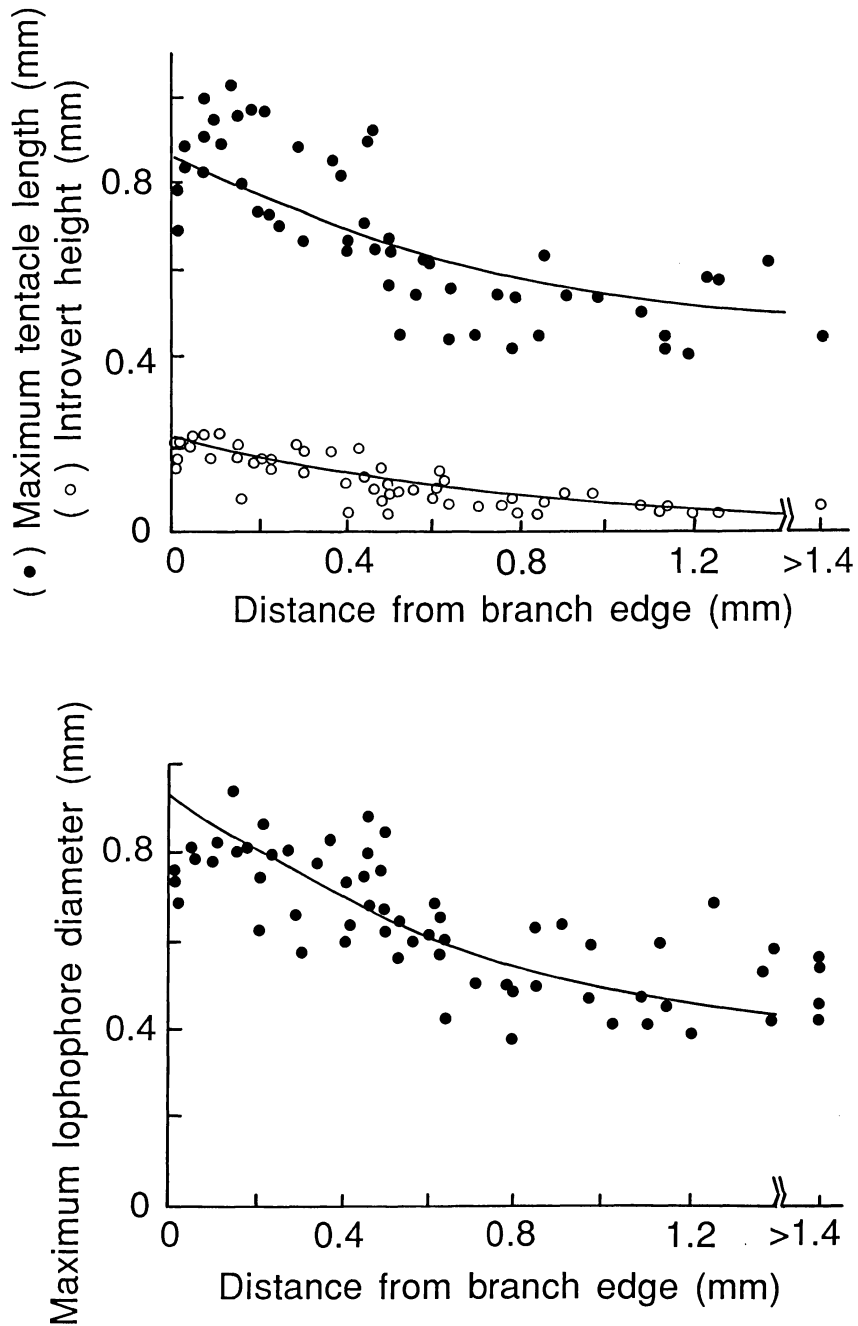
Fig. 4 - Plots of A, maximum tentacle length and introvert height, and B, maximum lophophore diameter against distance from branch edge *Schizotheca serratimargo*. For maximum tentacle length, $Y = 840.33 - 0.450X + 1.38 \times 10^{-4}X^2$, $r = -0.746$; for introvert height, $Y = 200.85 - 0.193X + 5.68 \times 10^{-5}X^2$, $r = -0.767$; for maximum lophophore diameter, $Y = 927.44 - 0.680X + 2.38 \times 10^{-4}X^2$, $r = -0.740$.
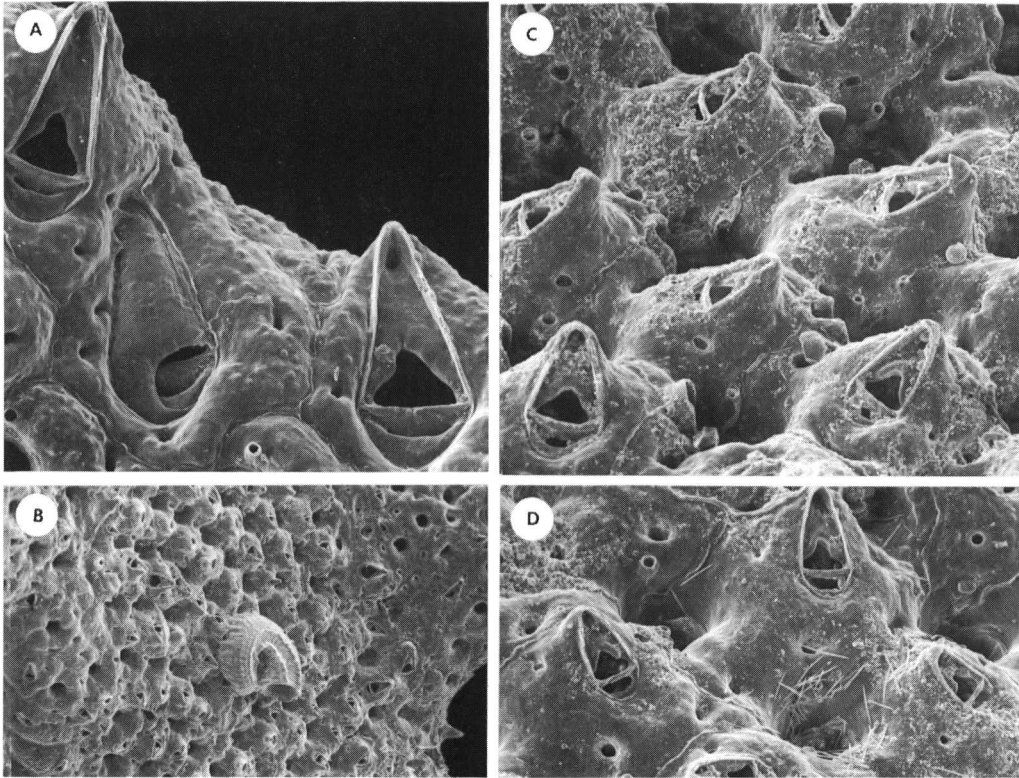
PLATE II - *Schizotheca serratimargo* (Hincks). A, SEM micrograph of three branch-margin avicu-
laria, x 110. B, SEM micrograph of area about 2 cm proximal to branch tip, where nume-
rous adventitious avicularia have been budded and a spirorbid annelid has fouled the
surface, x 22. C, SEM micrograph of adventitious avicularia that are added about 15 mm
proximal to branch tips, x 110. D, SEM micrograph of surface in proximal portion of a
colony that has been fouled by a sponge bearing monaxon spicules, X110.

