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Distribution and Ecology of Estuarine Ectoprocts: A Critical Review

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ABSTRACT: While most gymnolaemates are restricted to waters of normal salinity, at least 3–6% are able to penetrate some distance into mixohaline water. Of this group, which includes 9 species of cyclostomes, 35 species of ctenostomes, 55 species of anascan and 21 species of ascophoran cheilostomes, the cyclostomes and the ascophorans are least tolerant of diluted salinities, the ctenostomes and the anascans are most tolerant. Like many other groups of benthic organisms, ectoprocts show a decrease in numbers of species with decreasing salinity. Only 5 species can penetrate into waters of less than 3‰. About 20 species can be considered truly brackish-water organisms, being most abundant in mixohaline waters. Apparently these species possess some means of active osmoregulation, probably at the tissue level.

The distribution of brackish water ectoprocts depends not on salinity alone, but also on factors of temperature, substrate availability and the general stability of the environment.

Research most necessary before distribution patterns can be explained concerns the salinity tolerance of larvae and adults, larval behavior, and physiology. Also needed are faunal studies, particularly in tropical estuarine localities.

Introduction

The special ecological and physiological features of life in brackish waters have been reviewed many times (e.g. Remane and Schlieper 1971; Kinne 1964, 1970; Emery, Stevenson and Hedgpeth 1957; Day 1951; Green 1968, etc.) Estuarine and brackish water areas are usually poor in species, and those species living there often show adaptations enabling them to cope with fluctuating or stressful environmental conditions.

Many authors have noted that stenolaemate and gymnolaemate ectoprocts are usually restricted to normal sea water (salinity roughly 35‰). Ryland (1970) and Remane (1971) have given figures for the number of species of ectoprocts in varying salinities in the Baltic area from which a graphic picture of the gradual impoverishment of species in increasingly brackish water may be derived (Fig. 1). Remane has stressed that the decrease in the number of species cannot be simply correlated with salinity because the environments sampled vary also in such factors as substrate, depth of water, ice cover, O_2 levels, etc. Salinity does, however, appear to be the major environmental factor involved.

Several early studies of estuarine ectoprocts concerned morphological variation in waters of different salinities. Winther (1877) found variations in the stenolaemate *Crisia eburnea* in the Baltic area which correlated with variations in salinity. Stoliczka (1869), Annandale (1907a,b, 1908, 1911, 1915) and Robertson (1921) described several *Membranipora* species from Indian brackish water, with delicate walls, elaborate development of spines and a loose connection to the substrate. Robertson considered these morphological features to be effects of the low salinity environment. Loppens (1903, 1905, 1906, 1907) described variations in spination in a brackish water species which he called *Membranipora membranacea* from the Netherlands, later considered to be a variety of *Electra crustulenta* (Borg 1931).

Important contributions to the study of brackish water ectoprocts of the Baltic region were made by Borg (1931, 1936,

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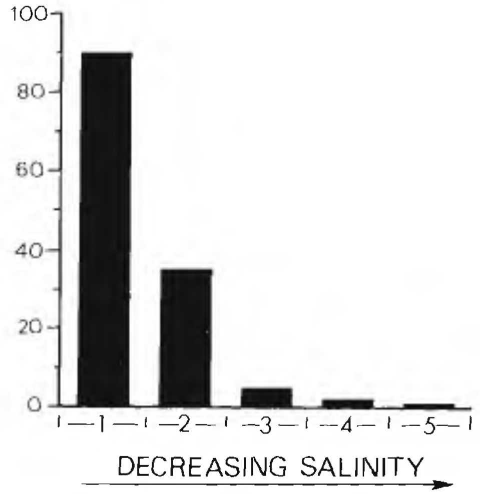


Fig. 1. Impoverishment of ectoproct species in the Baltic Sea (after data from Remane and Schlieper [1971] and Ryland [1970]). Area 1, salinity—20–30‰; area 2, salinity—10–20‰; area 3, salinity—6–10‰; area 4, salinity—3–6‰; area 5, salinity—<3‰.

1947), who distinguished between the mainly marine species *Membranipora membranacea* (Linnaeus), and the more truly brackish water species *Electra crustulenta* (Pallas). In the Baltic, Borg (1931) noted decrease in size and decreasing degree of calcification of zooids of *Electra* in more brackish water.

Hutchins (1941) studied the impact of environmental factors, especially salinity, on growth rates, calcification, and distribution of *Conopeum reticulum* (now identified by the author as a member of the *tenuissimum-seurati* group). Presence of lateral spines on the zooids was dependent on a salinity of at least 25‰.

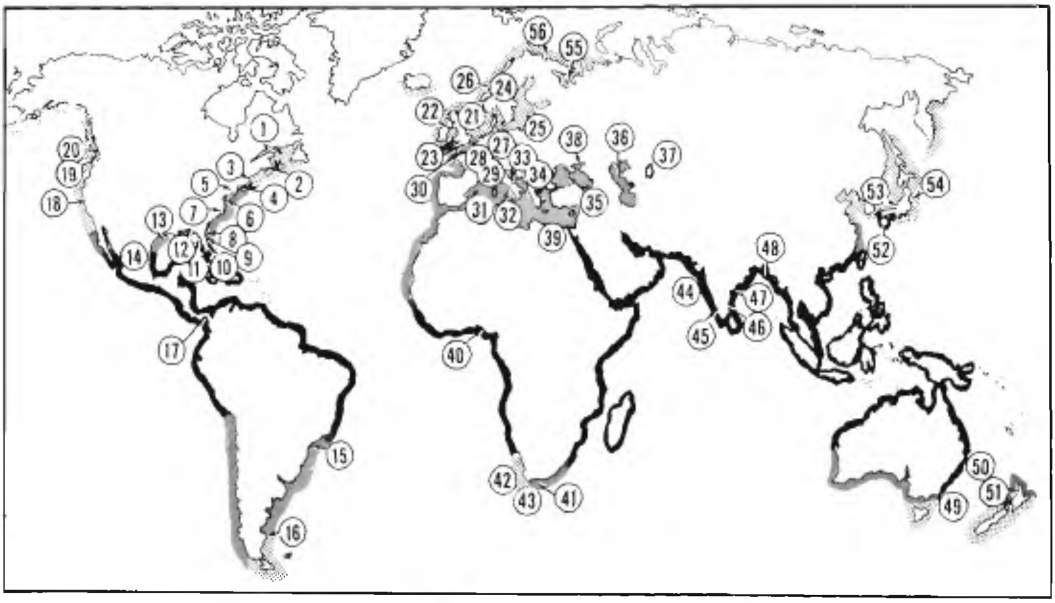
Osburn (1932, 1944) made a survey of the Bryozoa of Chesapeake Bay which has served as a classic reference on the penetration of marine ectoprocts into fresh water. Osburn described the change in the composition of the ectoproct fauna from the sea into the estuary, with ctenostomes and membraniporine cheilostomes being proportionately better represented, and cyclostomes and ascophoran cheilostomes more poorly represented in the Bay than in the sea. He also stressed that while the numbers of species were reduced, the numbers of individuals of these few species could be quite large at any given locality.

