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Alcyonidium nodosum O'Donoghue and de Watteville occurs on whelks, *Burnupena papyracea*, off the south and western Cape, South Africa. A description is given of colony structure and organization in relation to reproductive and inferred feeding functions. The thick, encrusting colony is mammillate, each mammilla comprising a group of large male zooids bearing tall, funnel-shaped lophophores. Between mammillae are smaller female zooids bearing shorter, goblet-shaped lophophores. At the time of collection, October to November, colonies were actively reproducing, with the coelom of male zooids full of mature sperm. The lophophore of female zooids incorporated an intertentacular organ, while ovaries with developing oocytes and free ovulated eggs were both present. Eggs were twice observed being discharged through an intertentacular organ. *Hippoporidra dictyota* sp. n., from rocky reefs off Beaufort, North Carolina, is described. Its colonies encrust pagurid-inhabited shells and display the same colonial, and inferred functional, characteristics as those of *A. nodosum*. Male zooids on the mammillae bear reduced, non-feeding lophophores and are surrounded by autozooids, many bearing ovicells and presumed female, with normal lophophores. The feeding currents and flow patterns found in mammillate colonies, and their role in sperm discharge, are discussed. It is concluded that these two unrelated, shell-encrusting bryozoans have evolved identical hydrodynamic feeding systems which have been utilized to benefit reproduction. The mammillae provide foci for exhalant currents: the placement of male zooids therein concentrates all the sperm in a strong discharge, rising clear of the parent and enhancing its water-borne passage between colonies.

KEYWORDS: Reproduction, oviparity, monticules, exhalant chimneys, sperm discharge, *Alcyonidium nodosum*, *Hippoporidra dictyota* sp n., *Paguristes*.

Introduction

Alcyonidium nodosum O'Donoghue and de Watteville is a ctenostome bryozoan that encrusts the shells of whelks, mainly *Burnupena* (formerly *Comminella*) *papyracea*

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(Bruguière) on the shore and subtidally in the cooler Atlantic waters off the Western Cape (South Africa). Branch *et al.* (1994) show the distributions of these species as extending from the Orange River to False Bay but *A. nodosum* is distributed further eastwards, at least to Port Elizabeth (Yvonne Dempster, personal communication), by utilizing the shell of another whelk, *B. pubescens* (Küster). The bryozoan colony is thick and mammillate; it is thought to be toxic and has been shown (Barkai and McQuaid, 1988) to protect the thin-shelled *B. papyracea* from predation by rock lobsters *Jasus lalandii* (Milne-Edwards). *Alcyonidium nodosum* occurs in orange-brown (figure 1A) and deep purple colour morphs, which have been illustrated by Branch *et al.* (1994: figures 48.5 and 76.5b).

The mammillate nature of *A. nodosum* was first described by O'Donoghue and de Watteville (1944). They observed that the mammillae were often 'almost in regular rows' (actually spiralling parallel to the whorls of the shell) but that this was not a consequence of shell sculpturing (the shell is so finely striate as to be almost smooth): the 'hemispherical nodules … are brought about by the presence … of a number of zooecia, varying from 4 to 20, which are much larger and deeper than the zooecia over the remaining, lower parts of the colony'. The authors adduced no explanation for these 'larger zooecia'. Cook (1977) published some inferences on colonial feeding currents based on the mammillate morphology which characterizes this species. Bryozoans feed by extracting particles from water which is driven downwards and outwards through the expanded lophophores. This results in a layer of water under pressure adjacent to the colony surface. The hydrodynamic solution of venting through 'excurrent chimneys' is now well known. It is achieved through a system of rather regularly arranged spaces, sometimes marked by an empty zooid from which surrounding lophophores bend away, out of which water flows upwards and away from the colony. Such exhalant 'chimneys' were first described by Banta *et al.* (1974) in the flat colonies of *Membranipora membranacea* (L.). Many bryozoans, such as species of *Celleporaria* and composite species of *Disporella*, as well as *Alcyonidium nodosum*, have a mammillate surface and it has been shown or inferred that such mammillae, or monticules, mark the sites of exhalant chimneys (Banta *et al.*, 1974; Cook, 1977; Taylor, 1979; Cook and Chimonides, 1980).

In the cheilostomate genus *Hippoporidra*, species of which also have mammillate colonies but live on shells occupied by hermit crabs, zooidal dimorphism occurs.

Fig. 1. *Alcyonidium nodosum* (A–F) and *Hippoporidra dictyota* (G, H). (A) *A. nodosum* (deep orange form) encrusting shell of the whelk *Burnupena papyracea* (shell length 44 mm). Specimen from Kalk Bay, South Africa, 3 November 1997. (B) Part of another colony showing mammillae and large, sperm-filled male zooids (frame size 12×9 mm). (C) Somewhat elongated mammillae with sperm-filled male zooids. (D) Single mammilla with five sperm-filled male zooids, and a number of intercalary buds (frame size 4×3 mm). (E) Vertical section through mammilla consisting of several sperm-filled (pink stain) male zooids and intercalary buds; photograph using Wild Makroskop M420 (illustrated section 1.8 mm long). (F) Photomicrograph of ovary, situated between the stomach caecum and the basal wall of the zooid (blue), containing developing oocytes, with nucleoli stained deep red (longer axis of ovary $\approx 100 \, \mu m$). (G) Six specimens of *Hippoporidra dictyota* sp. n., each a multilaminar colony encrusting a gastropod shell occupied by the anomuran *Paguristes tortugae*; from Black Rocks, off Beaufort, North Carolina, 4 August 1977. (F) One of the specimens embedded in resin, sawn transversely, and polished, showing how the contrasting colour bands of mammillae and surrounds elongate with the growth of the colony; the gastropod shell can be seen internally (horizontal diameter of colony = 12.25 mm).

The male zooids, each with much reduced non-feeding lophophore, are grouped on the mammillae (Cook, 1968, 1977; Ryland, 1979b; Cook and Chimonides, 1980; Ryland and Bishop, 1993). The surrounding feeding lophophores generate the current which outflows from the chimney, presumably carrying sperm which are shed through the terminal pore of some or all of the tentacles (cf. Silén, 1966, 1972;
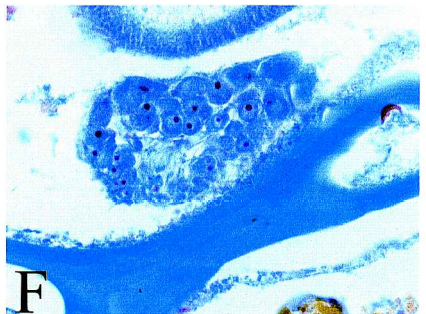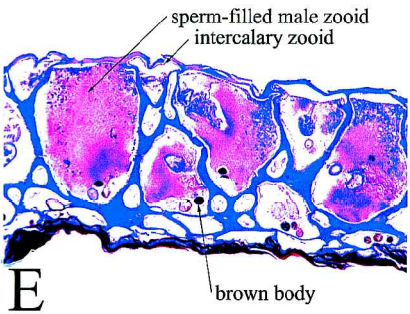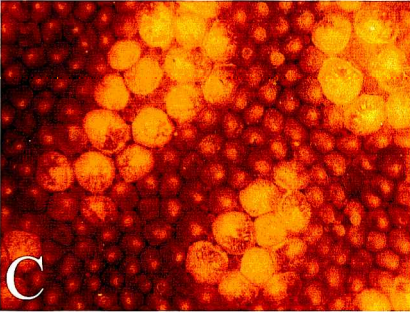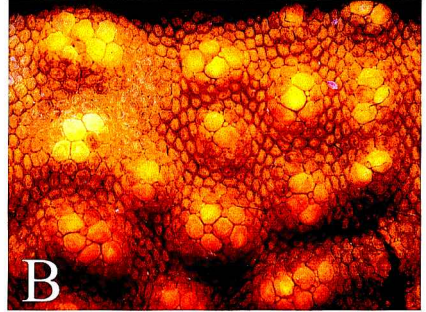
Bullivant, 1967). The chimneys are thus thought to provide a mechanism to aid the dispersal of sperm away from the colony. However, in several described species of *Alcyonidium*, zooids as well as colonies are hermaphroditic (Prouho, 1892; Cadman and Ryland, 1996).