Incurrent velocity above the mat of feeding lophophores averaged 0.94 mm/sec
(standard deviation = 0.37 mm/sec, N = 17). Food particles were filtered from the
water as it passed between tentacles of the lophophores. The filtered water then
flowed laterally between the base of the lophophores and the colony surface to-
wards the closer branch margin.

Outflow of filtered water was confined to a continuous strip along margins of
branches of normal widths, where water from both sides of the branch was combi-
ned into a single stream approximately 1.0 mm thick. Velocity of outflow where
measured for a branch 3.2 mm wide was 3.12 mm/sec (standard deviation = 1.25,
N = 11) when all lophophores were protruded and functioning.

Branches of adeoniform portions of colonies have widths clustered between 3
and 4 mm. Less than 3 % (6 of 221 measured) of the branches are >5.5 mm in
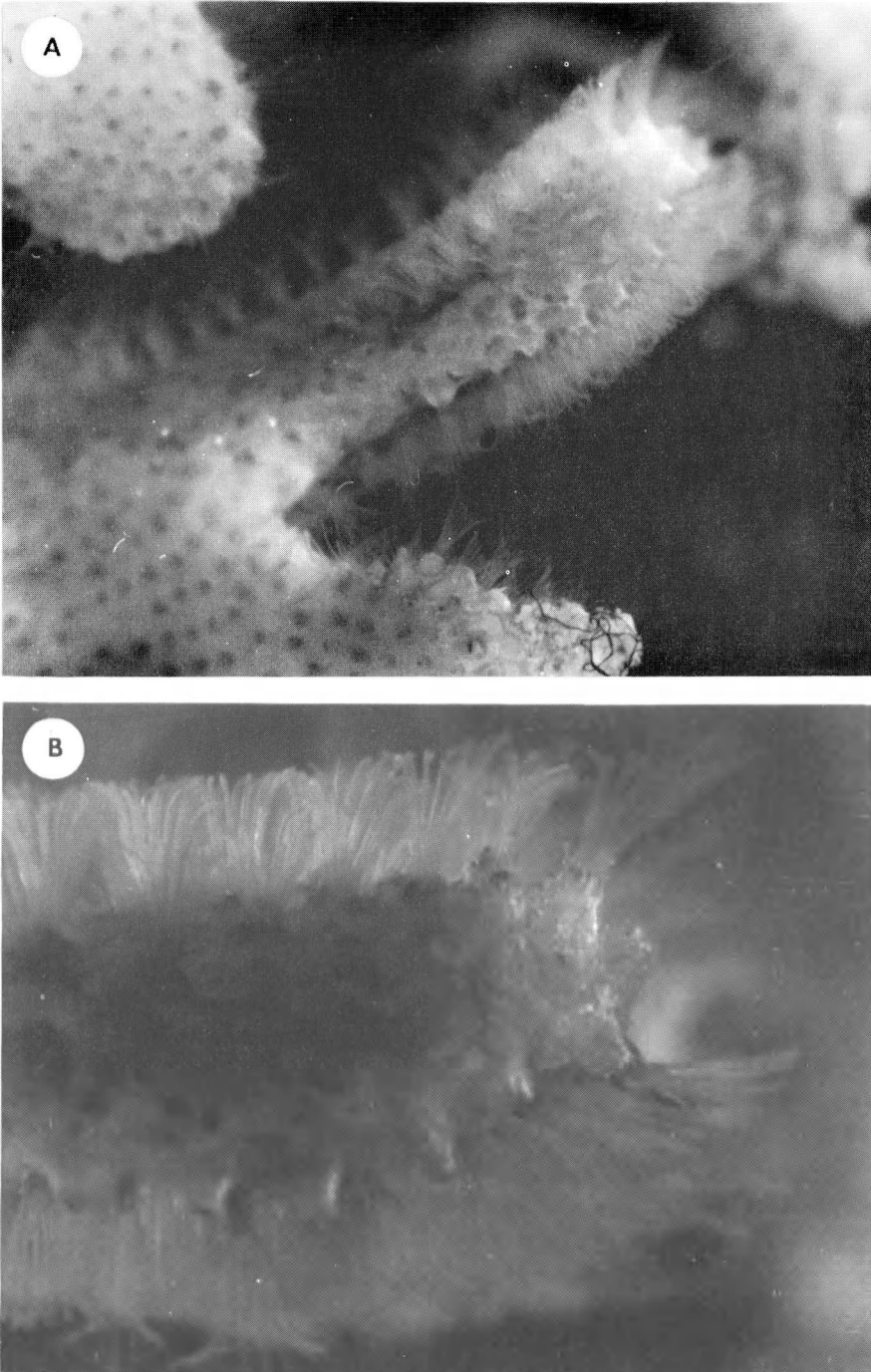width. These wider branches all have a median keel or sulcus. In the few instances