Probably the most comprehensive recent review of European brackish water species is found in Gautier's 1962 monograph. He found salinity to be a principal factor in the distribution of all cheilostomes, especially harbor-dwelling species and those characteristic of the brackish circum-Mediterranean lagoons (étangs). Gautier also noted a general improverishment of species, the occurrence of a large number of individuals of tolerant species in brackish water localities, and a change in the composition of the fauna, with the Membraniporidae, Cellularina and Ctenostomata being best able to tolerate a slight lowering of salinity, and the Cyclostomata and the ascophoran Cheilostomata being more completely stenohaline. His major contribution, however, was the description of a group of subspecies, the *Conopeum seurati* group, characteristically found in the very low salinity Mediterranean lagoons, and now shown to penetrate into the Pontocaspian brackish seas as well (Zevina and Kuznetsova 1965).

Most of the above works pertain to the European coast, especially the Baltic Sea. No comparative study has been made of ectoprocts recorded from mixohaline water in all parts of the world. Except for the above papers, the literature relating to the distribution of estuarine and brackish water ectoprocts is not easily accessible to readers since much of it is buried in fouling studies and confused by systematic revisions. In order to clarify the whole pattern of ectoproct distribution with respect to salinity the author has attempted to gather all the information on such species, from faunal lists of estuarine regions, studies of the ectoprocts of various regions of the world, and from studies on fouling organisms, into a thorough survey of their distribution. Because of the confusion in species identity and the diversity of the literature, a bibliography on the ecology and distribution of these organisms has been included.

Materials and Methods

Ninety-nine studies covering 56 worldwide localities were used in constructing the tables of estuarine species and the gradients of brackish water penetration. Fig. 2 shows the location of these areas with respect to



KEY: TROPICAL WARM-TEMPERATE BOREAL-ANTIBOREAL

Fig. 2. Estuarine and brackish-water ectoproct localities. 1. Gulf of St. Lawrence (Bassler and Osburn 1931; Brunel 1970). 2. Bay of Fundy (Powell and Crowell 1967). 3. Great Bay, N.H. (Winston, unpublished research). 4. Long Island Sound (Hutchins 1945). 5. Delaware Bay (Watts 1957; Maurer and Watling 1973). 6. Chesapeake Bay (Osburn 1944). 7. Beaufort, N.C. (Maturo 1947, 1959, 1968; Wells 1961). 8. Ponce de Leon Inlet, Daytona Beach, Fla. (Clapp and Richards 1944). 9. Mayport, Jacksonville, Harbor, Fla. (Joseph and Nichy 1955b). 10. Indian River, Fort Pierce, Fla. (Winston and Middleton [unpubl.]; Mook 1976). 11. Appalachee Bay, Fla. (Joseph and Nichy 1955a). 12. N.W. Florida (Shier 1964). 13. Texas and Louisiana Coasts (Gunter 1955; Gunter and Geier 1955; Cook 1966). 14. Tamiahua Lagoon, Veracruz, Mexico (Sandberg 1961). 15. Bay of Antonina, Brazil (Marcus 1941). 16. Ria Deseado, Argentina (Amor and Pallares 1965). 17. Panama Harbor, Panama (Powell 1971). 18. San Francisco Bay, Calif. (Filice 1958). 19. Admiralty Inlet, Puget Sound, Wash. (De Palma 1966). 20. Strait of Georgia, B.C. (Powell 1967; Johnson and Miller 1935). 21. New England Creek, Essex, England (Howes 1939; Cook 1960). 22. Mersey Estuary, England (Fraser 1938; Corlett 1948). 23. Tamar Estuary, and Plymouth England (Milne 1940; Mar. Biol. Assoc., U.K., 1958). 24. Baltic Sea, Kattegat Area (Borg 1930; Brattstrom 1954; Kramp 1918). 25. Baltic, including inner areas (Androsova 1962; Bock 1950; Braem 1951; Jebram 1969; Ryland 1970). 26. Western Norway (Nair 1961, 1962). 27. North Sea, Riveroff Canal, Elbe Estuary, Nordostsee Canal, Schleswig-Holstein (Jebram 1969a, b; Kuhl 1972; Schutz 1963; Hagmeier 1927). 28. Former Zuiderzee, Netherlands (Vorstman 1936; Van Benthem Jutting 1922). 29. Netherlands, all areas (Lacourt 1951). 30. River D'lc and Roscoff, France (Salmon 1959; Prenant and Teissier 1924). 31. Western Mediterranean (Gautier 1958). 32. Naples, Italy, "Lago di Patria," "Lago Fusaro" (Sacchi 1961a, b; Carrada and Sacchi 1966). 33. Adriatic—Lagoon of Venice (Neviani 1937; Gautier 1958). 34. Lagoon of Orbatello (Apolloni 1931). 35. Black Sea, Med-Azov (Lebedev 1963; Braiko 1960). 36. Caspian Sea (Abrikosov 1959; Zevina 1963; Petukhova 1963; Ryland 1967; Zevina and Kuznetsova 1963). 37. Aral Sea (Abrikosov 1959). 38. Sea of Azov (Lebedev 1963; Starostin and Permitin 1963). 39. Port Said, Egypt (Hastings 1927). 40. West Africa: vicinity of Lagos, Nigeria, and mouth of River Densu, Ghana (Cook 1968a, b). 41. Knysna Estuary, S. Africa (Day, Millard and Harrison 1952). 42. Milnerton Estuary, S. Africa (Day 1951). 43. Klein River Estuary, S. Africa (Scott, Harrison and McNae 1952). 44. Bombay Harbor, India (Karande 1968). 45. Cochin Harbor, India (Menon and Nair 1967, 1971). 46. Madras Harbor, India (Antony Raja 1959; Daniel 1954). 47. Visapakhatnam Harbor, India (Ganapati 1958). 48. Bay of Bengal, various areas (Annandale 1907a, b, 1908, 1911, 1915; Robertson 1921). 49. Sydney Harbor area, Australia (Allen and Wood 1950; Wisely 1959; Blick and Wisely 1964). 50. Brisbane River, Moreton Bay, Australia (Straughan 1967). 51. Auckland, New Zealand (Skerman 1959). 52. Sasebo, Japan (Rucker 1969). 53. Maizuru, Japan (Rucker 1969). 54. Matsusbima Bay, Japan (Toriumi 1944). 55. White Sea (Zevina 1963). 56. Kola Inlet, Murmansk Coast (Gurjanova 1924).

the littoral marine biogeographic provinces derived by Hedgpeth (1957). The figure demonstrates that most of the locations are in the boreal-antiboreal (21) and warm-temperate (22) provinces. Only 13 are found in the tropical region. The lack of information on tropical areas makes it impossible to get a true idea of tropical estuarine ectoproct diversity, although the locations can still be useful in obtaining some idea of the types of ectoproct species found in these areas and the factors influencing their ecology.

The 99 references selected from the bibliography were used to compile Table 1—a list of species collected at stations with diminished salinity. The list includes all species mentioned in those references even if they only occurred at one locality. However, since species which occurred only once could have been erroneously labelled and not truly euryhaline, only those which either occurred more than once, or occurred once but in water that was definitely mixohaline (<30‰) in character were included in the rest of the analysis. Wherever possible names have been changed to correspond with current nomenclature.

Figs. 3, 4 and 5 summarize gradient data from 9 of the most complete studies on the change in composition of the ectoproct fauna with increasing brackish water penetration.

