REPRODUCTIVE ECOLOGY OF SOME NORTHERN NEW ZEALAND BRYOZOA

by

D.P. Gordon (1)
Leigh Marine Laboratory, University of Auckland, New Zealand.

Résumé

L'auteur étudie la période de reproduction de 23 espèces de Bryozoaires à Goat Island Bay, Nouvelle-Zélande ; ces espèces se reproduisent suivant l'un des trois modes saisonniers suivants : période très courte, reproduction toute l'année ou période débutant au printemps et se terminant au début de l'hiver. Au plus fort de l'activité reproductrice, à peu près toutes les colonies de *Fenestrulina malusii* var. *thyreophora* de plus de 25 mm^2 de surface contiennent des embryons qui se développent dans les ovicelles de 25 p. 100, environ, des zoïdes. L'auteur indique la fréquence des divers types de chambre d'incubation chez les Chilostomes de Goat Island Bay. Il décrit le substrat sur lequel vivent les larves et la couleur des embryons et discute la présence anormale d'embryons albinos et ses implications chez les deux espèces. Les rapports entre les fluctuations annuelles de l'activité reproductrice, d'une part, et la température de l'eau de mer et l'abondance de nourriture, d'autre part, suggère que cette dernière possède une influence plus directe sur le déclenchement de la reproduction.

Introduction

This paper presents an account of the breeding seasons of cheilostome bryozoans from northern New Zealand. Apart from data on certain fouling species (Ralph and Hurley, 1952; Skerman, 1958, 1959, 1960 and Poore, 1968) there is practically no information on reproduction and larvae of New Zealand bryozoans. Three aims were the basis of the present study, viz., 1. to record patterns of breeding activity; 2. to gather data on larval colour, behaviour and substrate preferences; 3. to ascertain which environmental parameters are responsible for stimulating reproduction.

1. In the northern hemisphere, the breeding seasons of many species have been recorded. In her 1959 review, Hyman summarised what was known before this date, stating that the breeding season of bryozoa in that hemisphere "falls within the period from spring to autumn or even extends into early winter". Ryland (1963) suggests there is maximum output of larvae of shallow water species during the warmest months (in North Wales and Norway). Gautier (1962) distinguished three patterns of reproduction in Mediterranean species, viz., species with winter breeding maxima, species with summer maxima, and eurythermic species breeding year round. Eggleston

---

(1) Present address: Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada.

CAHIERS DE BIOLOGIE MARINE
Tome XI - 1970 - pp. 307-323

(1963) is cited by Ryland (1967) as finding three patterns of reproduction in Manx bryozoa such as Gautier found in the Mediterranean. I have recorded the seasonal reproductive activity of 23 species of bryozoa, of which *Fenestrulina malusii* (Audouin) var. *thyreophora* (Busk) was studied in most detail, to see if breeding patterns similar to those in Northern Hemisphere bryozoa could be discerned.

2. Ryland (1958) stressed the importance of embryo colour as a diagnostic feature in bryozoans. The embryo colours of 28 species from New Zealand were recorded and compared to colony colour to see if there is any colour relationship between embryo and colony, and to make this data available for species diagnoses.

3. Although much experimental work has been conducted to determine the effects of certain environmental parameters on released bryozoan larvae (of which good reviews are given by Hyman (1959) and Ryland (1967), it is not certain which parameters initiate events leading to larval production and release. Sea water temperatures and phytoplankton availability were measured throughout the duration of the study to try to ascertain any relationship between food, temperature and reproduction.

Materials and Methods

The species used in the study were found at Goat Island Bay, Leigh, New Zealand between November, 1967 and October, 1968. Various substrates bearing bryozoa were collected by hand in the intertidal zone and by SCUBA from depths up to 70' below mean sea level. The substrates bearing the colonies (rocks, seaweeds, etc.), were kept in aquaria with constantly flowing sea water, at the Leigh Marine Laboratory and examined within a few hours of their collection under a binocular microscope. Embryos were counted with a hand tally counter. In the case of *F. malusii* var. *thyreophora,* the total number of zooids in each colony were counted and the percentage number of zooids with embryos calculated. Weekly (sometimes twice weekly), collections of substrates were examined in this way.

To assess embryo colour objectively, the method described by Eggleston and cited by Ryland (1963) was used. Developing embryos were dissected out and their colour measured against a standard colour notation (the Nickerson Color Fan of the Munsell Color Company, Baltimore). Embryos are mounted in a drop of water on a slide. This is then placed on the colour standard and moved from panel to panel until the shade and intensity of the embryo are matched by the background. In the case of colonies, the colour panels were held alongside. The colonies matched in this way were growing on a uniform grey sandstone.

Sea water surface temperatures were recorded continuously at the Marine Laboratory by five thermistor thermometers embedded in the intertidal rock and connected to a strip-chart recorder. Daily temperatures were also taken manually with a centigrade thermometer. Information concerning weekly variations in phytoplankton standing crop was kindly given by Dr F.J. Taylor, phytoplanktologist at the Laboratory, who conducted weekly net tows in Goat Island Bay.

RESULTS

Reproductive seasons.

The seasonal occurrence of embryos in 23 species is shown in Figure 1. It is apparent from the figure that there are broadly three breeding patterns that the species exhibit, viz., a very restricted