PLATE III - *Schizotheca serratimargo* (Hincks). A, light micrograph of feeding colony, ~X10. B, light micrograph of branch margin of feeding colony, showing asymmetry and lateral inclination of marginal lophophores, ~X25.

where such unusually broad branches were examined while colonies were feeding, the median keels and sulci served as supplementary loci of outflow.

In one small specimen, parallel branches had fused into a continuous bifoliate sheet, resulting in an eschariform portion 56 x 24 mm (see Pl. 1, Fig. B). The fused former margins of the branches were less strongly colored than the general orange-peach surface of the colony, were characterized by giant vicarious avicularia, and commonly were of a slightly different elevation from the general surface of the sheet. Elongate chimneys with vigorous outflow occurred over these regions. They were spaced an average of 3.04 mm (standard deviation = 0.65 mm, N = 5) from center-to-center and averaged 2.80 mm (standard deviation = 0.57 mm, N = 6) in length and 0.47 mm (standard deviation = 0.10 mm, N = 6) in width. The ratio of chimney area to incurrent area was 1 : 7.5.

DISCUSSION

Schizotheca serratimargo exhibits both adeoniform and eschariform morphologies. Therefore, it provides a good test of the hypotheses that adeoniform colonies expel filtered water only along the branch margins, that this limits branch width, and that eschariform colonies expel filtered water from chimneys as well as frond margins. Results of this study support each of the three hypotheses.

Variations in polypide characteristics, including size and tentacle number, have been shown to be affected by quality of food in laboratory cultures of other gymnolaemate bryozoans (Jebram 1973, 1979), and numerous authors have reported variation in tentacle number within bryozoans that grew in their native habitat. *Schizotheca serratimargo* exhibited neither lateral nor proximal gradient in tentacle number; almost all zooids had 14 tentacles. The gradients toward branch margins in tentacle length, lophophore shape, and introvert height, do not appear to be related to differences in nutrition, because incurrent velocity of food-bearing water was uniform across the branch surface. In addition, nutrients can be passed laterally among zooids through interzooidal communication pores, thereby at least partially offsetting local variations in nutrition within the feeding portions of a colony. The gradients toward branch margins in characteristics of the zooidal feeding structures appears to result from a gradient in functional requirements, as discussed below.

In every case in which adeoniform branches of typical width were examined while feeding, venting of filtered water appeared to be exclusively along the branch margins. A rough check for presence of visually undetected chimneys on the adeoniform branches may be made based on the principle of continuity, which would require that incurrent velocity (Ui) times incurrent area (Ai) be equal to velocity of outflow (Uo) times area of outflow (Ao), i.e. :

$$UiAi = UoAo.$$

If branch margins constitute the only escape for filtered water, then Uo and Ao are simple terms for velocity and area at colony margins. Solving this for both sides of the 3.2 mm-wide branch with incurrent velocity of 0.94 mm/s, escape velocity at branch margins of 3.12 mm/s, and width of outflow at branch margins approximately 1.0 mm,

$$[0.94\text{mm/s}][2(3.2 \text{ mm})L) = [3.12 \text{ mm/s}][2(1.0 \text{ mm})L]$$
$$3.01 \text{ mm}^2/\text{s}.L = 3.12 \text{ mm}^2/\text{s}.L,$$

where L = some specified length of branch. The integer 2 in the left term of the unsolved equation is required to account for inflow towards both sides of the branch; the integer 2 in the right term is required to account for outflow from both branch margins. The discrepancy in the two figures is less than 3 % of their value, which is well within the range one would expect given the potential error for some of the measurements.