It was already apparent from the observations of O'Donoghue and de Watteville (1944), and of Cook (1977), that zooidal dimorphism occurs in *A. nodosum*. The object of the present investigation was to determine the nature of this dimorphism and, especially (in view of a contrary indication in Cook, 1997), whether the mammillae were associated with male zooids and the dispersal of sperm. When this was established (see below), the extraordinary similarities between *A. nodosum* and a species of *Hippoporidra* (a bryozoan genus only distantly related), which I had observed earlier (Ryland, 1979b; Ryland and Bishop, 1993) became apparent. I had not been able to identify the species of *Hippoporidra* at the time and it has become clear from subsequent work (Taylor and Cook, 1981) that it is undescribed. A taxonomic description is therefore included, to present a fuller account of the colonial morphology and facilitate a proper comparison between *Alcyonidium nodosum* and the *Hippoporidra*.

Material and methods

A visit to Cape Town in 1997 provided an opportunity to examine live colonies of *Alcyonidium nodosum*. Whelks bearing *A. nodosum* were collected on 31 October and 2 November from the intertidal reef at Woolley's Pool, Kalk Bay, on the False Bay side of the Cape Peninsula. The whelks and associated bryozoans were maintained under circulation and aeration in the Department of Zoology, University of Cape Town. Observations were made under a stereo-microscope with the whelks in small containers. Several peels of the *Alcyonidium*, with some attached periostracum, were fixed in formalin (10% commercial formaldehyde in sea water) and returned to Swansea. *Alcyonidium* often does not section well following wax embedding; therefore, a double embedding protocol was followed. After dehydration through a graded ethanol series, the primary embedding was in two 24 h changes of 1% solution of Merck Necoloidine (Stanvis) in diethyl ether mixed with an equal volume of absolute (synthetic grade) ethanol, followed by ~15 h in chloroform. Secondary embedding was in three 8 h changes of Merck pastillated Gurr Paramat paraffin wax blended with synthetic polymers (58°C). Blocks were sectioned at 7 μm and stained with Mallory's Triple for optical microscopy. Measurements were made with an eyepiece linear scale or (nearest neighbours) concentric rings micrometer.

The original specimens of *Hippoporidra* were obtained by scuba from the '10 fathom fishing banks' or 'Black Rocks' (Pearse and Williams, 1951; Maturo, 1968), which lie ~10 nautical miles SSW of Cape Lookout, near Beaufort, North Carolina, on 4 August 1977. These banks, the outermost of which approximate the landward boundary of the Gulf Stream, are noted for their Floridian–Caribbean benthic fauna (Cerame-Vivas and Gray, 1966; Maturo, 1968). The colonies were photographed (figure 1G) and examined alive under a stereo-microscope, with the notes and sketches made using measurements providing the basis for subsequent drawings (Ryland and Bishop, 1993). Additional specimens, very similar in appearance and from approximately the same locality, collected in July 1983, have also been used for taxonomic description. One of these has been examined with a scanning electron microscope after treatment with bleach, to remove soft parts, ultrasonic cleaning, and gold coating.

Description and morphology

Alcyonidium nodosum O'Donoghue and de Watteville, 1944

The colony of *A. nodosum* is thick, mammillate, and deep orange or purple in colour. The mammillae, with a nearest neighbour distance of ∼2.6 mm (table 1), are elevated ∼1 mm above the surround; they appear to follow a spiral course parallel to the whorls of the shell, although the shell itself is almost smooth. The summits of mammillae are occupied by large zooids, the surrounding area by smaller zooids. Those occupying the mammillae, as O'Donoghue and de Watteville (1944) noted, are very large (∼0.65 × 0.55 mm, table 1) and polygonal, but often associated with small intercalary zooids (figures 1D, E). Sectioning showed these large zooids to be deeper than wide (figures 1E, 2A), extending virtually to the base of the colony. They overlay a few small, defunct and presumably neanic zooids.

The area between the mammillae comprises much smaller (∼0.43 × 0.38 mm), variously polygonal zooids (figures 1B–D, 2B). The mammilla zooids in freshly collected specimens everted tall lophophores of 11–12 tentacles, each raised on an elongated 'neck' composed partly of an oral papilla and partly of the evaginated tentacle sheath (see figure 6). The lophophores displayed marked departure from radial symmetry, the adneural tentacles being longest. Surrounding zooids had less elevated lophophores, which were smaller though comprising more (15–16) tentacles, and displayed little departure from radial symmetry. The tentacles of both types of lophophore appeared to carry the normal complement of cilia and were feeding. The lophophores of surrounding zooids emerged readily in the vigorously moving water of the holding tanks but were reluctant to do so in small containers under the microscope. Though several authors have inferred that mammillae determine the position of permanent exhalant chimneys (Banta *et al.*, 1974; Cook, 1977; Taylor, 1979; Cook and Chimonides, 1980), the failure of lophophores to emerge in large numbers made it impossible to verify this.

The mammilla zooids are closed by a sphincter muscle (figure 2A), have a functional polypide with conspicuous retractor muscle fibres, and generally contained several small brown bodies. At the time of collection, at the end of October, these zooids had conspicuously white contents (figure 1B–D), which suggested that they contained spermatozoa. The sections confirmed that the vast coelomic lumen was filled with developing and mature spermatozoa (figure 1E). They suggest that testes were situated along the lateral and frontal zooid walls, where signs of spermatogenesis and clusters of sperm morulae were apparent. The remaining volume was packed with mature sperm. No ovary was ever seen, so that zooids are assumed to be male only.