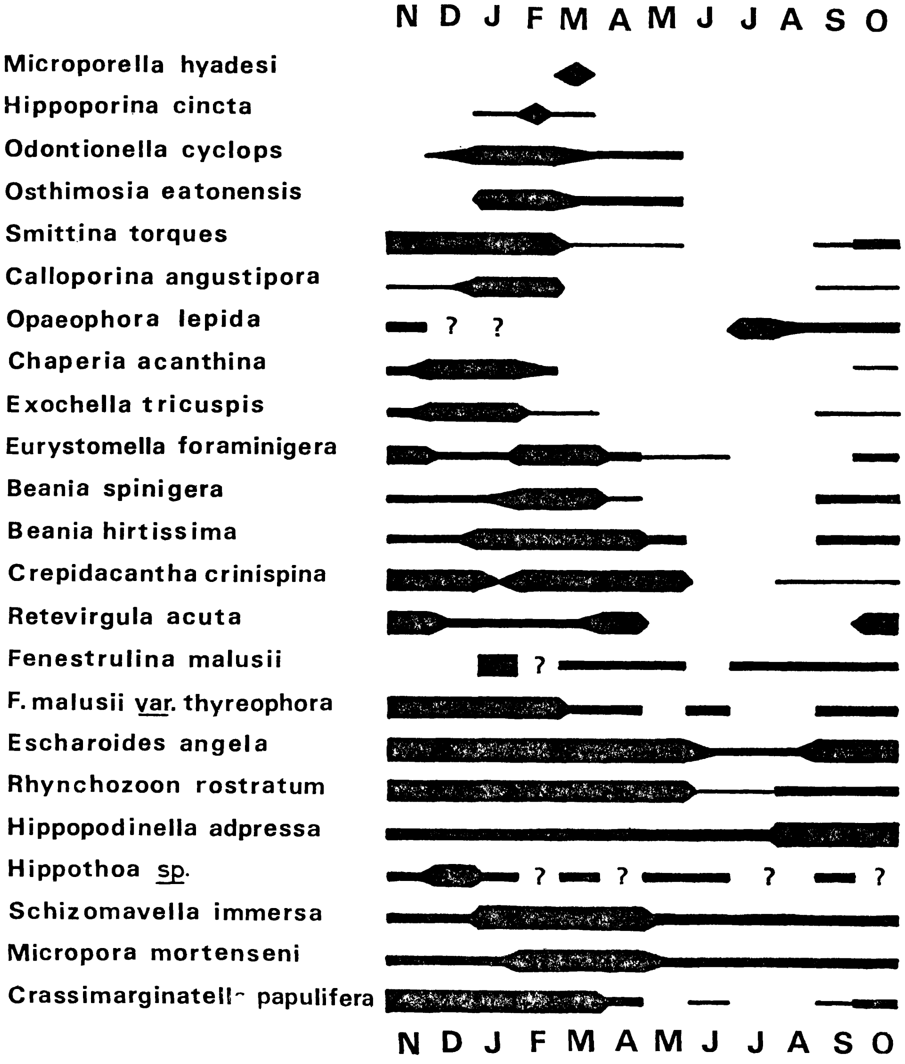

FIG. 1.

The seasonal occurrence of embryos from November, 1967 to October, 1968.

The bars have three thicknesses, based on averages for three or more colonies of each species per month. Full width denotes that embryos were very common; half width, present, but not in great numbers; a line, only one or two embryos per colony. A question mark indicates that the species was not found in that month and it is not known if embryos were present or not. A gap indicates that the species was found and embryos were absent.

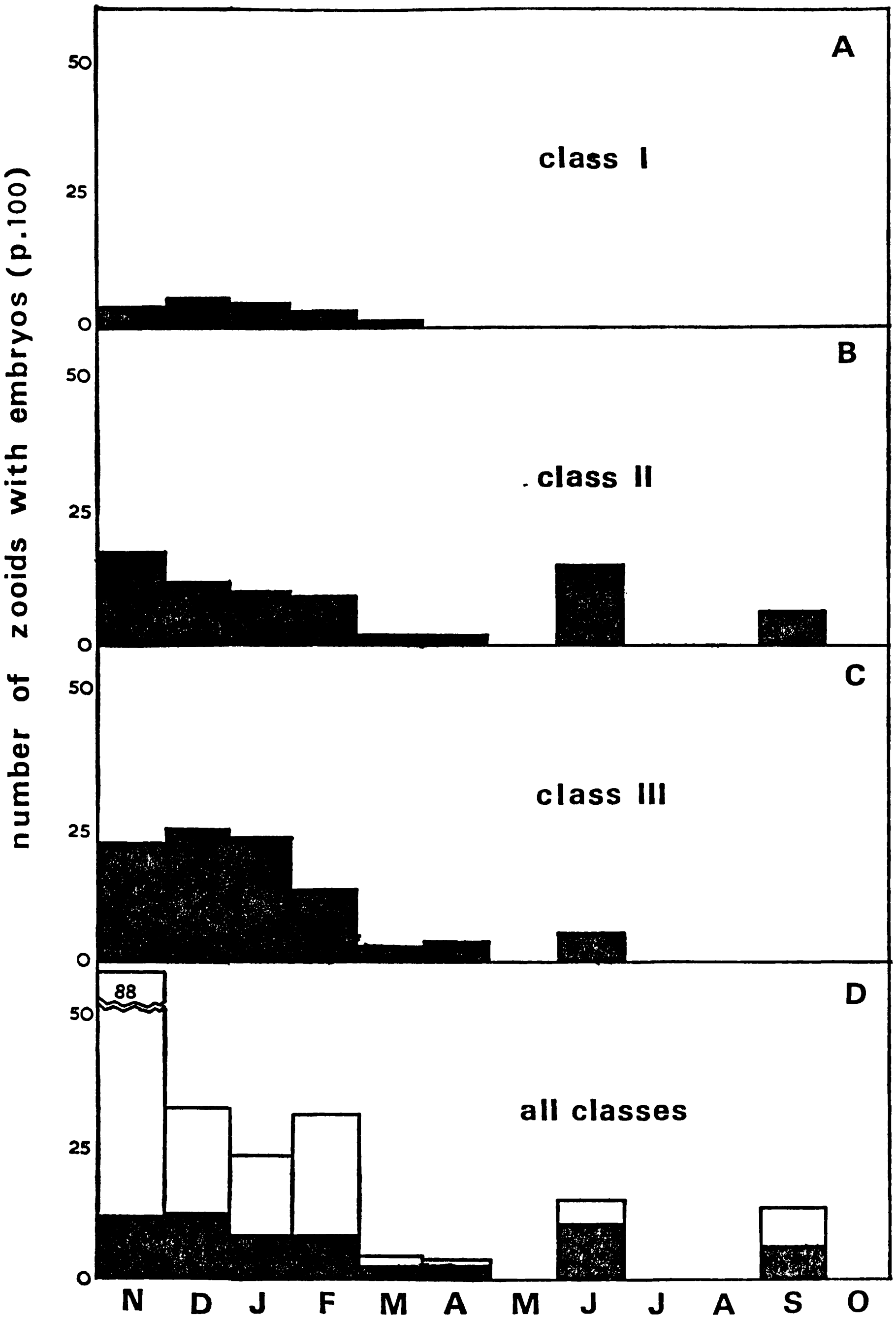

FIG. 2.

Fecundity of *F. malusii* var. *thyreophora*, in terms of the percentage number of zooids with embryos (average for all colonies in the size class indicated).

A. class I (1-25 mm^2); B. class II (26-100 mm^2); C. class III (101 + mm^2), few colonies grew to 400 mm^2 or more in area; D. all classes (Black = average values; white = upper limit of range). The high value for class I in June results from an unusually high number of embryos found in one colony. Few colonies were found breeding in this month thus the average is misleadingly high.

breeding season (*Microporella hyadesi, Hippoporina cincta*); a year round breeding season with usually a slight decline in winter (*Escharoides angela, Rhynchozoon rostratum, Schizomavella immersa, Micropora mortenseni, Fenestrulina malusii?, Hippopodinella adpressa*) and a season from spring to early winter (the remainder of the species in the figure).