Table 2 gives the salinity ranges of species collected at stations with diminished salinity. Station salinities were used if available; otherwise, salinities were estimated from other literature on the hydrography and physical conditions of the area. The species were grouped in categories according to the salinity classification of Remane and Schlieper (1971, p. 87): (1) Stenohaline marine organisms or halobionts (live in euhaline range 35–40‰ to about 30‰); (2) Euryhaline marine organisms or halobionts of the first degree (I)—range from sea (35–40‰) to 30–18‰ salinity; (3) Euryhaline marine organisms of the second degree (II) or pleiomesohaline organisms—range from the sea into water of 18–8‰; (4) Euryhaline marine organisms of the third degree (III) or meiomesohaline organisms—penetrate from the sea into salinities of 8–3‰; (5) Euryhaline marine organisms of the fourth degree (IV) or oligohaline marine organisms—those which can survive in water of less than 3‰. Table 2 also includes those euryhaline marine organisms for which brackish water conditions appear to be optimal for survival and reproduction or the true brackish water species.

The salinity categories used in this paper follow those given in Remane and Schlieper (1971, p. 5–6) adapted from the "Venice System" classification (Symposium in the classification of brackish waters, 1959):

$$
\begin{aligned}
\text{hyperhaline} &= >40‰\\
\text{euhaline} &= 30\text{–}40‰\\
\text{mixohaline} &= <30‰\\
\text{polyhaline} &= 30\text{–}18‰\\
\left.\begin{aligned}\text{pliohaline} &= 18\text{–}8‰\\ \text{miohaline} &= 8\text{–}3‰\end{aligned}\right\} &\ \text{mesohaline}\\
\text{oligohaline} &= 3\text{–}0.5‰\\
\text{limnetic} &= 0.5‰
\end{aligned}
$$

Table 3 lists the estuarine and brackish water ectoprocts characteristic of the various biogeographic provinces as delimited by Hedgpeth (1957). In the case of species which also occur in marine environments, the table lists only their records from the brackish water localities; their biogeographic distribution in euhaline waters may be broader.

Results

Brackish Water Gymnolaemate Species

The list (Table 1) of those species occurring at least once at a station of diminished salinity contains 16 species of cyclostomes, 52 ctenostomes, 92 anascan cheilostomes, and 43 ascophoran cheilostomes, or 203 species in all, representing only 6% of the 3500 or so Recent ectoproct species. Those species which occurred more than once or were definitely shown to occur in brackish water include 9 species of cyclostomes, 35 species of ctenostomes, 55 species of anascans and 21 species of ascophorans, only 120 species in all, or, 3% of the total Recent ectoproct fauna. Thus, only 3 to 6% of gymnolaemate ectoprocts are known to have penetrated into brackish water.

Considering the number of genera involved, it appears that there are 4 genera of cyclostomes, 18 genera of ctenostomes, 21 genera of anascan cheilostomes and 19 genera of ascophoran cheilostomes known to occur in brackish water. Bassler (1953) lists 58 genera of Recent cyclostomes, 33 genera of ctenostomes, 174 of anascan, and 207 of ascophoran cheilostomes. Therefore, about 7% of the total cyclostome genera (representing only 2 of the 5 suborders), 55% of the ctenostome genera, 12% of anascan

TABLE 1. List of species collected at stations with diminished salinity

Species	Locations	Geographic Affinity
Cyclostomes		
1. *Crisia* sp.	49	Tropical
2. *Crisia denticulata* (Lamarck)	29	Boreal
3. *Crisia eburnea* (L.)	3, 4, 6, 24, 25, 26, 29, 56	Boreal, Warm-temp.
4. *Crisia elongata* Milne-Edwards	33	Warm-temp.
5. *Crisia geniculata* Smitt	56	Boreal
6. *Crisidia cornuta* (L.)	29	Boreal
7. *Crisiella producta* (Smitt)	25, 56	Boreal
8. *Diastopora flabellum* (Reuss)	33	Warm-temp.
9. *Lichenopora hispida* (Fleming)	25	Boreal
10. *Lichenopora intricata* (Busk)	17	Tropical
11. *Lichenopora verrucaria* (Fabricius)	4, 24, 25, 26	Warm-temp., Boreal
12. *Plagioecia patina* (Lamarck)	26	Boreal
13. *Tubulipora flabellaris* (Fabricius)	19, 20, 25, 26, 34	Boreal, Warm-temp.
14. *Tubulipora liliacea* (Pallas)	4, 25, 26, 29	Boreal, Warm-temp.
15. *Tubulipora lobulata* Hassall	24, 25	Boreal
16. *Tubulipora phalangea* Couch	24, 25	Boreal
Ctenostomes		
1. *Aeverrillia armata* (Verrill)	4, 6, 7, 12, 15	Warm-temp.
2. *Aeverrillia setigera* (Hincks)	4, 7, 39, 44	Warm-temp., Tropical
3. *Alcyonidium chondroides* O'Donoghue & DeWatteville	41	Warm-temp.
4. *Alcyonidium gelatinosum* (L.)	16, 24, 25, 26, 29, 33	Boreal, Warm-temp.
5. *Alcyonidium hauffi* Marcus	7	Warm-temp.
6. *Alcyonidium hirsutum* (Fleming)	24, 25, 28, 29, 56	Boreal
7. *Alcyonidium mamillatum* Alder	7, 15, 29	Boreal, Warm-temp.
8. *Alcyonidium mytili* Dalyell	1, 24, 30	Boreal, Warm-temp.
9. *Alcyonidium parasiticum* (Fleming)	6, 12, 25, 29	Boreal, Warm-temp.
10. *Alcyonidium polyoum* (Hassall)	2, 3, 4, 5, 6, 7, 12, 16, 17, 23, 25, 26, 28, 29, 30	Boreal, Warm-temp.
11. *Alcyonidium proliferans* Lacourt	29	Boreal
12. *Alcyonidium rhomboidale* O'Donoghue	41	Warm-temp.
13. *Alcyonidium verrilli* Osburn	4, 5, 6, 7	Warm-temp.
14. *Amathia* sp.	13	Warm-temp.
15. *Amathia* sp.	43	Tropical
16. *Amathia alternata* Lamouroux	12	Warm-temp.
17. *Amathia convoluta* Lamouroux	5, 6, 7, 11, 12	Warm-temp.
18. *Amathia distans* Busk	7	Warm-temp.
19. *Amathia vidovici* (Heller)	4, 5, 6	Warm-temp.
20. *Anguinella palmata* Van Beneden	4, 5, 6, 7, 12, 28, 29	Boreal, Warm-temp.
21. *Arachnidium clavatum* Hincks	35	Warm-temp.
22. *Arachnidium fibrosum* Hincks	15	Warm-temp.
23. *Bowerbankia* sp.	13	Warm-temp.
24. *Bowerbankia* sp. (=*B. imbricata caspia*)	38	Warm-temp.
25. *Bowerbankia* sp.	43	Tropical
26. *Bowerbankia* sp.	45	Tropical
27. *Bowerbankia* sp.	46	Tropical
28. *Bowerbankia* sp. (Indian River sp.)	10	Tropical
29. *Bowerbankia gracilis* Leidy	3, 4, 5, 6, 7, 12, 15, 16, 24, 25, 27, 28, 29, 30, 32, 35, 44, 46, 47, 53	Boreal, Warm-temp., Tropical
30. *Bowerbankia imbricata* (Adams)	3, 16, 22, 23, 26, 29, 30, 33	Boreal, Warm-temp.
31. *B. imbricata caspia* (Abrikosov)	35?, 36	Warm-temp.
32. *Bowerbankia imbricata aralensis* (Abrikosov)	37	Warm-temp.
33. *Bowerbankia pustulosa* (Ellis and Solander)	23, 33	Warm-temp.
34. *Bulbella abscondita* Braem	25, 27	Boreal
35. *Buskia nitens* Alder	25, 29	Boreal
36. *Farrella repens* (Farre)	28, 29	Boreal
37. *Flustrellidra hispida*	1, 2, 3, 4, 24, 25, 26, 29, 30, 56	Boreal, Warm-temp.