In order to accommodate filtered water approaching branch margins of adeoniform branches if *S. serratimargo* were wider, either a) introverts must become longer, b) velocity of the confined flow must increase, c) incurrent velocity must be reduced, or some combination of the three means of accommodation must occur. None of these seems particularly appropriate. Reduced incurrent velocity has the obvious disadvantage of reduction in nutrient capture, with attendant reduction in growth and reproductive potential.

After water passes through lophophores, its passage to the branch margin is resisted by friction generated by the colony surface as well as by interference provided by the introverts of other lophophores encountered (McKinney 1986 b). Therefore, because of the greater distance that it must travel within the confined space and the greater number of introverts that it must pass, water processed by the median zooids in a branch is subject to more resistance to its movement than is that processed by more marginal zooids. In addition, each rank of zooids towards the colony margin adds another increment to the volume of flow; therefore, velocity would increase linearly because of these regular incremental additions to volume if cross-sectional area of flow were to remain constant. With regard to resistance to flow of water towards lateral margins of branches, each introvert is a cylinder oriented perpendicular to the direction of flow. An approximation of drag (D) generated by each is:

$$D = \frac{C_D \, e \, AU^2}{2}$$

where C_D is a coefficient for drag that must be recalculated each time that velocity, size, density, or viscosity is changed, e is density (1.028 for average seawater), A is cross-sectional area of the cylinder, and U is velocity (Vogel, 1981). It is clear that a linear increase in velocity raises drag generated by the introverts by the second power of the amount of increase in velocity. This would have a greater metabolic cost than if velocity did not increase.

This would be the case if introverts were the same length across the branch. However, introvert length increases steadily from <40 μm near centers of branch surfaces to about 200 μm at branch margins, which allows an approximately constant velocity of flow between colony surface and lophophore base, thereby preventing such geometric increase in resistance to flow towards branch margins.

Longer introverts would result in a linearly proportional increase in shear forces on them due to drag. The introverts mechanically are cantilever beams with respect to the lateral outflow, and as such, the stress (σ) along the introvert is:

$$\sigma = \frac{4Dh}{\pi r^3},$$

where D is the deforming force (drag), h is the height above the point where the center of force is located (length of introvert/2), and r is radius of the introvert at the point in question (Wainwright et al., 1976). Progressively longer introverts do accommodate outflow of a progressively greater discharge of filtered water towards the branch edge without an increase in velocity, thereby circumventing a second power increase in stress on the introverts due to drag. But still, stress increases geometrically because increase in introvert length increases both D and h. Placement of the lophophore at a greater distance from the refuge in the skeleton might also result in higher predation rates.

The appropriate values have not been measured or calculated to quantitatively assess an approximate limit on adeoniform branch width for S. serratimargo. However, 95 % of the branches are less than 5.5 mm wide, which suggests empirically that it is disadvantageous for S. serratimargo to produce branches broader than this and that 5.5 mm or slightly less approaches the limit in this species for efficiently functioning branches in which outflow of filtered water is confined to their margins.

The only eschariform surface of S. serratimargo that was seen live in this study possessed regularly spaced chimneys with size, spacing, and area relative to incurrent regions consistent with the attributes of chimneys previously described for encrusting species (Banta et al., 1974; Cook, 1977; Winston, 1978, 1979; Cook & Chimonides, 1980; Lidgard, 1981). Even though a single occurrence does not demonstrate a pattern, the presence of chimneys in the single living colony observed demonstrates that they do occur in this eschariform example, which is consistent with prediction (McKinney 1986 a). In addition, the presence of chimneys on the eschariform surface, which is well beyond 5.5 mm wide, is consistent with the notion that S. serratimargo has a maximum branch width above which marginal outflow of filtered water must be supplemented by flow out of chimneys.

ACKNOWLEDGMENTS

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