The seasonal reproduction of *F. malusii* var. *thyreophora* was followed in detail to find out if fecundity varies with colony size and what proportion of the population breeds during the reproductive season. To determine the fecundity of this species over the peak breeding period, colonies of all sizes were examined for embryos. The colonies were each assigned to one of three size classes and the percentage number of zooids with mature or developing embryos calculated for each colony. The number of colonies in each size class that were not breeding were also recorded.

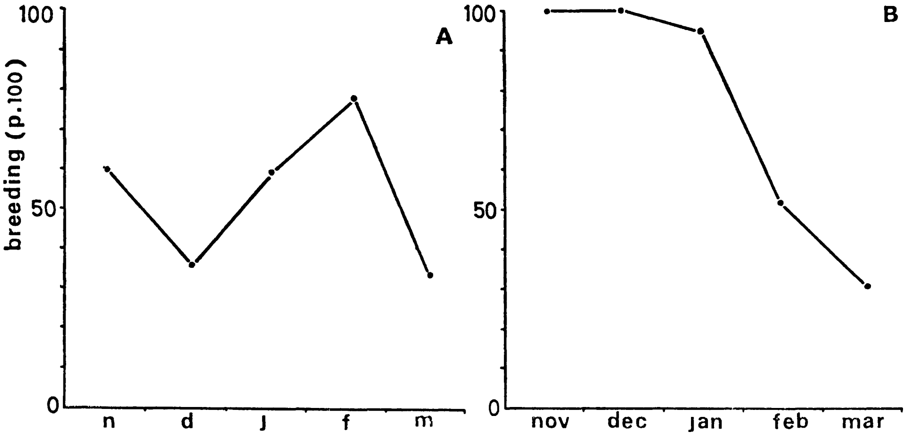

Fig. 3.

Percentage number of colonies of *F. malusii* var. *thyreophora* breeding during peak reproductive activity.

A. Class I; B. classes II and III.

The average fecundity of a number of colonies in each class per month is shown in Figure 2, A-D. No colonies were found breeding in May or July of 1968 but, since some were found with embryos in June, it is thought that a small proportion of the population may have been breeding that were missed in those months. Many colonies die during winter and the chances of finding breeding colonies are rather small.

During the main breeding season usually not more than 25 p. 100 of the zooids in a colony contain embryos in their ovicells (Plate 1), although the percentage range may deviate considerably from the average. For example, one class II colony (80 mm^2) had mature or near mature embryos in ovicells of 88 p. 100 of the zooids in November of 1967. This represents approximately 440 embryos. Usually the average number of embryos seen in a colony of this size in this month was 60.

The number of colonies containing embryos over the main summer breeding period is very high. Of 94 colonies examined in November and December of 1967, *all* above 25 mm^2 in area (60 colonies) had embryos but this percentage quickly tailed off to 30 p. 100 by late summer (March, 1968) (Fig. 3).

Brooding habits

The brooding habits and structures associated with these, are very varied in cheilostome bryozoa (Hyman, 1959) and among the species at Leigh five types of brood chamber are found. The frequency of occurrence of these types is shown in Figure 4.

A. Most cheilostomes possess ovicells (also very varied) which are distal extensions of the body wall in which the fertilised ovum completes its development. Typically only one embryo at a time develops in the ovicell.

B. Another method of incubation is the retention of the fertilised ovum in the parent zooid, usually in a sac, in which case an ovicell is absent. (Calvet, 1900; Waters, 1912; Mawatari, 1952; Cook, 1968, etc.). Because the developing embryo takes up so much space in the zooid, the polypide typically degenerates. In ovicelled species, the polypide can still function.

C. A third method of brooding was that seen in the anascan *Macropora grandis* (Hutton) var. *levinseni* Brown. In this species are globoid structures larger than autozooids which appear to occupy the place of autozooids in the zooidal rows. They have the general appearance of ovicells and are even closed by the operculum of the proximal autozooid, but because of their size and position are probably best regarded as gonoecia. Brown (1952) had this in mind when he suggested they might be gonozooids. Powell (1967a) distinguished a gonoecium as "a zooid which is frequently enlarged for the incubation of eggs within the zoecial cavity", and a gonozooid as a "sexually differentiated zooid, the female comprising a dwarf zooid and an ovicell". Dissection of five gonoecia of a *Macropora* colony revealed that two or four embryos mature in a single gonoecium.

D. Species of *Hippothoa* brood their embryos in gonozooids and this is well documented (Marcus, 1938; Rogick, 1956; Powell, 1967b).

E. Also well documented is the method of brooding seen in the cosmopolitan *Aetea anguina* (L.). The embryo is brooded in a sac, on the outside of the frontal membrane (Osburn, 1912; Hastings, 1943). I do not know if this is also the case in *A. truncata* (Landsborough), which is also found at Goat Island Bay.

Certain species (*Electra pilosa* (L.), *Conopeum seurati* Canu, *Membranipora* spp.) do not brood their embryos; development is completed in the sea. The larvae (cyphonautes) are long living and planktotrophic. All other cheilostomes in the vicinity of Leigh are believed to produce lecithotrophic larvae.

D.P. GORDON

PLATE 1.

A class III colony of *Fenestrulina malusii* var. *thyreophora* in December 1967, showing the central dead periancestrular region, the middle, reproductive zone in old season's zooids, and the outer whitish growing region. The number of larvae (yellow objects) is about 16 p. 100 of the total number of zooids in the colony (c. 1120).