An intertentacular organ was present in many of the lophophores of the surrounding zooids. The intertentacular organ is a small, internally ciliated, funnel located between the dorso-medial tentacles in lophophores of the anascan bryozoans *Conopeum*, *Electra* and *Membranipora*, and in some species of *Alcyonidium*, at certain seasons of the year. It was similar to that occurring in *A. mytili* Dalyell (see Cadman and Ryland, 1996) and in an unidentified species occurring on the west coast of Canada and northern USA (unpublished observation). In *Electra*, *Membranipora* and *Alcyonidium mytili* the intertentacular organ has been shown to function for the discharge of ova and either as a site for fertilization or for the ingress of sperm (Silén, 1966; Cadman and Ryland, 1996; Temkin, 1996), occurring only—with the

Table 1. Characteristics of mammilla (male) and surrounding (female or non-reproductive) zooids in *Alcyonidium nodosum* and *Hippoporidra dictyota*; measurements based on stereo-microscope eyepiece units, ×10 or ×20; smallest measurements are only approximations.

Attribute	*Alcyonidium nodosum*		*Hippoporidra dictyota*	
	Mammilla zooids	Surrounding zooids	Mammilla zooids	Surrounding zooids
Mammilla nearest neighbour distance	2.56 (±0.33) mm (n=20)		2.79 (±0.34) mm (n=20)	
Dimensions of mammillae (*A. nodosum*) or maculae[1] (*H. dictyota*)	A: No. of zooids: 6.40 (±2.78) 1.81 (±0.61)× 1.30 (±0.33) mm (ratio 1.42:1) (n=20) B: No. of zooids 9.85 (±7.40) 2.42 (±1.41)×1.40 (±0.31) mm (ratio 1.78:1) (n=20)		3.1 (±0.6)× 2.6 (±0.3) mm (n=20)	
Zooid dimensions[2] (mean (±SD))	667.5 (±69.4)× 552.5 (±89.6) μm ratio 1.24:1 (n=20)	425.0 (±69.4)× 376.4 (±23.6) μm ratio 1.13:1 (n=20)	558.5 (±74.5)× 414.5 (±41.2) μm ratio 1.36:1 (n=20)	—
Zooid surface area[3]	—	341.9 (±33.9) μm^2	—	—
Orifice dimensions (mean (±SD))	—	—	86.3 (±5.1)× 65.5 (±4.6) μm ratio 1.32:1 (n=20)	96.0 (±11.2)× 86.5 (±8.9) μm ratio 1.11:1 (n=20)
Total height of extended lophophore	1.25–1.75 mm	0.55 mm	~0.80–0.90 mm	~0.70 mm (max.)
Vertical height of funnel	0.75 mm	0.40–0.50 mm	~0.50 mm[4]	~0.35 mm (mid)
Top diameter of funnel	0.45–0.60 mm	0.40–0.50 mm	<0.20–0.25 mm[5]	0.35–0.50
Vertical height: diameter	~1.5:1	~1:1	—[5]	0.7:1
Longest tentacles	0.90 mm	est. 0.75 mm	est. 0.50 mm (shortest 0.40 mm)	0.45–0.63 mm
Number of tentacles	11–12 (n=10)	15–16 (n=8)	4	12
Peristome height	0.25 mm	not measured	—	—
Height of peristome+ introvert	0.75 mm	0.15–0.20 mm	—	—
Lophophore base diameter	0.125 mm	not measured	not measured	not measured
Intertentacular organ (ITO)	No	Yes	No	No
Egg in ITO: major and minor axes	—	~100×~50 μm	—	—
Egg diameter	—	~60 μm	—	—

Notes: 1, maculae: in *Hippoporidra* the spots (not equivalent to the mammillae or the sum of the mammilla zooids); mammillae: in *Alcyonidium* the sum of the mammilla zooids (for two colonies, A and B). 2, maximum linear dimensions. 3, (max. length+ min. length)/2 × (max. width+ min. width)/2. 4, based on the longer pair of tentacles. 5, the four tentacles were commonly not spread at all.

apparent anomaly of *Alcyonidium diaphanum* (Hudson)—in species that are oviparous. The presence of the intertentacular organ on the lophophore of the surrounding zooids indicated that they were actually or potentially female. This was confirmed when the process of egg discharge was observed. A slenderly ovoid object was observed just below the intertentacular organ in each of two neighbouring zooids. Shortly afterwards in one of the zooids this object, evidently an egg, was noted as being in the chamber of the intertentacular organ. Both lophophores were then retracted. The one with the egg in the intertentacular organ soon everted, with the egg now more distally situated. The egg slowly moved to the opening of the funnel, assuming spherical shape as it did so, until it was free and dropped down to the surface of the colony, where it remained. An egg of this size, approximately 60 μm diameter, is clearly destined to develop into a small cyphonautes larva (see Cadman and Ryland, 1996).

The serial sections showed that, between mammillae, the smaller zooids are multi-laminar, and only those near the frontal surface of the colony contain polypides (figure 2B). Such zooids contain a few small brown bodies whereas the more basal, enclosed zooids contain many. This suggests that each zooid supports several generations of polypides before being overgrown, presumably by zooid buds of intercalary origin as described in *A. mytili* (see Cadman and Ryland, 1996). The very small size of the accumulated brown bodies suggests that at least two arise from each polypide degeneration, as happens in certain other species of *Alcyonidium*. These zooids were female only and retained their functional lophophores whilst the oocytes were developing. Ovaries were present in many of these zooids, situated between the base of the stomach caecum and the body wall, and usually quite close to the latter (figures 1F, 2C–F). Small ovaries appear subspherical but later, when some of the oocytes are larger (figure 2E), they have a hollow, lens shape. At no stage of oogenesis, from small ovaries (figure 2C) through to the laying of eggs, was there any evidence of polypide degeneration. This accords with what has been described in the oviparous *A. mytili* (Cadman and Ryland, 1996); but in *A. nodosum* it is not known either whether the polypide degenerates prior to commencement of oogenesis or at what stage the intertentacular organ appears.

All developing oocytes contain a large germinal vesicle, which stains less densely with Mallory's than the ooplasm and yolk, and contains a single, prominent nucleolus (figures 1F, 2D–F). It appears that the follicle cells of the ovary dissociate and/or break down to release free oocytes into the coelomic lumen. These lack the germinal vesicle and nucleolus (figure 2G), which accords with what Temkin (1996) has described in an unidentified oviparous *Alcyonidium* from the Pacific coast of North America. The present observations are therefore consistent with Temkin's demonstration that fertilization (syngamy) occurs at about the time of ovulation of eggs from the ovary (though sperm transfer and insemination may occur earlier). Very few free eggs have been found in the sections cut, suggesting that they are spawned soon after ovulation (which contrasts with the species from North America, which may contain vast numbers of eggs, personal observation).

Sperm are presumed to be liberated in the usual bryozoan manner, via all or just the adneural tentacles, but no observations were possible with the magnification of a stereo-microscope. The huge production of sperm is one of the most striking features of reproduction in *A. nodosum* and emphasizes once again the need for bryozoans to overcome problems of dilution by diffusive and turbulent processes during sperm transfer. It was noted that the whelks tended to occur on the shore in

little groups, perhaps aggregating for mating purposes, but cross-fertilization between *Alcyonidium* colonies on different whelks will still present major problems (see Levitan, 1995; and Levitan and Petersen, 1995, for general discussion on sperm limitation and appropriate references).

Hippoporidra dictyota sp. n.

Hippoporidra Canu and Bassler, 1927 (family Hippoporidridae).