TABLE 1. (Cont'd)

TABLE 1. List of species collected at stations with diminished salinity

Species	Locations	Geographic Affinity
38. *Mimosella gracilis* Hincks	33	Warm-temp.
39. *Nolella* sp.	44	Tropical
40. *Nolella papuensis* (Busk)	44, 45	Tropical
41. *Nolella gigantea* (Busk)	7	Warm-temp.
42. *Paludicella* sp.	48	Tropical
43. *Paludicella articulata* (Ehrenberg)	29	Boreal
44. *Sundanella sibogae* (Harmer)	7, 12, 15	Warm-temp.
45. *Tanganella mulleri* (Kraepelin)	25	Boreal
46. *Triticella elongata* (Osburn)	4, 5, 6, 7	Warm-temp.
47. *Triticella pedicellata* (Alder)	25	Boreal
48. *Valkeria uva* (L.)	24, 25, 27, 28, 29, 31	Boreal, Warm-temp.
49. *Vesicularia spinosa* (L.)	29	Boreal
50. *Victorella bergi* (Abrikosov)	37	Warm-temp. ?
51. *Victorella pavida* Saville Kent	6, 7, 24, 25, 27, 28, 29, 32, 35, 36, 44?, 45, 48, 54	Boreal, Warm-temp., Tropical
52. *Zoobotryon verticillatum* (Delle Chiaje)	7, 12, 11, 13, 31, 32, 33, 44	Warm-temp., Tropical
Cheilostomes		
ANASCA		
1. *Aetea anguina* (L.)	4, 6, 7, 12, 16, 40	Boreal, Warm-temp., Tropical
2. *Aetea ligulata* Busk	16	Boreal
3. *Aetea sica* (Couch)	16	Boreal
4. *Aetea truncata* (Landsborough)	25, 26	Boreal
5. *Alderina arabiensis* Menon and Nair	45	Tropical
6. *Alderina smitti* (Smitt)	44	Tropical
7. *Amphiblestrum flemingii* (Busk)	26	Boreal
8. *Amphiblestrum trifolium* (Searles Wood)	35	Boreal
9. *Antropora tincta* (Hastings)	17	Tropical
10. *Aplousina gigantea* Canu and Bassler	7	Warm-temp.
11. *Aspidelectra densuense* Cook	40	Tropical
12. *Aspidelectra melolontha* (Landsborough)	27, 29, also England	Boreal
13. *Beania costata* (Busk)	16	Boreal
14. *Beania inermis* (Busk)	16	Boreal
15. *Beania intermedia* (Hincks)	10	Tropical
16. *Beania magellanica* (Busk)	16	Boreal
17. *Bicellariella ciliata* (L.)	23, 29	Boreal
18. *Bugula* sp.	8	Warm-temp.
19. *Bugula* sp.	9	Tropical
20. *Bugula avicularia* (L.)	48	Warm-temp.
21. *Bugula californica* Robertson	52, 53	Warm-temp., Boreal
22. *Bugula cucullata* Busk	45	Tropical
23. *Bugula ditrupae* Busk	33	Warm-temp.
24. *Bugula flabellata* (Thompson)	51	Warm-temp.
25. *Bugula gracilis* (Busk)	4, 33	Warm-temp.
26. *Bugula neritina* (L.)	7, 8, 9, 10, 11, 12, 17, 31, 32, 33, 29, 44, 45, 49, 50, 51, 52, 53	Boreal (?), Warm-temp., Tropical
27. *Bugula pacifica* Robertson	20	Boreal
28. *Bugula plumosa* (Pallas)	29, 33	Warm-temp.
29. *Bugula spicata* (Hincks)	33	Warm-temp.
30. *Bugula simplex* Hincks	5, 8, 31	Warm-temp.
31. *Bugula stolonifera* Ryland	3, 7, 10, 17, 31, 32, 33	Boreal, Tropical, Warm-temp.
32. *Bugula turrita* (Desor)	3, 4, 5, 6, 7, 13	Boreal, Warm-temp.
33. *Callopora aurita* (Hincks)	2, 3, 4, 24, 25, 35	Boreal, Warm-temp.
34. *Callopora craticula* (Alder)	4, 24, 25, 26	Boreal, Warm-temp.
35. *Callopora lineata* (L.)	25, 26, 29, 33, 34	Boreal, Warm-temp.
36. *Carbasea carbasea* Ellis & Solander	24	Boreal

TABLE 1. (Cont'd)

TABLE 1. List of species collected at stations with diminished salinity

Species	Locations	Geographic Affinity
37. *Caulibugula* sp.	44	Tropical
38. *Chaperia patula* (Hincks)	7	Warm-temp.
39. *Conopeum* sp.	44	Tropical
40. *Conopeum reticulum* (L.)	2, 4, 15, 21, 23, 27, 29, 30, 35 (?), 49, 50	Boreal, Warm-temp., Tropical
41. *Conopeum seurati* (Canu)	10, 21, 25, 27, 29, 30, 31, 32, 35 (?), 36, 38	Boreal, Warm-temp., Tropical
42. *Conopeum tenuissimum* (Canu)	3, 5, 6, 7, 8, 9 (?), 10, 12, 13, 40	Boreal, Warm-temp., Tropical
43. *Conopeum truitti* Osburn	6	Warm-temp.
44. *Cribrilina annulata* (Fabricius)	20, 24, 25, 26	Boreal
45. *Cribrilina cryptooecium* Norman	2	Boreal
46. *Cribrilina punctata* (Hassall)	2, 3, 4, 24, 25, 29	Boreal, Warm-temp.
47. *Cribrilina spitzbergensis* (Norman)	55	Boreal
48. *Cupuladria canariensis* (Busk)	11	Tropical
49. *Electra* sp.	14	Tropical
50. *Electra* sp.	43	Tropical
51. *Electra bellula* (Hincks)	10, 12, 40	Warm-temp., Tropical
52. *Electra bengalensis* (Stolickzka)	17, 45, 48	Tropical
53. *Electra crustulenta* (Pallas)	2, 21, 23, 24, 25, 27, 28, 29, 45, 54, 55	Boreal, Warm-temp., Tropical?
54. *Electra monostachys* Marcus	2, 4, 5, 6, 7, 8, 17, 21, 29	Boreal, Warm-temp.
55. (near) *Electra monostachys*	43	Boreal
56. *Electra pilosa* (L.)	3, 4, 6, 23, 24, 25, 26, 28, 29, 34, 35, 55, 56	Boreal, Warm-temp.
57. *Electra tenella* (Hincks)	52, 53	Boreal, Warm-temp.
58. *Electra verticillata* (Ellis and Solander)	26, 40	Boreal, Tropical
59. *Electra zostericola* (Von Nordman)	35	Warm-temp.
60. *Eucratea loricata* (L.)	24, 25, 29, 56	Boreal
61. *Flustra foliacea* (L.)	2, 24, 25, 29	Boreal
62. *Membranipora* sp. (not *membranacea)*	6	Warm-temp.
63. *Membranipora* sp. (may be *Conopeum tenuissimum*)	13	Warm-temp.
64. *Membranipora* sp. (as *Acanthodesia* sp.)	13	Warm-temp.
65. *Membranipora* sp. (as *Acanthodesia* sp.	14	Tropical
66. *Membranipora* sp.	42	Boreal
67. *Membranipora* sp. (as *Acanthodesia* sp.)	43	Tropical
68. *Membranipora* sp.	46	Tropical
69. *Membranipora* sp.	47	Tropical
70. *Membranipora arborescens* (Canu and Bassler)	7, 12, 17, 18	Boreal, Warm-temp., Tropical
71. *Membranipora annae* Osburn	17, 40	Tropical
72. *Membranipora devinensis* (Robertson)	48	Tropical
73. *Membranipora hugliensis* (Robertson)	48	Tropical
74. *Membranipora membranacea* (L.)	22, 24, 25, 26, 27 ?, 29 ?	Boreal
75. *Membranipora savartii* (Audouin)	11, 12, 13, 17, 39, 44, 45, 49	Warm-temp., Tropical
76. *Membranipora tenuis* Desor	4, 5, 6, 7, 11, 12, 29, 35	Boreal, Warm-temp., Tropical
77. *Membranipora tuberculata* (Bosc)	5, 6, 13, 40	Warm-temp., Tropical
78. *Membranipora villosa* Hincks	20	Boreal
79. *Membraniporella nitida* (Johnston)	25, 26, 29	Boreal
80. *Menipea marionensis* Busk	41	Warm-temp.
81. *Parellisina curvirostris*	17	Tropical
82. *Scruparia ambigua* D'Orbigny	16, 26, 31	Boreal, Warm-temp.
83. *Scruparia chelata* (L.)	31	Warm-temp.
84. *Scrupocellaria* sp.	51	Warm-temp.
85. *Scrupocellaria bertholettii* (Audouin)	31, 33, 35, 39	Warm-temp.
86. *Scrupocellaria jolloisii* (Audouin)	39	Warm-temp.