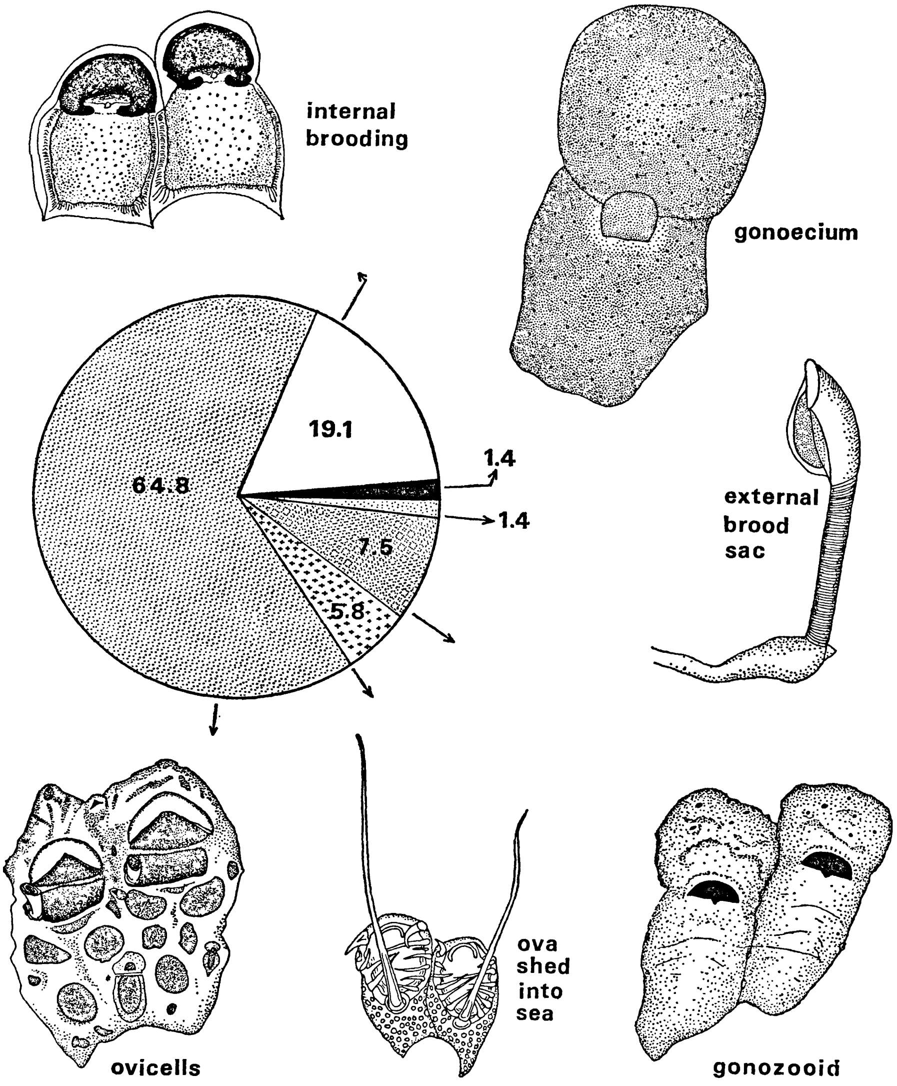

FIG. 4.

The frequency of occurrence of the various brooding methods among cheilostomes at Goat Island Bay.

From the top going clock-wise are, *Steginoporella neozelanica* var. *magnifica* (internal brooding), *Macropora grandis* var. *levinseni* (gonoecium), *Aetea anguina* (external brood sac), *Hippothoa* sp. (gonozooid), *Electra pilosa* (ova not brooded) and *Arachnopusia unicornis* (ovicells). The numbers in the circle represent percentages based on 70 species of cheilostomata (Appendix 1).

Larval biology

A. Colour.

Cheilostome larvae exhibit a wide range of colour. This is due primarily to a number of carotenoids, especially carotenes and xanthophylls which account for red, yellow and orange larvae (Ryland, 1958).

The embryo colour of 29 species are recorded in Table 1; the colours of the colonies are included for comparison. As an embryo matures, its colouration usually becomes less intense, said to be due to metabolic changes, and the free larva may be paler. This is indicated where appropriate in the Table.

Both colony colour and embryo colour are generally consistent in the species at Leigh, although there are minor variations due to aging (colonies tend to darken and embryos to lighten with age). However, two notable exceptions to constancy of embryo colour were found that deserve special mention.

The embryos of *Crassimarginatella papulifera* (MacGillivray) and *Micropora mortenseni* Livingstone are normally coloured, but white embryos were discovered in a few zooids near the growing edge of a colony of each species. These embryos were almost full size and did not occupy the ovicells which had not yet developed completely. Instead, they occupied the body cavity, which may or may not have been at the expense of the polypides, which were still developing. The embryos of other parts of the colony in each species were normally coloured. The unusual occurrence of these white embryos poses two important questions, viz., were they fertilised, and why were they white when the others in the colony were coloured?

In the first place, the embryos were large. At this size, they are normally presumed to have been fertilised. However, they cannot have been fertilised because this presumably takes place during transference to the ovicell (Silén, 1966) and this, of course, had not happened. There are two possible explanations—parthenogenesis or fertilisation by some unknown means.

The problem of albinism is a little easier account for. It is said that animals cannot manufacture their own carotenoids but get them from plant material (Fox and Hopkins, 1966). Since the polypides had not fed, this tells us something of the restricted nature of the supposed diffusion of substances between zooids; presumably carotenoids or the form in which they are incorporated into the yolk of an embryo cannot be transferred from zooid to zooid.

Precocious development of gametes in a growing zone is not unknown (Bullivant, 1967) but albinism of embryos that are normally coloured does not seem to have been noted before.

B. Larval release and settlement.

Prior to release the embryo typically moves around in its membrane inside the ovicell and presumably in other types of brood structure also, although this cannot be as easily seen. In many species, the operculum which closes the orifice also closes the entrance to the ovicell and departure of the larva necessitates the opening of the operculum in such cases. The larva takes several seconds to escape. Three types of movement were seen in released larvae of *Eurystomella foraminigera* (Hincks) and this seems to be fairly general, viz., 1. a rapid, anticlockwise upward spiralling, followed by; 2. fairly straight directional movements of some distance, interrupted by periodic visits to the substrate where the larva exhibits; 3. rather slow exploratory manoeuvres (one larva was timed at 0.5 mm/3 se-

TABLE 1.
Embryo colour and colony colour.