Generic diagnosis.   Colonies encrusting, multilaminar, mammillate or nodular, typically on pagurid-occupied gastropod shells. Autozooids dimorphic: a network of jumbled, standard-sized zooids surrounding mammillae of larger, more regular zooids (which have a smaller orifice). Frontal wall a cryptocyst with marginal pores. Orifice 'cleithridiate', the sub-oval outline constricted by prominent condyles into larger anter and smaller poster (figure 3C, D); no oral spines. Ovicell prominent, imperforate, not closed by the zooidal operculum. Avicularia dimorphic: small adventitious or large vicarious. Type species *Cellepora edax* Busk, 1859.

Background.   The eastern Atlantic species of *Hippoporidra* have been revised by Taylor and Cook (1981). *Hippoporidra edax* is a fossil species from the Coralline Crag of Suffolk, England, and is not known from Recent seas. It is not the marine species described, for example, by Hincks (1880: 311) or Hayward and Ryland (1979: 214) as *H. edax*—that is *H. lusitania* Taylor and Cook, 1981. From the western Atlantic off Florida, Smitt (1873) recorded three 'forms' referred to *H. edax* (f. *typica*, f. *calcarea* and f. *janthina*), none associated with pagurids. Two species occur off North Carolina (Maturo, 1968): *H. calcarea* (Smitt's f. *calcarea*) and an unnamed species, perhaps that from the 'fishing banks' identified as *H. edax* by Osburn (in Pearse and Williams, 1951). If the latter is the present species it is quite unlike *H. lusitania*. The present species is accordingly described as new.

Type specimens.   HOLOTYPE: BMNH 1999.12.17.1 (figure 1G, 1). Type locality: Black Rocks, ∼ 10 nautical miles SSW of Cape Lookout, North Carolina, 34°20′N, 76°35′W, chart depth ∼ 10 fathoms (= 18 m) at MLW; 4 August 1977. Paratypes from type locality: BMNH 1999.12.17.2-3. Additional paratypes: Smithsonian Institution USNM 21601 collected by F. K. McKinney from approximately the same area, July 1983.

Description.   Colonies of massive form, ovoid or somewhat irregular, 18–30 mm long, originating on a pagurid-occupied shell; in some cases the distal part clearly overgrowing a small, whorled shell, suggesting later free growth as a carcinoecium; strongly patterned, mid to dark brown against off-white to pale buff, with roundish

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FIG. 2.   *Alcyonidium nodosum.* (A) Vertical section (VS) through group of non-mammilla (female) zooids (section length 12.5 mm; photograph using Wild Makroskop). (B) VS through male zooid: polypide with sphincter muscle and coelom full of mature sperm (frame 0.85 × 0.65 mm). (C) VS through female zooid with small ovary between the peripheral funiculus and the funicular cord to the caecum (frame 0.45 × 0.35 mm). (D) VS female zooid, with ovary of developing oocytes lying close to the peripheral funiculus (frame 0.23 × 0.17 mm). (E) Horizontal section (HS) through female zooid, the plane of section passing near the base of the lophophore and through the cardiacaecum of the stomach: ovary with oocytes in various stages of development (frame 0.45 × 0.35 mm). (F) HS through female zooid: ovary with fully developed oocytes, apparently close to discharge into the coelom (frame 0.23 × 0.17 mm). (G) HS female zooids with two free eggs in coelom (frame 0.45 × 0.35 mm).

or polygonal spots (maculae) of one colour separated by thin, intersecting stripes of the other (figure 1G), as in netting (hence *dictyota*, from Greek *dictyon*, net); the pattern visible in sections as radiating stripes (figure 1H); the centre of each macula
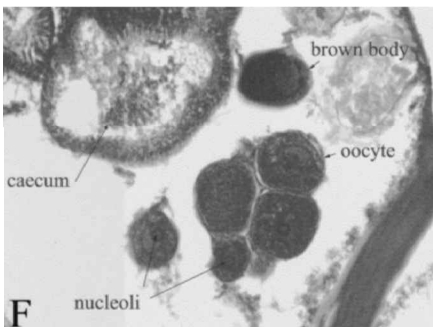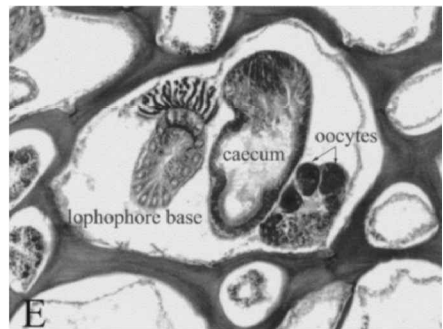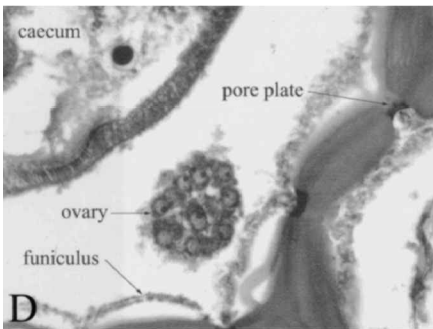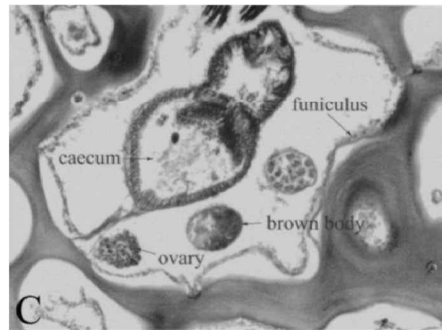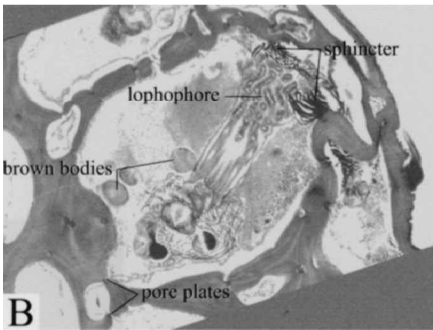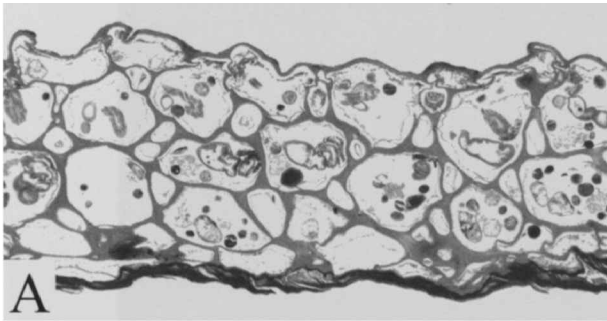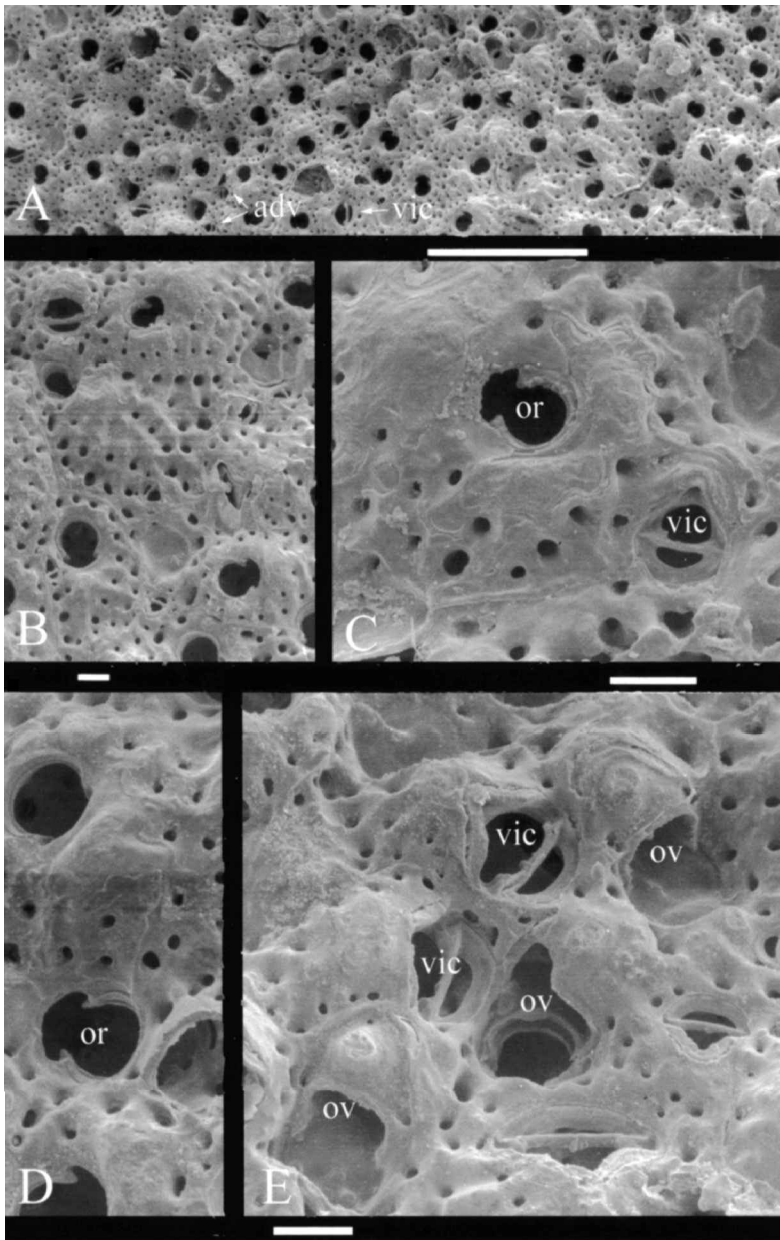
FIG. 3. *Hippoporidra dictyota* n. sp., scanning electron micrographs, paratype specimen (USNM: 21601). (A) Portion of surface, scale bar = 1 mm. (B) A mammilla, with male zooids and avicularia, scale bar 100 μm. (C) Orifice of male zooid and vicarious avicularium, scale bar 100 μm. (D) Orifice of female zooid, scale bar 100 μm. (E) Ovicells and vicarious avicularia (scale as D). adv, adventitious avicularium; or, orifice; ov, ovicell; vic, vicarious avicularium.