TABLE 1. (Cont'd)

TABLE 1. List of species collected at stations with diminished salinity

Species	Locations	Geographic Affinity
87. *Scrupocellaria reptans* (L.)	26	Boreal
88. *Scrupocellaria scabra* (van Beneden)	24, 29	Boreal
89. *Scrupocellaria scruposa* (L.)	24, 26, 29, 44 (?)	Boreal, Tropical (?)
90. *Securiflustra securifrons* (Pallas)	24, 29	Boreal
91. *Tegella unicornis* (Fleming)	25, 26, 29	Boreal
92. *Thalamoporella gothica* (var. *floridana*) Osburn	11, 12	Warm-temp., Tropical
Ascophora		
1. *Celleporaria aperta* (Hincks)	39, 52, 53	Boreal, Warm-temp.
2. *Celleporella hyalina* (L.)	3, 4, 6, 7, 16, 19, 20, 23, 24, 25, 26	Boreal, Warm-temp.
3. *Celleporina hassallii* (Johnston)	29, 56, 26	Boreal
4. *Chorizopora brogniartii* (Audouin)	34	Warm-temp.
5. *Codonellina montferrandii* (Audouin)	52	Warm-temp.
6. *Cryptosula pallasiana* (Moll)	2, 3, 4, 7, 8, 9, 20, 23, 26, 29, 31, 32, 33, 34, 35, 53, 50	Boreal, Warm-temp., Tropical
7. *Discopora turgenewi* Ostroumoff	35	Warm-temp.
8. *Escharella immersa* (Fleming)	2, 24, 25	Boreal
9. *Escharina spinifera* (Johnston)	24	Boreal
10. *Euteleia evelinae* Marcus	40	Tropical
11. *Fenestrulina malusii* (Audouin)	34, 53	Boreal, Warm-temp.
12. *Hippodiplosia* sp.	3	Boreal
13. *Hippodiplosia pertusa* (Esper)	23, 29	Warm-temp., Boreal
14. *Hippopodina feegeensis* (Busk)	17	Tropical
15. *Hippoporella gorgonensis* (Hastings)	17	Tropical
16. *Hippoporidra janthina* (Smitt)	7	Warm-temp.
17. *Hippoporina americana* (Verrill)	7, 40	Warm-temp.
18. *Hippoporina verrilli* Maturo and Schopf	10, 17	Tropical
19. *Cleidochasma contractum* (Waters)	11	Tropical
20. *Celleporaria mordax* (Marcus)	12	Warm-temp.
21. *Mamillopora* sp.	44	Tropical
22. *Microporella californica* (Busk)	20	Boreal
23. *Microporella ciliata* (Pallas)	4, 6, 7, 12, 20, 29	Boreal, Warm-temp.
24. *Microporella umbracula* (Audouin)	17	Tropical
25. "*Parasmittina trispinosa*"	4, 7, 12, (also Puget Sound)	Warm-temp., Boreal?
26. *Parasmittina crosslandi* (Hastings)	17	Tropical
27. *Pasythea tulipifera* (Ellis and Solander)	40	Tropical
28. *Rhynchozoon rostratum* (Busk)	7, 17	Warm-temp., Tropical
29. *Savignyella lafontii* (Audouin)	39, 45	Warm-temp., Tropical
30. *Schismopora americana* (Osburn)	4	Warm-temp.
31. *Schizobrachiella sanguinea* (Norman)	33	Warm-temp.
32. *Schizomavella auriculata* (Hassall)	35	Warm-temp.
33. *Schizomavella linearis* (Hassall)	29, 35, 45	Boreal. Warm-temp., Tropical
34. *Schizoporella* sp.	35	Warm-temp.
35. *Schizoporella* sp.	44	Tropical
36. *Schizoporella biaperta* (Michelin)	4	Warm-temp.
37. *Schizoporella cornuta* (Gabb and Horn)	7	Warm-temp.
38. *Schizoporella errata* (Waters)	3, 4, 6. 7, 31, 33	Boreal, Warm-temp.
39. *Schizoporella unicornis* (Johnston)	8, 9, 10, 11, 12, 20, 30, 39, 43, 52	Boreal, Warm-temp., Tropical
40. *Smittoidea prolifica* Osburn	52, 53	Boreal, Warm-temp.
41. *Umbonula verrucosa* (Esper)	33	Warm-temp.
42. *Vittaticella uberrima* Harmer	40	Tropical
43. *Watersipora subovoidea* (D'Orbigny)	10, 31, 40, 45, 49, 52, 53	Boreal, Warm-temp., Tropical