Species	Embryo colour Munsell designation	Colony colour Munsell designation
Crassimarginatella papulifera	vivid yellow 2.5Y 8/12	unpigmented
Chaperia acanthina	moderate orange-yellow 7.5YR 8/8	unpigmented
Chaperia rubida	strong orange 2.5YR 6/12	strong orange-yellow 7.5YR 7/11
Micropora mortenseni	vivid red 5R 5/13; then light yellowish-pink 2.5YR 9/3	unpigmented
Opaeophora lepida	strong orange-yellow 7.5YR 7/11 (1)	unpigmented
Odontionella cyclops	strong orange 2.5YR 6/12	strong orange 2.5YR 7/10
Beania hirtissima	strong orange-yellow 10YR 7/10	strong yellowish-brown 10YR 5/6
Beania bilaminata	vivid yellow 2.5Y 8/12	strong yellowish-brown 10YR 5/6
Caberea zelandica	strong red 2.5R 5/12, then strong orange 5YR 7/11	dark orange-yellow 7.5YR 6/9
Arachnopusia unicornis	strong red 5R 4/12	light orange 5YR 8/7
Exochella tricuspis	strong reddish-orange 7.5R 5/13	essentially unpigmented
Escharoides angela	strong orange-yellow 7.5YR 7/11 then light orange 2.5YR 8/6	strong orange 2.5YR 7/10
Escharoides excavata	strong orange 2.5YR 6/12	strong orange 2.5YR 7/10
Eurystomella foraminigera	strong purplish-red 10RP 5/12 then strong orange 2.5YR 6/12	moderate red 2.5R 4/10
Hippothoa sp.	pale orange-yellow 7.5YR 9/4	unpigmented
Schizomavella immersa	dark reddish-orange 7.5R 4/11	strong reddish-orange 10R 5/11
Calloporina angustipora	strong reddish-orange 10R 6/12	deep pink 2.5R 6/11
Fenestrulina malusii	strong orange 2.5YR 6/12	unpigmented
Fenestrulina malusii var. *thyreophora*	strong orange-yellow 10YR 7/10	unpigmented
Microporella hyadesi	strong reddish-orange 10R 6/12	unpigmented
Smittina torques	strong orange 2.5YR 6/12	strong reddish-orange 10R 6/12
Smittina maplestonei		strong orange 2.5YR 6/12
Parasmittina unispinosa	strong orange-yellow 7.5YR 7/11	essentially unpigmented
Hippopodinella adpressa	deep yellowish-pink 5R 6/11	moderate orange-yellow 7.5YR 8/8
Hippoporina cincta	7.5YR 7/11 (1) strong orange-yellow	vivid greenish-yellow 7.5Y 8/12
Crepidacantha crinispina	pale orange-yellow 7.5YR 9/4	unpigmented
Osthimosia eatonensis	strong reddish-orange 7.5R 4/11	strong reddish-orange 10R 6/12
Rhynchozoon rostratum	strong orange 2.5YR 6/12	
Rhynchozoon larreyi	strong orange 2.5YR 6/12	dark red 5R 3/7

(1) Denotes nearest available colour on Fan. In both cases a more brilliant yellow.

conds) involving a great deal of body flexure. (These observations were made on larvae released from colonies on rocks in a small aquarium. Progress was followed with a binocular microscope and although the light source was moderately strong, the larvae did not seem to respond to this as they exhibited the same repertoire of movements when the light was dimmed considerably.)

A lot has been written about the responses of bryozoan larvae to a wide range of experimental stimuli, the attractive factors in settlement and factors influencing metamorphosis. Good reviews are given by Hyman (1959) and Ryland (1967), and the bibliographies of Ryland (1962a, b) are worth consulting for details.

In the course of the investigation, certain observations were made that were contrary to expectations. It was originally noticed for *Eurystomella* and later for *Smittina torques* Powell and *Hippopodinella adpressa* (Busk), that as many as a dozen or more larvae from an actively breeding colony may settle and metamorphose on the colony. It is not unusual to find a larva which has settled across the operculum of a live zooid, or right against the growing edge of a parent colony. The larvae evidently have no respect for their own colony surface. An ancestrula of *Eurystomella* and one of *Steginoporella neozelanica* Busk var. *magnifica* Livingstone were found perched precariously on hydroid stems. The hydroid (*Plumularia setacea* Ellis) is seasonal so larvae settling on this substrate stand no chance of survival.

Larvae of most species settle on a wide range of substrates (Table 2). There are a few exceptions; *Hippopodinella adpressa* is found almost exclusively on gastropod shells, and *Fenestrulina malusii* from the intertidal shows a preference for algae, especially holdfasts of *Ecklonia radiata* (C. Ag.) J. Ag. (Gordon, 1967).

Initiation of reproductive activity

The colony size at which egg production occurs was noted for three species. *F. malusii* var. *thyreophora* is capable of reproducing at a minimum size of 80 zooids, *Eurystomella foraminigera* at 130 zooids and *Crassimarginatella papulifera* at 56 zooids. It is not known what exactly initiates gametogenesis or what causes distribution of sexuality in polymorphic species, but it is probably a combination of factors. A colony of *Hippothoa* sp. was found, in which a number of male zooids developed along a line which represented a previous check in growth, where there would otherwise have been autozooids (Fig. 5). Silén (1966) found a similar situation in *Electra posidoniae* Gautier where, with few exceptions, gametogenesis was initiated in parts of colonies whose vegetative growth was checked due to collision with other colonies.

Sea water temperature and phytoplankton standing crop were measured weekly to see what relationship exists between these parameters and the commencement and intensity of breeding. A large number of species resumed breeding after winter, in September of 1968. (There was a spectacular resumption or burst of growth in most species at this time too, as indicated by the paler zone of new

TABLE 2.
The occurrence of bryozoans on various types of substrate.

Species	rock	shell	crabs	algae	glass	ascidians	bryozoans	brachiopods	wood	rubber	iron	stainless steel	tin
Aetea anguina	C	R		C			C						
Aetea truncata							O						
Scruparia ambigua		R		C	O		C						
Membranipora membranacea				C									
Conopeum seurati		C							C				
Electra pilosa		R		C									
Spiralaria denticulata	O	C											
Crassimarginatella papulifera	C	O									R		R
Retevirgula acuta	C			O	R								
Chaperia acanthina	C	O		O	R						R	R	R
Chaperia cervicornis	C	O		O		O				R			
Chaperia rubida	C			O					R				
Steginoporella neozelanica var. *magnifica*	C	R					O		R			R	R
Opaeophora lepida	C	O											
Micropora mortenseni	C	O			R								
Odontionella cyclops	C	R				R							R
Macropora grandis	C					R						R	
Caberea zelandica	O			C									
Beania decumbens	C						O						
Beania spinigera	C			R		R	O						
Beania bilaminata	C												
Beania magellanica	C					R							
Beania hirtissima	C	R	R	R		R	O			R			
Arachnopusia unicornis	C	O		O								R	
Umbonula bicuspis	O	C											
Exochella tricuspis	C	O			R								
Escharoides angela	C	O	R	O								R	
Escharoides excavata	C	O		C						R			R
Eurystomella foraminigera	C	O		R	R						R		R
Hippothoa sp.	R	C		C	C								
Hippothoa cancer				C									
Hippothoa distans				C									
Hippothoa buskiana				C									
Arthropoma circinata	R	O											
Schizomavella immersa	C												
Calloporina angustipora	C			R									
Microporella hyadesi	C	O			R			O					
Fenestrulina malusii	R	R		C				R					
Fenestrulina malusii var. *thyreophora*	C	O				R					R		R
Hippoporina cincta	C	R											
Osthimosia eatonensis	C	C		O	R		R		R				
Smittina torques	C	R									R		R
Smittina maplestonei	C												
Smittoidea acaroensis	R			C									
Parasmittina unispinosa	C												
Crepidacantha crinispina	O	O						R			R	R	R
Cryptosula pallasiana	O	R				R			C				
Hippopodinella adpressa	R	C	O		R								

Notation: C = common; O = occasional; R = rare.