raised, forming a mammilla; nearest neighbour distance of mammillae ∼ 2.8 mm (table 1). Zooids dimorphic, those of the mammillae larger than those of the sur-round (figure 3). Mammilla zooids few, more or less elevated, directed up and partly

comprising the mammilla, polygonal (commonly hexagonal), longer than wide (maximum ~0.60 × ~0.40 mm; table 1; figure 3B, C); the frontal wall raised as an imperforate suboral mucro, peripheral calcification thick, nodular and porous; orifice cleithridiate, ~80 × ~65 μm, with prominent, narrowly triangular condyles separating the level, subcircular anter from the upward-slanting, almost semicircular poster (figure 3C; operculum in figure 4B). Surrounding zooids smaller, ~0.40 × ~0.24 mm; away from the mammillae increasingly jumbled, close-packed, vertical in orientation; frontally budded so that a layer of functional zooids overlays the previous layer in which orifices appear more or less occluded (figure 3A); the orifice surrounded by a convex collar of frontal wall ~200 μm diameter, cleithridiate, ~100 × ~85 μm, the pointed condyles swept back towards the poster (figure 3D); operculum in figure 4A. Ovicells only present away from the mammillae, prominent, smooth, imperforate, ~160 × ~160 μm, with a less calcified triangle or crescent above the opening (figure 3E). Large broad vicarious avicularia scattered abundantly among the autozooids, even close to the mammillae; mandibles broader than high, subtriangular, with the free sides distinctly sinuous (figures 3C, E, 4E, F). Some zooids with a small adventitious avicularium in variable orientation near to the orifice; mandible in figure 4C, D. Lophophores dimorphic: in mammilla zooids (assumed male) each comprised two pairs of rigidly erect, unciliated tentacles, the dorsal pair being the longer, ~500 μm (figure 5C); in surrounding zooids (assumed female) the lophophores comprised 12 normally ciliated tentacles in a symmetrical funnel, ~380 μm top diameter (figure 5B); toward the mammillae the lophophores become bilaterally symmetrical, with the nearer (and morphologically dorsal) tentacles the longer (figure 5A). The pagurid associated with the 1977 specimens was identified as *Paguristes tortugae* Schmitt, distributed from North Carolina to Surinam (Williams, 1984).

Related species. The most similar congener is *H. senegambiensis* (Carter, 1882) from West Africa. This has the same pattern of dark spots against a pale ground, or *vice versa* (Cook, 1964). However, the colonies grow away from the shell as several (up to 10) long arms, producing an irregular, three-dimensional star. The large vicarious avicularia are highly variable, with the mandible spathulate, slenderly triangular, or shallowly triangular, almost semicircular. This last is somewhat like that of *H. dictyota* (figure 5E, F), except that the free edges are convex rather than sinuous; other shapes have not been seen in *H. dictyota*.

Western Atlantic species have been reported from North Carolina (Pearse and Williams, 1951; Maturo, 1968), around Florida (Smitt, 1873; Osburn, 1914;
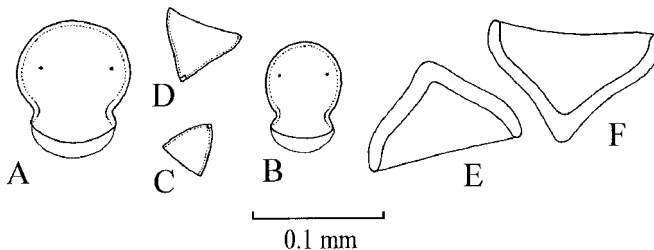