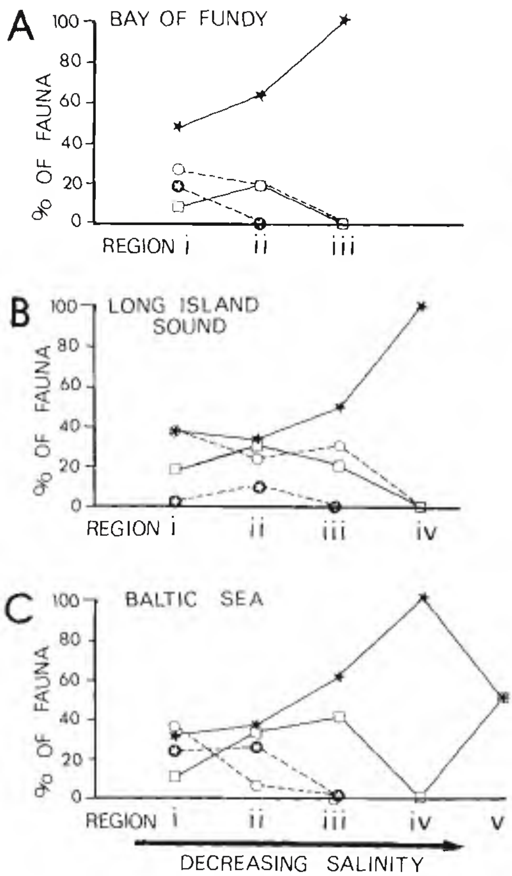


Fig. 3. Changes in composition of ectoproct faunas from marine to brackish water in boreal localities. (A) Bay of Fundy, N.S.: i, outer Bay stations; ii, inner Bay stations; iii, brackish-water stations (based on data in Powell and Crowell 1967). (B) Long Island Sound: i, localities with salinities above 28‰; ii, localities with salinities 20–28‰; iii, typical oyster ground species; iv, inner harbor species (based on data in Hutchins 1945). (C) Baltic Sea: i, western Norway (marine); ii, Baltic transitional zone; iii, s.w. part of the Sea; iv, central part of the Sea (with bays); v, river mouths (based on data in Bock 1950; Androsova 1962; Jebram 1969a, 1969b). Data given as percent of total ectoproct fauna each group comprises in each region: open squares, ctenostomes; stars, anascan cheilostomes; open circles, ascophoran cheilostomes; starred circles, cyclostomes.

cheilostome genera, and 9% of ascophoran cheilostome genera have been found in brackish water. Cyclostomes and ascophoran cheilostomes appear least tolerant of diluted salinities, while anascans (mainly membraniporine forms) are somewhat more tolerant, and ctenostomes contain a majority of genera able to survive at least some dilution of salinity.

Changes in Composition of Ectoproct Fauna in Brackish Water

A few of the references used were complete enough to allow interpretation of

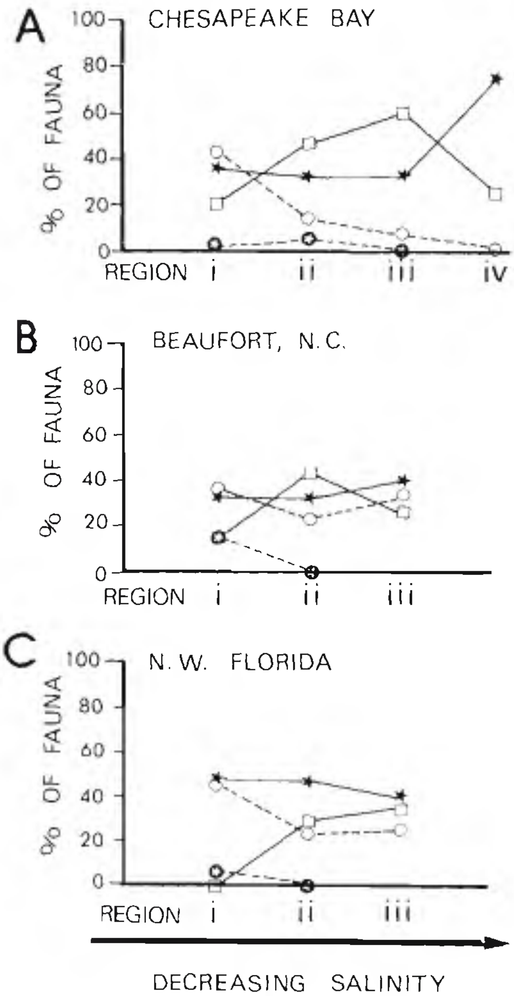


Fig. 4. Changes in composition of ectoproct faunas from marine to brackish water in North American warm-temperate localities. (A) Chesapeake Bay-Atlantic Shelf: i, Atlantic Shelf (marine); ii, Bay localities with salinity greater than 18‰; iii, Bay localities with salinity 10–18‰; iv, Bay localities with salinity less than 10‰ (based on data in Osburn 1944; Maturo 1968). (B) Estuarine-offshore localities, Beaufort, N.C.: i, offshore (marine); ii, estuarine-sound; iii, estuarine (based on data in Maturo 1957, 1959, 1968). (C) N.W. Florida: i, Gulf of Mexico (marine); ii, marginal stations; iii, brackish stations (based on data in Shier 1964). Data given as percent of total ectoproct fauna each group comprises in each region: open squares, ctenostomes; stars, anascan cheilostomes; open circles, ascophoran cheilostomes; starred circles, cyclostomes.

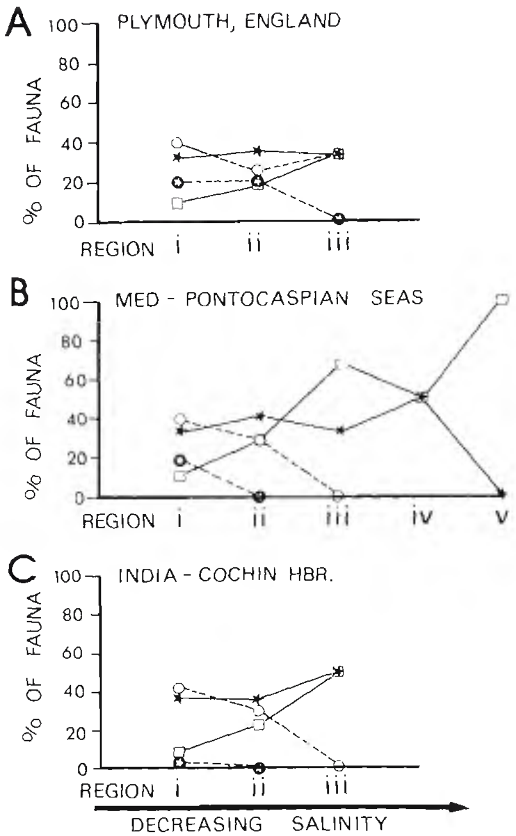


Fig. 5. Changes in composition of ectoproct faunas from marine to brackish water in Old World warm-temperate and tropical localities. (A) Plymouth, England: i, outside breakwater, Plymouth Sound; ii, inside breakwater, Plymouth Sound; iii, estuarine stations (based on data in Marine Biological Association, 1957). (B) Mediterranean-Pontocaspian Seas: i, Adriatic (marine); ii, Black Sea; iii, Caspian Sea; iv, Sea of Azov; v, Aral Sea (based on data in Friedl 1917; Abrikosov 1959; Braiko 1960; Lebedev, Permitin and Karayeva 1963; Starostin and Permitin 1963; Zevina and Kuznetsova 1965). (C) India: i, Indian marine waters; ii, Cochin Harbor, salinity greater or equal to 28‰; iii, Cochin Harbor, salinity 2–33‰ (based on data in Menon and Nair 1967a, 1971). Data given as percent of total ectoproct fauna each group comprises in each region: open squares, ctenostomes; stars, anascan cheilostomes; open circles, ascophoran cheilostomes; starred circles, cyclostomes.

faunal changes with increasing penetration into brackish water. In some cases, two or more studies were combined to show the changes occurring over a salinity gradient. Figs. 3, 4 and 5 show 9 locations for which some gradient data was available. Although it was not possible to equate the different localities with respect to salinity, the gradients still are useful in determining general patterns.

Fig. 3 shows gradient patterns for 3 boreal areas: (A) the Bay of Fundy, (B) Long Island Sound, and (C) the Baltic Sea. Fig. 4 illustrates patterns for North American warm-temperate localities: (A) Chesapeake Bay, (B) Beaufort, N.C., and (C) Northwest Florida. Fig. 5A shows the pattern for Plymouth, England (warm-temperate), while 5B shows the change in composition of the ectoproct fauna from the Mediterranean (Adriatic) to the Pontocaspian region. Patterns for a tropical region (India) are shown by Fig. 5C.