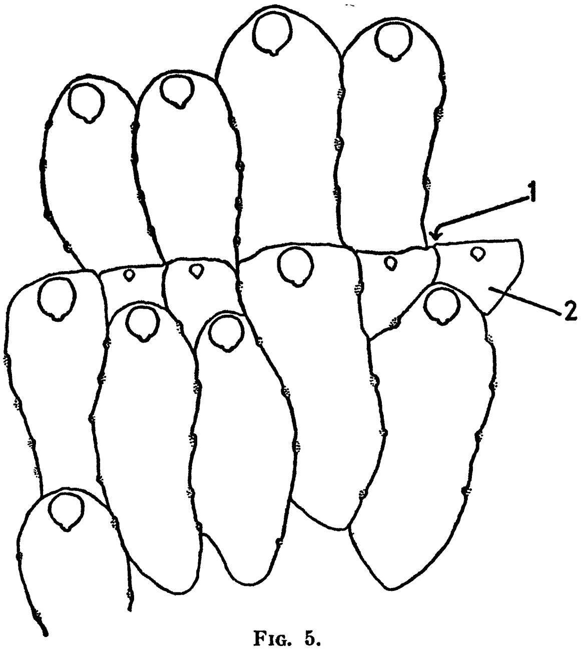

Fig. 5.

Hippothoa sp. showing initiation of sexual characters by a check (cause unknown) in growth.

1. limit of previous growth of colony; 2. male zooid.

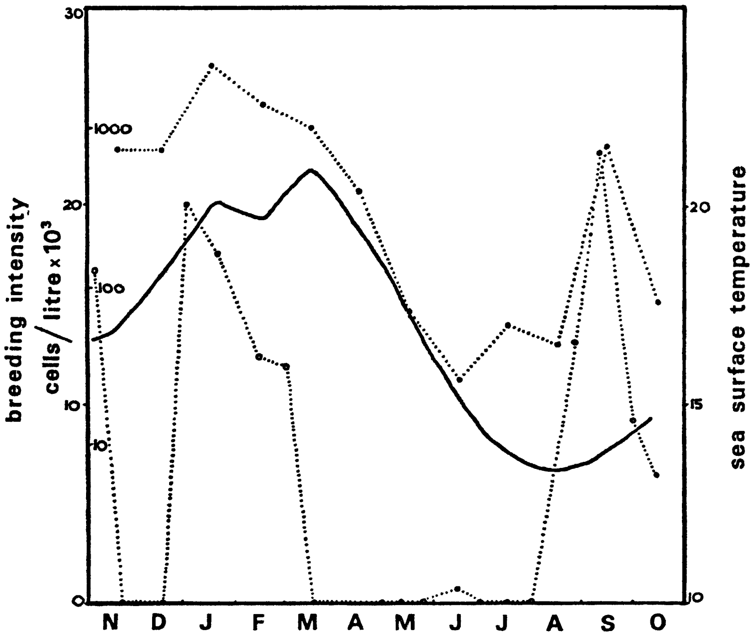

Fig. 6.

Seasonal changes in breeding intensity (upper dotted line), sea water temperature (middle unbroken line) and phytoplankton standing crop (lower dotted line), from November 1967 to October 1968.

Breeding intensity is plotted as the number of species observed to contain embryos each month.

season's zooids separated by a marked line from the darker, older parts of colonies). Since sea water temperatures were still very low at this time, an explanation for this vigorous reproductive activity was looked for in food availability.

The events leading up to the September activity were as follows. Shortly after March and throughout the winter of 1968, dinoflagellates predominated in the inshore phytoplankton, though in relatively low numbers, of which the dominant species was *Gonyaulax polyedra* Stein. Microflagellates also occurred in low numbers in the winter phytoplankton. The dinoflagellates declined during August and by August 26 the long chain diatom *Leptocylindrus danicus* Cleve was predominant. Since this diatom's appearance seemed to coincide with reproductive activity in the local bryozoans, mouth sizes of some species were measured to see if ingestion of the diatom were possible. The average diameter of the diatom is 2.5 µ. The measured mouth sizes in the bryozoans ranged from 25 µ in diameter in *Smittina torques* to 42.5 µ in *Beania magellanica*. However, *L. danicus* occurs in chains up to 125 µ in length. These do not typically fragment and thus it seems unlikely that this is a food species. An examination of the guts of some bryozoans proved fruitless as the contents were unrecnisable. The seasonal relationships between reproduction, phytoplankton standing crop and sea water temperature are plotted in Figure 6, in which it may be noted how closely the spring rise in breeding intensity parallels the increase in plankton availability.

DISCUSSION

Reproductive seasons

As indicated in the results, three breeding patterns can be discerned, but these are not the same as Gautier's. For example, there are no bryozoans at Goat Island Bay which were observed to have winter breeding maxima. His second group of species, with summer maxima, is represented by most species. Of the cosmopolitan, eurythermic element, not all breed throughout the year at Goat Island Bay. *Beania hirtissima* (Heller), for example, which might reasonably be described as comospolitan, is at or near the southern limit of its distribution in New Zealand and this may explain the absence of embryos from June to August. *Fenestrulina malusii* was not found every month. The gaps in the figure result from this, although again, New Zealand is at or near the southern limit of its distribution and it may not breed year round at Goat Island Bay.

Hippopodinella adpressa ranges from Chile to California and Hawaii and the Indo-Pacific region. It is shown in the Figure as breeding year round but this may be more apparent than real. The breeding season in the Figure is based on the presence of male polypides (Gordon, 1968) throughout the year but this may not reflect a seasonal production of embryos. Unfortunately embryos cannot be detected unless one dissects numerous zooids; they are brooded internally and the heavily calcified frontal wall precludes casual observation of their presence.

Rhynchozoon rostratum (Busk) is probably best described as tropicopolitan, being found in the Panamic region, California and Hawaii, and also from New England to Brazil (Soule & Soule, 1967). It breeds year round at Goat Island Bay with a slight decline in winter.

Schizomavella immersa, Micropora mortenseni and *Escharoides angela* are conspicuous winter breeders which are endemic to New Zealand. *Microporella hyadesi* is a little anomalous. According to Powell (1967b), this species ranges from antarctic to tropical waters, and one might expect its breeding season at Goat Island Bay to be reflected in its eurythermy. However, although colonies were collected at all times of the year, embryos were found only during March.

Larval biology

Although Ryland stressed the importance of embryo colour in segregating closely related species (particularly ctenostomes) (1958), he also suggested (1963) its use as a generic character. There are probably too few congeneric species in Table 1 to support this claim but it many be noted that both species of *Rhynchozoon* have identically coloured embryos.