FIG. 4. *Hippoporidra dictyota* n. sp. Opercula and avicularian mandibles. (A) Operculum of non-mammilla (presumed female) zooid. (B) Operculum of mammilla (presumed male) zooid. (C, D) Mandibles of adventitious avicularia. (E, F) Mandibles of vicarious avicularia. Specimen from Black Rocks, Beaufort, North Carolina.
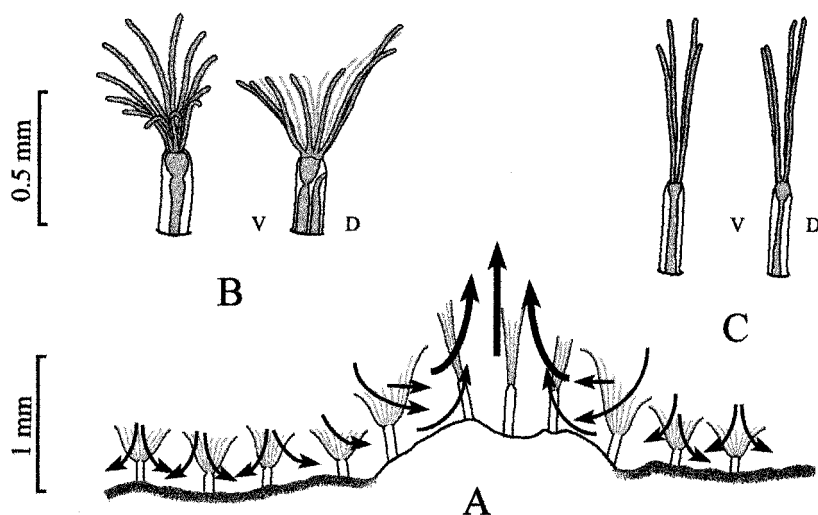
FIG. 5. *Hippoporidra dictyota* n. sp. (A) Reconstruction of a mammilla in vertical section, showing three male zooids, surrounded by non-mammilla autozooids; arrows indicate presumed directions and magnitude of flow (see text). (B) Lophophore of non-mammilla autozooid in ventral (left) and side (right) views. (C) Lophophore of male zooid in ventral (left) and side (right) views. V, ventral, D, dorsal.

Deichmann, 1954) and in the Gulf of Mexico (Canu and Bassler, 1928). The large and distinctive 'Texas Longhorns' (Deichmann, 1954), in which the *Hippoporidra* colony extends outwards from the shell as a pair of long (to 12 cm or more across), tapering—and presumably balanced—projections, have been referred to *H. edax*, though such identification clearly requires revision following Taylor and Cook's (1981) clarification of that species. According to Williams (1984) the hermit crab associated with the 'Texas Longhorns' in *Paguristes hummi* Wass. *Hippoporidra calcarea* (Smitt, 1873) may be nodular or have similar form but is smaller and uniformly pale; the mandibles of the vicarious avicularia are almost triradiate in shape. Neither of these species has spotted coloration, though such forms do occur in the Gulf (F. J. S. Maturo, personal communication in Ryland, 1979b). While Osburn (in Pearse and Williams, 1951) identified specimens from the North Carolina fishing banks as '*H. edax*' he had earlier (Osburn, 1914) regarded *H. calcarea* as inseparable from '*H. edax*'. Maturo (1968) recorded *H. calcarea* off North Carolina and as ranging southwards from Cape Hatteras. Smitt's (1873) third species, *H. janthina*, has darkly pigmented violet or blue-black colonies.

General discussion

Water flow patterns and their relations to colonial organization

Bryozoan lophophores as feeding structures and the influence of colonial morphology on flow patterns have been extensively studied in recent years (see McKinney and Jackson, 1989, and references therein), but certain aspects are still not well explored. For example, encrusting bryozoan colonies tend to have zooid shapes that maximize close-packing (Ryland and Warner, 1986; Thorpe and Ryland, 1987) and, in general, the area covered by the lophophore approximately equals the surface area of the bearing zooid (Thorpe and Ryland, 1987). However, recent studies,

using different assumptions and algorithms, have modelled the consequences of close-packing lophophores in bryozoan colonies (Grünbaum, 1995; Okamura and Eckman, 1997; Eckman and Okamura, 1998). Grünbaum argued that isolated lophophores will outperform close-packed lophophores: consequently, the larger the colony the less the average flow per zooid (figure 9 in Grünbaum, 1995). Presumably, despite the interference between lophophores, close-packing is still advantageous, and Eckman and Okamura (1998) have demonstrated that total colony feeding rates are higher—especially under low ambient flow conditions—with close packing. Both *Alcyonidium nodosum* and *Hippoporidra dictyota* have colonies organized with the feeding zooids, which surround the small groups of mammilla zooids, having close-packed lophophores.

All encrusting bryozoans encounter another problem affecting feeding efficiency—the impermeable nature of their own surface causes filtered water to be immediately deflected sideways, dramatically increasing viscous resistance to flow (Grünbaum, 1995). This problem is reduced by the presence of edges or areas without lophophores, such as the chimneys of *Membranipora membranacea* (Banta *et al.*, 1974) and other species. However, because the components of water velocity normal to the surface decay with distance more rapidly than tangential velocity components (Grünbaum, 1995), a compounding problem for a flat colony is that feeding lophophores will laterally entrain previously filtered water from directly above the excurrent chimney. This effect will be reduced by elevating the chimney above the level of the surrounding lophophores, such that discharge is achieved with minimal recycling (see Eckman and Okamura, 1998). In the two species described in this paper the mammillae are inferred to provide the hydrodynamically necessary chimneys, and their elevation is indeed to about that of the surrounding lophophores (figures 5A, 6) as required to prevent recycling. An important consequence of this is considered below.
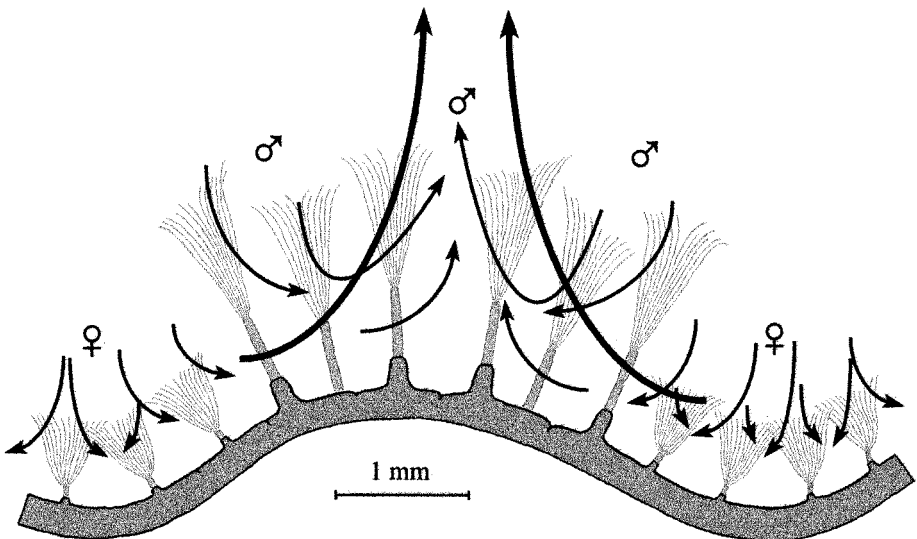

FIG. 6. *Alcyonidium nodosum*. Diagrammatic reconstruction of a mammilla showing male zooids surrounded by female zooids; thickness and substance of colony arbitrary. Arrows indicate suggested directions and strengths of water flows.