Salinity Tolerances of Ectoproct Species

Table 2 summarizes the literature on salinity tolerances of various ectoproct species occurring in brackish water. The largest number of species (76), including 9 cyclostomes, 11 ctenostomes, 34 anascans and 22 ascophorans, penetrate only into the polyhaline region (salinity 30–18‰).

Only 30 species reach the upper part of the mesohaline region (18–8‰). Of these, 14 are ctenostomes, 13 are anascans and 3 are ascophorans. The ascophorans reach their limit in this region, with *Cryptosula pallasiana* apparently having the greatest tolerance.

Only 11 species (5 ctenostomes and 6 anascans) have been recorded from salinities between 8 and 3‰ (meiomesohaline zone). Three percent appears to be about the lowest salinity that members of the membraniporine group can tolerate, although Ryland (1971) has reported *Electra crustulenta* living at salinities of less than 2‰ in the Baltic and *Conopeum seurati* enduring salinities down to 1‰.

Three species of ctenostome have been recorded from the oligohaline region (<3‰). *Victorella pavida* is most commonly recorded. *Victorella bergi* is a species reported from the Aral Sea (Abrikosov 1959) as distinct from *V. pavida*. Finally, the fresh water ctenostome *Paludicella articulata* can tolerate salinities within the oligohaline range (Prenant and Bobin 1956).

TABLE 2. Salinity ranges of species collected at stations with diminished salinity.

I. Remane's "Euryhaline marine organisms of the first degree;" found in euhaline and polyhaline regions. To 18‰.

Cyclostomes
1. *Crisia eburnea*[1]
2. *Crisiella producta*[1]
3. *Lichenopora hispida*[1]
4. *Lichenopora intricata*
5. *Lichenopora verrucaria*[1]
6. *Tubulipora flabellaris*[1]
7. *Tubulipora liliacea*[1]
8. *Tubulipora lobulata*[1]
9. *Tubulipora phalangea*[1]

Ctenostomes
1. *Aeverrillia setigera*
2. *Alcyonidium mamillatum*[2]
3. *Alcyonidium mytili*
4. *Alcyonidium parasiticum*
5. *Amathia convoluta*
6. *Arachnidium clavatum*
7. *Arachnidium fibrosum*[2]
8. *Bowerbankia* sp. (Indian River sp.)
9. *Nolella papuensis*
10. *Sundanella sibogae*[2]
11. *Zoobotryon verticillatum*

Anascans
1. *Aetea anguina*
2. *Amphiblestrum trifolium*
3. *Antropora tincta*
4. *Bicellariella ciliata*[1,2]
5. *Bugula avicularia*[2]
6. *Bugula californica*
7. *Bugula gracilis*
8. *Bugula neritina*
9. *Bugula plumosa*[2]
10. *Bugula simplex*
11. *Bugula stolonifera*
12. *Bugula turrita*
13. *Callopora craticula*[1]
14. *Callopora lineata*[1]
15. *Cribrilina annulata*[1]
16. *Cribrilina punctata*[1]
17. *Electra bellula*
18. *Electra monostachys*
19. *Electra tenella*
20. *Electra verticillata*
21. *Eucratea loricata*[1]
22. *Flustra foliacea*[1]
23. *Membranipora annae*
24. *Membranipora arborescens*
25. *Membranipora savartii*
26. *Membranipora tuberculata*
27. *Membraniporella nitida*[1]
28. *Parellisina curvirostris*
29. *Scruparia ambigua*
30. *Scrupocellaria bertholettii*
31. *Scrupocellaria scabra*[1]
32. *Scrupocellaria scruposa*[1]
33. *Securiflustra securifrons*[1]
34. *Thalamoporella gothica* var. *floridana*

Ascophorans
1. *Celleporaria aperta*
2. *Celleporina hassallii*
3. *Discopora turgenewi*
4. *Escharella immersa*[1]
5. *Escharina spinifera*[1]
6. *Fenestrulina malusii*
7. *Hippopodina feegeensis*
8. *Hippodiplosia pertusa*[2]
9. *Hippoporella gorgonensis*
10. *Hippoporina verrilli*
11. *Microporella ciliata*
12. *Microporella umbracula*
13. *Parasmittina crosslandi*
14. *Parasmittina trispinosa*
15. *Pasythea tulipifera*
16. *Phynchozoon rostratum*
17. *Savignyella lafontii*
18. *Schizomavella auriculata*
19. *Schizomavella linearis*
20. *Schizoporella unicornis*
21. *Smittoidea prolifica*
22. *Watersipora subovoidea*

II. "Euryhaline marine animals of the second degree;" occur from the sea into the pleiomesohaline zone 18–8‰ (Pleiomesohaline marine organisms).

Cyclostomes

None

Ctenostomes
1. *Alcyonidium gelatinosum*
2. *Alcyonidium hirsutum*
3. *Alcyonidium parasiticum*
4. *Alcyonidium polyoum*
5. *Alcyonidium verrilli*
6. *Amathia vidovici*
7. *Anguinella palmata*
8. *Bowerbankia imbricata*
9. *Buskia nitens*
10. *Farrella repens*
11. *Flustrellidra hispida*
12. *Triticella elongata*
13. *Triticella pedicellata*
14. *Valkeria uva*

Anascans
1. *Aetea truncata*
2. *Aspidelectra densuense*[2]
3. *Aspidelectra melolontha*[2]
4. *Callopora aurita*
5. *Carbasea carbasea*
6. *Conopeum truitti*
7. *Electra bengalensis*[2]
8. *Electra pilosa*
9. *Electra zostericola*
10. *Membranipora devinensis*[2]
11. *Membranipora hugliensis*
12. *Membranipora membranacea*
13. *Tegella unicornis*

Ascophorans
1. *Celleporella hyalina*
2. *Cryptosula pallasiana*
3. *Schizoporella errata*

TABLE 2. (Cont'd)

III. "Euryhaline marine organisms of the third degree;" occur from the sea to 8–3‰ (Meiomesohaline marine organisms).

Cyclostomes
None

Ctenostomes
1. *Bowerbankia gracilis*
2. *Bowerbankia imbricata caspia*
3. *Bowerbankia imbricata aralensis*
4. *Bulbella abscondita*
5. *Tanganella mulleri*[2]

Anascans
1. *Conopeum reticulum*
2. *Conopeum seurati*
3. *Conopeum tenuissimum*
4. *Electra crustulenta*
5. *Membranipora* sp. [Ches. Bay sp.]
6. *Membranipora tenuis*

Ascophorans
None

IV. "Euryhaline marine organisms of the fourth degree;" to < 3‰ (Oligohaline marine organisms).

Cyclostomes
None

Ctenostomes
1. *Victorella bergi*[2]
2. *Victorella pavida*
3. *Paludicella articulata*

Anascans
1. *Conopeum seurati*
2. *Electra crustulenta*

Ascophorans
None

Of the above species the following may be considered true brackish water species according to the definition of Remane and Schlieper (1971), "Brackish water species are those which abound in brackish water and occur only occasionally in the sea or in fresh water."