There does not seem to be any hard and fast relationship between colony colour and embryo colour. Red embryos, for example, are found in red, orange and colourless colonies. However, whitish embryos are typically found in white or transparent colonies (e.g. *Hippothoa* sp. and *Crepidacantha crinispina* Levinsen).

Initiation of reproductive activity

Isolating factors initiating gametogenesis in any organism is not easy. It is most likely that the factors triggering reproduction in bryozoans are food and temperature and also, as Silén (1966) discovered, mechano-physiological stimuli play a part as well. The action of this kind of stimulus, as in the example of *Electra posidoniae* cited by Silén, could be interpreted as a curbing of budding (asexual reproduction) of which the energy is channelled into sexual reproduction.

The observations on temperature and food availability at Goat Island Bay suggest that the latter has a more direct influence. Sea water temperatures were low when reproduction (sexual and asexual) started or increased in September. Numbers of *Leptocylindrus* were high and numbers of other phytoplankters were low. It appeared that *Leptocylindrus* could not be ingested, however. It may be that the dissolved organic nutrients that are now known to exist in sea water (vitamins, amino acids, etc.) and which stimulate plant growth, also influence animal growth and reproduction. Shiraishi and Provasoli (1959) have demonstrated that varying amounts of vitamins in solute form can affect growth in a marine copepod. Possibly this phenomenon occurs in bryozoa, but this of course, is pure speculation.

Summary

The breeding seasons of 23 species of Bryozoa from Goat Island Bay, New Zealand are recorded. These species broadly show three breeding patterns; a very restricted breeding season, a year round breeding season and a season from spring to early winter. During the peak of reproductive activity almost all colonies of *Fenestrulina malusii* var. *thyreophora* above 25 mm^2 in area contained embryos, and these are found in ovicells of 25 p. 100 of the zooids, on the average. The frequency of occurrence of various types of brood chamber among the cheilostomes at Goat Island Bay is recorded. Tables of substrate habitation of larvae and colours of embryos are given, and the abnormal occurrence of albino embryos in two species and its implications are discussed. Annual fluctuations in breeding activity are compared to sea water temperature and food availability and it is suggested that the latter has a more direct influence on initiation of reproduction.

Zusammenfassung

Die Reproduktionszeiten von 23 Arten der Bryozoen aus der Goat Island Bay, Neuseeland, werden verzeichnet. Diese Arten zeigen, grob gesagt, drei Muster im Reproduktionsvorgang ; eine sehr begrenzte Reproduktionsperiode, eine ganzjährige Reproduktionsperiode und eine Periode vom Frühjahr bis zum Frühwinter. Zur Hauptzeit der reproduktiven Aktivität enthielten fast alle über 25 mm^2 großen Kolonien von *Fenestrulina malusii* var. *thyreophora* Embryos, und diese finden sich in den Ovizellen von durchschnittlich 25 Prozent der Zooiden. Die Vorkommenshäufigkeit verscheidener Arten von Bruthöhlen bei den Cheilostomen in der Goat Island Bay wird verzeichnet. Tabellen zu Siedlungsböden von Larven und zur Färbung von Embryos werden gegeben, und das abnorme Vorkommen von Albino-Embryos in zwei Gattungen und seine Bedeutung werden diskutiert. Schwankungen der Reproduktionsaktivität in einem Jahr werden zur Seewassertemperatur und zur vorhandenen Nahrungsmenge in Beziehung gesetzt, und es wird vermutet, daß letztere einen direkteren Einfluß auf die Auslösung des Reproduktionsprozesses ausübt.

Acknowledgements

This study was carried out at the Leigh Marine Laboratory. I am grateful to the Director, Dr W.J. Ballantine for the use of facilities and for many helpful suggestions during the course of this work. I also wish to thank Roger V. Grace, Tony Ayling and John H. Laxton for collecting bryozoa from the sublittoral, and Dr F.J. Taylor for information on the seasonal abundance of phytoplankton. Dr Eric L. Mills (Institute of Oceanography, Dalhousie University, Halifax), and Dr William C. Banta (Smithsonian Institution, Washington D.C.) read the manuscript, for which I am grateful.

REFERENCES

BROWN, D.A., 1952. — *The Tertiary Cheilostomatous Polyzoa of New Zealand.* British Museum (Nat. Hist), London.

BULLIVANT, J.S., 1967. — Release of sperm by bryozoa. *Ophelia*, 4, *pp.* 139-142.

CALVET, L., 1900. — Contribution à l'histoire naturelle des Bryozoaires ectoproctes marins. *Trav. Inst. Zool. Univ. Montpellier*, 8, *pp.* 1-488.

COOK, P.L., 1968. — Observations on living bryozoa. *Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano*, 108, *pp.* 155-160.

EGGLESTON, D., 1963. — *The Marine Polyzoa of the Isle of Man. Thesis*, University of Liverpool, 297, *pp.* (Not seen).

FOX, D.L. & HOPKINS, T.S., 1966. — The comparative biochemistry of pigments, in *Physiology of Echinodermata*, ed. R.A. Boolootian, John Wiley & Sons, pp. 277-300.

HASTINGS, A.B., 1943. — Polyzoa (Bryozoa). — I. *Discovery Rep.* 22, *pp.* 301-510.

GAUTIER, Y.V., 1962. — Recherches écologiques sur les Bryozoaires Cheilostomes en Méditerranée occidentale. *Rec. Trav. St mar. Endoume*, 38, *pp.* 9-434.

GORDON, D.P., 1967. — A report on the ectoproct Polyzoa of some Auckland shores. *Tane*, 13, *pp.* 43-76.

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

HYMAN, L.H., 1959. — *The Invertebrates: V Smaller Coelomate Groups*, McGraw-Hill, New York, 783 *pp.*

MARCUS, E., 1938. — Bryozoarios marinhos Brasileiros. *Bol. Faculd. Philos., Sci. e Letr.*, IV, *Zool.*, 2, *pp.* 1-196.

MAWATARI, W., 1952. — On *Watersipora cucullata*, a common marine fouling bryozoan. *Misc. Rep. Res. Inst. Nat. Resour. Tokyo*, 28, *pp.* 17-27.

POORE, G.C.B., 1968. — Succession of a wharf-pile fauna at Lyttelton, New Zealand. *N.Z. Jl mar. Freshwat. Res.*, 2, *pp.* 577-590.

POWELL, N.A., 1967a. — Sexual dwarfism in *Cribrilina annulata* (Cribrilinidae - Bryozoa). *J. Fish. Res. Board Can.*, 24, *pp.* 1905-1910.

POWELL, N.A., 1967b. — Polyzoa (Bryozoa) Ascophora from North New Zealand. *Discovery Rep.*, 34, *pp.* 199-394, pls 1-17.