Sexual allocation and reproductive function in relation to colonial organization

Bryozoans are colonial hermaphrodites comprising either hermaphroditic, and usually protandrous, or gonochoric zooids (Reed, 1991, for review). In *Alcyonidium* various combinations are known: *A. albidum* Alder and *A. mytili* (both oviparous) are simultaneous zooidal hermaphrodites (Prouho, 1892; Cadman and Ryland, 1996); *A. diaphanum* and *A. duplex* Prouho are protandrous zooidal hermaphrodites (Prouho, 1892; Grellet, 1958); *A. hirsutum* (Fleming) has a mixture of male, female and hermaphroditic zooids, with both zooidal and colonial protandry (Owrid and Ryland, 1991); *A. nodosum*, from the single sample available, appears to have gonochoric zooids with colonial protandry. In cheilostomes, when zooids are gonochoric, the zooecia may be di- or heteromorphic, as in *Celleporella*, *Epistomia*, *Hippodiplosia* and *Thalamophorella* (Marcus, 1938, 1941; Ryland, 1979a; Nielsen, 1981; Dyrynda and King, 1982; Hughes, 1987; Cancino and Hughes, 1988), and such dimorphism characterizes all cyclostomates (Borg, 1926).

Sometimes the sex of the zooid is not manifested in the form of the zooecia but is apparent in polypide morphology: in *Hippopodinella adpressa* (Busk), for example, male and female zooecia are indistinguishable but male polypides have an aborted gut and a lophophore comprising only eight non-ciliated tentacles (Gordon, 1968). In *Celleporella* both male and female zooecia are smaller than autozooecia and have reduced polypides. In contrast to both of these genera, the male zooids of *Alcyonidium nodosum* are larger than autozooids and the lophophore—despite a slightly smaller number of tentacles—is certainly not reduced. Various species of *Hippoporidra* also have male zooecia which are larger than auto- (or female) zooecia, though the orifice of male zooecia is smaller and the lophophore is much reduced, and comparable to that of male *H. adpressa*. Male zooids in *Hippoporidra senegambiensis* have six non-ciliated tentacles: two long, two of medium length, and two short, which remain adpressed when the lophophore is protruded (Cook, 1968). In *H. dictyota* the male lophophores seem to comprise the two longer pairs observed in *H. senegambiensis* (I could sometimes see a rudimentary third, abneural pair when observing live colonies of *H. dictyota*). The dimorphism of zooecia, with those on the mammillae being larger, though with smaller orifices, than the surrounding zooecia, applies also to *H. edax* and *H. lusitania* (see Taylor and Cook, 1981), so that it may be inferred that the presence of hypertrophied male zooecia with reduced, non-feeding polypides is a characteristic of the genus. Sperm discharge (or, indeed, even sperm presence) has not yet been observed in any *Hippoporidra* but Gordon (1968) noted mature sperm inside the male zooids of *Hippopodinella adpressa*. Cook (1968) observed the male lophophores in *H. senegambiensis* making movements similar to those of other bryozoans when discharging spermatozoa (as described by Silén, 1966).

Alcyonidium nodosum, *H. dictyota* and other species of *Hippoporidra* thus have in common the location of a cluster of large male zooids on rather regularly spaced mammillae. The hydrodynamic advantages of mammillae, in terms of feeding, have already been discussed. The benefit of this organization to reproductive success is that sperm released in an excurrent chimney will be propelled well clear of the colony, the elevation ensuring that there will be little likelihood of their being entrained in the feeding inflow and drawn into the surrounding female lophophores (see discussion above). The prospects for cross-fertilization are thus enhanced (Ryland and Bishop, 1993). The large size of the similarly situated male zooids, in two only distantly related genera, must be significant, and may be related to the

habitat of the bryozoans concerned: *A. nodosum* encrusts the shells of whelks, and many *Hippoporidra* spp. from associations with pagurid crabs. Both whelks and pagurids only occasionally come together for copulation and the breeding cycle of the bryozoans must clearly match that of its host. It will be advantageous for the achievement of cross-fertilization if a large amount of sperm can be liberated in a short time, not simply to catch a transitory approximation of colonies but to ensure that adequate amounts of sperm will reach the female zooids in the mate colony (equations in Denny, 1988; general discussion in Levitan and Petersen, 1995). Fertilization success is heavily dependent on the quantity and rate of sperm output particularly in the turbulent habitat of *Alcyonidium nodosum*, even though the colonies may be rather close at the time.

References

BANTA, W. C., MCKINNEY, F. K. and ZIMMER, R. L., 1974, Bryozoan monticules: excurrent water outlets?, *Science, N. Y.*, **185**, 783–784.
BARKAI, A. and MCQUAID, C., 1988, Predator–prey role reversal in a marine benthic eco-system, *Science, N. Y.*, **242**, 62–64.
BORG, F., 1926, Studies on Recent cyclostomatous Bryozoa, *Zoologiska Bidrag från Uppsala*, **10**, 181–507.
BRANCH, G. M., GRIFFITHS, C. L., BRANCH, M. L. and BECKLEY, L. E., 1994, *Two Oceans. A Guide to the Marine Life of Southern Africa* (Cape Town and Johannesburg: David Philip).
BULLIVANT, J. S., 1967, Release of sperm by Bryozoa, *Ophelia*, **4**, 139–142.
CADMAN, P. S. and RYLAND, J. S., 1996, The characters, reproduction and growth of *Alcyonidium mytili* Dalyell, 1848 (Bryozoa: Ctenostomatida), in D. P. Gordon, A. Smith and J. Grant-Mackie (eds) *Bryozoans in Space and Time* (Wellington: NIWA), pp. 69–79.
CANCINO, J. M. and HUGHES, R. N., 1988, The zooidal polymorphism and astogeny of *Celleporella hyalina* (Bryozoa: Cheilostomata), *Journal of Zoology (London)*, **215**, 167–181.
CANU, F. and BASSLER, R. S., 1928, Fossil and Recent Bryozoa of the Gulf of Mexico region, *Proceedings of the United States National Museum*, **72**(14), 1–199.
CARTER, H. J., 1882, Remarkable forms of *Cellepora* and *Palythoa* from the Senegambian coast, *Annals and Magazine of Natural History*, Ser 5, **9**, 416–419.
CERAME-VIVAS, M. J. and GRAY, I. E., 1966, The distributional pattern of benthic invertebrates of the continental shelf off North Carolina, *Ecology*, **47**, 260–270.
COOK, P. L., 1964, Polyzoa from West Africa. Notes on the genera *Hippoporina* Neviani, *Hippoporella* Canu, *Cleidochasma* Harmer and *Hippoporidra* Canu and Bassler (Cheilo-stomata, Ascophora), *Bulletin of the British Museum (Natural History), Zoology*, **12**(1), 1–35.
COOK, P. L., 1968, Observations on living Bryozoa, *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **108**, 155–160.
COOK, P. L., 1977, Colony-wide currents in living Bryozoa, *Cahiers de Biologie Marine*, **18**, 31–47.
COOK, P. L. and CHIMONIDES, P. J., 1980, Further observations on water currents in living Bryozoa, *Cahiers de Biologie Marine*, **21**, 393–402.

DEICHMANN, E., 1954, The 'Texas longhorn shells' from the Florida waters, *The Nautilus*, **67**, 76–80.

DENNY, M. W., 1988, *Biology and the Mechanics of the Wave-swept Environment* (Princeton: Princeton University Press).

DYRYNDA, P. E. J. and KING, P. E., 1982, Sexual reproduction in *Epistomia bursaria* (Bryozoa: Cheilostomata), an endozooidal brooder without polypide recycling, *Journal of Zoology (London)*, **198**, 337–352.

ECKMAN, J. E. and OKAMURA, B., 1998, A model of particle capture by bryozoans in turbulent flow: significance of colony form, *American Naturalist*, **152**, 861–880.

GORDON, D. P., 1968, Zooidal dimorphism in the polyzoan *Hippopodinella adpressa* (Busk), *Nature, London*, **219**, 633–634.

GRELLET, P., 1958, Histologie du testicule et spermatogénèse chez *Alcyonidium gelatinosum* (L.), *Bulletin du Laboratoire Maritime de Dinard*, **43**, 1–24.

GRÜNBAUM, D., 1995, A model of feeding currents in encrusting bryozoans shows interference between zooids within a colony, *Journal of Theoretical Biology*, **174**, 409–425.

HAYWARD, P. J. and RYLAND, J. S., 1979, British ascophoran bryozoans, *Synopses of the British Fauna, N.S.*, **14**, 1–312.

HINCKS, T., 1880, *A History of the British Marine Polyzoa*, 2 vols (London: van Voorst).

HUGHES, D. J., 1987, Gametogenesis and embryonic brooding in the cheilostome bryozoan *Celleporella hyalina*, *Journal of Zoology*, **212**, 691–711.

LEVITAN, D. R., 1995, The ecology of fertilization in free-spawning invertebrates, in L. R. McEdwards (ed.) *Ecology of Marine Invertebrate Larvae* Boca Raton, FL: CRC Press), pp. 123–156.

LEVITAN, D. R. and PETERSEN, C., 1995, Sperm limitation in the sea, *Trends in Ecology and Evolution*, **10**, 228–231.

MARCUS, E., 1938, Bryozoarios marinhos brasileiros—II, *Boletim da Faculdade de Filosofia Ciencias e Letras Universidade de São Paulo, Zoologia*, **4**, 1–137.

MARCUS, E., 1941, Sobre Bryozoa do Brasil, *Boletim da Faculdade de Filosofia Ciencias e Letras Universidade de São Paulo, Zoologia*, **5**, 3–208.

MATURO, F. J. S., 1968, The distributional pattern of the Bryozoa of the east coast of the United States exclusive of New England, *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **108**, 261–284.

McKINNEY, F. K. and JACKSON, J. B. C., 1989, *Bryozoan Evolution* (Boston: Unwin Hyman).

NELSEN, C., 1981, On morphology and reproduction of '*Hippodiplosia*' *insculpta* and *Fenestrulina malusii* (Bryozoa, Cheilostomata), *Ophelia*, **20**, 91–125.

O'DONOGHUE, C. H. and WATTEVILLE, D. DE, 1944, Additional notes on Bryozoa from South Africa, *Annals of the Natal Museum*, **10**, 407–432.

OKAMURA, B. and ECKMAN, J. E., 1997, Modelling particle capture rates by encrusting bryozoans: adaptive significance of colony form. *Proceedings of the 8th International Coral Reef Symposium*, **2**, 1077–1080.

OSBURN, R. C., 1914, The Bryozoa of the Tortugas islands, Florida, *Publications of the Carnegie Institution of Washington*, **182**, 181–222.

OWRID, G. M. A. and RYLAND, J. S., 1991, Sexual reproduction in *Alcyonidium hirsutum* (Bryozoa: Ctenostomata), in F. P. Bigey (ed.) *Bryozoaires actuels et fossiles: Bryozoa living and fossil*, *Bulletin de la Societé des Sciences Naturelles de l'Ouest de la France*, **HS 1**, 317–326.

PEARSE, A. S. and WILLIAMS, L. G., 1951, The biota of the reefs off the Carolinas, *Journal of the Elisha Mitchell Scientific Society*, **67**, 133–161.

PROUHO, H., 1892, Contributions a l'histoire des Bryozoaires, *Archives de Zoologie Expérimentale et Générale*, **10**, 557–656.

REED, C. G., 1991, Bryozoa, in A. C. Giese, J. S. Pearse and V. B. Pearse (eds) *Reproduction of Marine Invertebrates*, Vol. 6, *Echinoderms and Lophophorates* (Pacific Grove: Boxwood Press), pp. 85–245.

RYLAND, J. S., 1979a, *Celleporella carolinensis* sp. nov. (Bryozoa Cheilostomata) from the Atlantic coast of America, in G. P. Larwood and M. B. Abbott (eds) *Advances in Bryozoology* (London: Academic Press), pp. 611–619.

RYLAND, J. S., 1979b, Structural and physiological aspects of coloniality in Bryozoa, in B. R. Rosen and G. P. Larwood (eds) *Biology and Systematics of Colonial Organisms* (London: Academic Press), pp. 211–242.

RYLAND, J. S. and BISHOP, J. D. D., 1993, Internal fertilisation in hermaphroditic colonial invertebrates, *Oceanography and Marine Biology: An Annual Review*, **31**, 445–477.

RYLAND, J. S. and WARNER, G. F., 1986, Growth and form in modular animals: ideas on the size and arrangement of zooids, *Philosophical Transactions of the Royal Society of London (B)*, **313**, 53–76.

SILÈN, L., 1966, On the fertilization problem in the gymnolaematous Bryozoa, *Ophelia*, **3**, 113–140.

SILÈN, L., 1972, Fertilization in the Bryozoa, *Ophelia*, **10**, 27–34.

SMITT, F. A., 1873, Floridan Bryozoa, collected by Count L. F. de Pourtales, Part II, *Kongelige Svenska Vetenskaps-Akademiens Handlingar*, **11**(4), 1–82.

TAYLOR, P. D., 1979, The inference of extrazooidal feeding currents in fossil bryozoan colonies, *Lethaia*, **12**, 47–56.

TAYLOR, P. D. and COOK, P. L., 1981, *Hippoporidra edax* (Busk, 1859) and a revision of some fossil and living *Hippoporidra* (Bryozoa), *Bulletin of the British Museum (Natural History), Geology*, **35**, 243–251.

TEMKIN, M. H., 1996, Comparative fertizilation biology of gymnolaemate bryozoans, *Marine Biology*, **127**, 329–339.

THORPE, J. P. and RYLAND, J. S., 1987, Some theoretical limitations on the arrangement of zooids in encrusting Bryozoa, in J. R. P. Ross (ed.) *Bryozoa: Present and Past* (Bellingham: Western Washington University), pp. 277–283.

WILLIAMS, A. B., 1984, *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida* (Washington, DC: Smithsonian Institution).