RALPH, P.M. et HURLEY, D.E., 1952. — The settling and growth of wharf pile fauna in Port Nicholson, Wellington, New Zealand. *Zool. Publ. Victoria Univ. Coll.*, 19, *pp.* 1-22.

ROGICK, M.D., 1956. — Studies on marine bryozoa VII. *Hippothoa. Ohio Jour. Sci.*, 56, *pp.* 183-191.

RYLAND, J.S., 1958. — Embryo colour as a diagnostic character in Polyzoa. *Ann. Mag. Nat. Hist.* xiii, 1, *pp.* 552-556.

RYLAND, J.S., 1962a. — The association between polyzoa and algal substrata. *J. Anim. Ecol.*, 31, *pp.* 331-338.

RYLAND, J.S., 1962b. — The effect of temperature on the photic responses of polyzoan larvae. *Sarsia*, 6, *pp.* 41-48.

RYLAND, J.S., 1963. — Systematic and biological studies on Polyzoa (Bryozoa) from western Norway. *Sarsia*, 14, *pp.* 1-59.

RYLAND, J.S., 1967. — Polyzoa. *Oceanogr. Mar. Biol. Ann. Rev.*, 5, *pp.* 343-369.

SHIRAISHI, K. et PROVASOLI, L., 1959. — Growth factors as supplements to inadequate algal foods for *Tigriopus japonicus*. *Tohoku Jour. Agric. Res.*, 10, *pp.* 89-96.

SILÉN, L., 1966. — On the fertilisation problem in the gymnolaematous Bryozoa. *Ophelia*, 3, *pp.* 113-140.

SKERMAN, T.M., 1958. — Marine fouling at the port of Lyttelton. *N.Z. J. Sci.*, 1, *pp.* 224-257.

SKERMAN, T.M., 1959. — Marine fouling at the port of Auckland. *Ibid.*, 2, *pp.* 57-94.

SKERMAN, T.M., 1960. — The recent establishment of the polyzoan *Watersipora cucullata* (Busk) in Auckland Harbour, New Zealand. *Ibid.*, 3, *pp.* 615-619.

SOULE, D.F. et SOULE, J.D., 1967. — Faunal affinities of some Hawaiian Bryozoa (Ectoprocta). *Proc. California Acad. Sci.*, 35, *pp.* 265-272.

WATERS, A.W., 1912. — A structure in *Adeonella* (*Laminopora*) *contorta* (Michelin) and some other Bryozoa, with remarks on the Adeonidae. *Ann. Mag. Nat. Hist.*, 9, *pp.* 489-500.

APPENDIX 1

Provisional list of cheilostomes of Goat Island Bay and vicinity, to accompany Figure 4. The method of brooding is indicated in parentheses after each species (IB = internal brooding; G = gonoecium; GZ = gonozooid; ES = external sac; O = ovicells; NB = ova not brooded).

Cheilostomata Anasca

Inovicellata:

- *Aetea anguina* (Linnaeus) (ES)
- *Aetea truncata* (Landsborough) (?)

Scrupariina:

- *Scruparia ambigua* d'Orbigny (O)

Malacostega:

- *Membranipora membranacea* (Linnaeus) (NB)
- *Membranipora* sp. (NB)
- *Conopeum seurati* (Canu) (NB)
- *Electra pilosa* (Linnaeus) (NB)
- *Spiralaria denticulata* Busk (O)
- *Crassimarginatella papulifera* (MacGillivray) (O)
- *Retevirgula acuta* (Hincks) (O)
- *Odontionella cyclops* (Busk) (O)
- *Chaperia acanthina* (Lamaroux) (IB)

Chaperia cervicornis (Busk) (O)
Chaperia rubida (Hincks) (O)
Patsyella flemingi Brown (IB)

Coelostega:

Steginoporella neozelanica (Busk) var. *magnifica* Harmer (IB)
Steginoporella neozelanica (Busk) var. *typica* (Busk) (IB)
Micropora mortenseni Livingstone (O)
Opaeophora lepida (Hincks) (O)
Macropora grandis (Hutton) var. *levinseni* Brown (G)

Pseudostega:

Cellaria tenuirostris (Busk) (O)

Appendix 1 continued

Cellularina:

Emma rotunda Hastings (O)
Caberea zelandica (Gray) (O)
Bicellariella sp. (O)
Bugula neritina (Linnaeus) (O)
Bugula sp. (?)
Beania hirtissima (Heller) (IB)
Beania magellanica (Busk) (IB)
Beania spinigera (MacGillivray) (IB)
Beania decumbens MacGillivray (IB)
Beania bilaminata (Hincks) (IB)
Beania conferta MacGillivray (IB)

Cheilostomata Ascophora

Ascophora Imperfecta:

Umbonula bicuspis (Hincks) (O)
Escharoides excavata (MacGillivray) (O)
Escharoides angela (Hutton) (O)
Exochella tricuspis (Hincks) (O)
Arachnopusia unicornis (Hutton) (O)
Celleporaria hastigera (Busk) (O)
Celleporaria sp. (O)
Eurystomella foraminigera (Hincks) (O)

Ascophora Vera:

Hippothoa distans MacGillivray (GZ)
Hippothoa cancer (Hutton) (GZ)
Hippothoa buskiana (Hutton) (GZ)
Hippothoa sp. (GZ).
Hippothoa sp. (GZ).
Spiroporina grandipora (Waters) (O)
Spiroporina polypora Brown (O)
Arthropoma circinatum (MacGillivray) (O)
Schizomavella immersa Powell (O)
Osthimosia eatonensis (Busk) (O)
Osthimosia bicornis (Busk) (O)
Celleporina sp. (O)
Microporella hyadesi (Jullien) (O)
Microporella ciliata (Pallas) (O)
Fenestrulina malusii (Audouin) (O)
Fenestrulina malusii var. *thyreophora* (O)
Calloporina angustipora (Hincks) (O)
Hippoporina cincta (Hincks) (O)
Hippomenella vellicata (Hutton) (O)
Hippopodinella adpressa (Busk) (IB)
Cryptosula pallasiana (Moll) (IB)
Watersipora arcuata Banta (IB)
Lagenipora nitens? MacGillivray (O)
Smittina maplestonei (MacGillivray) (O)
Smittina torques Powell (O)
Smittoidea acaroensis (Levinsen) (O)
Parasmittina unispinosa (Waters) (O)
Crepidacantha crinispina Levinsen (O)
Rhynchozoon rostratum (Busk) (O)
Rhynchozoon larreyi (Audouin) (O)

I wish to thank Dr A.B. Hastings for identifying the species of *Hippothoa* and Dr D. Jebram for identifying *Conopeum seurati*.