Cyclostomes
None

Ctenostomes
1. *Triticella elongata*
2. *Bowerbankia gracilis*
3. *Bowerbankia imbricata caspia*
4. *Bowerbankia imbricata aralensis*
5. *Bulbella abscondita*
6. *Tanganella mulleri*
7. *Victorella bergi*
8. *Victorella pavida*

Anascans
1. *Aspidelectra melolontha*
2. *Aspidelectra densuense*[2]
3. *Conopeum reticulum*
4. *Conopeum seurati*
5. *Conopeum tenuissimum*
6. *Conopeum truitti*
7. *Electra crustulenta*
8. *Electra zostericola*
9. *Membranipora deviensis*
10. *Membranipora hugliensis*
11. *Membranipora* sp. (Ches. Bay sp.)
12. *Membranipora tenuis*

Ascophorans
1. *Cryptosula pallasiana* (possibly)

[1] May occur at a lower salinity in Baltic.
[2] No salinity given at any locations, estimated position.

Brackish Water Biogeography of Ectoprocts

In Table 3 the species occurring in brackish water are grouped according to the biogeographic regions (boreal-antiboreal, warm-temperate and tropical) in which they occur. Seventy-four species are characteristic of the boreal-antiboreal region, including 8 cyclostomes, 17 ctenostomes, 34 anascans and 15 ascophorans. Seventy-seven species are found in the warm-temperate region: 4 cyclostomes, 25 ctenostomes, 32 anascans and 16 ascophorans. In the tropical region there are 41 species: 1 species of ctenostome, 22 species of anascans and 11 species of ascophoran cheilostomes recorded.

Discussion

Distribution of Ectoprocts in Brackish Water

Gradient patterns

Distribution patterns for the boreal region are best illustrated by the data from the Bay of Fundy (Fig. 3A) and the Baltic Sea (Fig. 3C). The number of cyclostomes shows a slight increase into the upper polyhaline zone, but then decreases rapidly to 0. The number of ctenostomes shows a percent increase from euhaline into mixohaline water, then decreases to 0. Ascophorans make up a large percentage of the ectoproct species of the euhaline zone, then show a grad-

TABLE 3. Estuarine and brackish water ectoprocts characteristic of various biogeographic regions.

I. Boreal and Antiboreal Regions

Cyclostomes

1. *Crisia eburnea*
2. *Crisiella producta*
3. *Lichenopora hispida*
4. *Lichenopora verrucaria*
5. *Tubulipora flabellaris*
6. *Tubulipora liliacea*
7. *Tubulipora lobulata*
8. *Tubulipora phalangea*

Ctenostomes

1. *Alcyonidium gelatinosum*
2. *Alcyonidium hirsutum*
3. *Alcyonidium mamillatum*
4. *Alcyonidium mytili*
5. *Alcyonidium parasiticum*
6. *Alcyonidium polyoum*
7. *Anguinella palmata*
8. *Bowerbankia gracilis*
9. *Bowerbankia imbricata*
10. *Bulbella abscondita*
11. *Buskia nitens*
12. *Farrella repens*
13. *Flustrellidra hispida*
14. *Paludicella articulata*
15. *Tanganella mulleri*
16. *Triticella pedicellata*
17. *Victorella pavida*

Anascan Cheilostomes

1. *Aetea anguina*
2. *Aetea truncata*
3. *Amphiblestrum trifolium*
4. *Aspidelectra melolontha*
5. *Bicellariella ciliata*
6. *Bugula avicularia*
7. *Bugula californica*
8. *Bugula neritina(?)*
9. *Bugula stolonifera*
10. *Bugula turrita*
11. *Callopora aurita*
12. *Callopora craticula*
13. *Callopora lineata*
14. *Carbasea carbasea*
15. *Conopeum reticulum*
16. *Conopeum seurati*
17. *Conopeum tenuissimum*
18. *Cribrilina annulata*
19. *Cribrilina punctata*
20. *Electra crustulenta*
21. *Electra monostachys*
22. *Electra pilosa*
23. *Electra tenella*
24. *Eucratea loricata*
25. *Flustra foliacea*
26. *Membranipora arborescens*
27. *Membranipora membranacea*
28. *Membranipora tenuis*
29. *Membraniporella nitida*
30. *Scruparia ambigua*
31. *Scrupocellaria scruposa*
32. *Securiflustra securifrons*
33. *Tegella unicornis*

Ascophoran Cheilostomes

1. *Celleporaria aperta*
2. *Celleporella hyalina*
3. *Celleporina hassallii*
4. *Cryptosula pallasiana*
5. *Escharella immersa*
6. *Escharina spinifera*
7. *Fenestrulina malusii*
8. *Hippodiplosia pertusa*
9. *Microporella ciliata*
10. *Parasmittina trispinosa(?)*
11. *Schizomavella linearis*
12. *Schizoporella errata*
13. *Schizoporella unicornis*
14. *Smittoidea prolifica*
15. *Watersipora subovoidea*

II. Warm Temperate Region

Cyclostomes

1. *Crisia eburnea*
2. *Lichenopora verrucaria*
3. *Tubulipora flabellaris*
4. *Tubulipora liliacea*

Ctenostomes

1. *Aeverrillia armata*
2. *Aeverrillia setigera*
3. *Alcyonidium gelatinosum*
4. *Alcyonidium mamillatum*
5. *Alcyonidium mytili*
6. *Alcyonidium parasiticum*
7. *Alcyonidium polyoum*
8. *Alcyonidium verrilli*
9. *Amathia convoluta*
10. *Amathia vidovici*
11. *Anguinella palmata*
12. *Arachnidium clavatum*
13. *Arachnidium fibrosum*
14. *Bowerbankia gracilis*
15. *Bowerbankia imbricata*
16. *Bowerbankia imbricata caspia*
17. *B. imbricata aralensis(?)*
18. *Bowerbankia* sp. (Indian River sp.)
19. *Bowerbankia pustulosa*
20. *Flustrellidra hispida*
21. *Sundanella sibogae*
22. *Triticella elongata*
23. *Victorella bergi(?)*
24. *Victorella pavida*
25. *Zoobotryon verticillatum*

Anascan Cheilostomes

1. *Aetea anguina*
2. *Beania intermedia*
3. *Bugula avicularia*
4. *Bugula californica*
5. *Bugula gracilis*
6. *Bugula neritina*
7. *Bugula plumosa*
8. *Bugula simplex*
9. *Bugula stolonifera*
10. *Bugula turrita*
11. *Callopora aurita*
12. *Callopora craticula*
13. *Callopora lineata*

TABLE 3. (Cont'd)

14. *Conopeum reticulum*	32. *Thalamoporella gothica*
15. *Conopeum seurati*	**Ascophoran Cheilostomes**
16. *Conopeum tenuissimum*	1. *Celleporaria aperta*
17. *Conopeum truitti*	2. *Celleporella hyalina*
18. *Cribrilina punctata*	3. *Cryptosula pallasiana*
19. *Electra bellula*	4. *Discopora turgenewi*
20. *Electra crustulenta*	5. *Fenestrulina malusii*
21. *Electra monostachys*	6. *Hippodiplosia pertusa*
22. *Electra pilosa*	7. *Hippoporina verrilli*
23. *Electra tenella*	8. *Microporella ciliata*
24. *Electra zostericola*	9. *Parasmittina trispinosa*
25. *Membranipora* [Ches. Bay sp.]	10. *Savignyella lafontii*
26. *Membranipora arborescens*	11. *Schizomavella auriculata*
27. *Membranipora savartii*	12. *Schizomavella linearis*
28. *Membranipora tenuis*	13. *Schizoporella errata*
29. *Membranipora tuberculata*	14. *Schizoporella unicornis*
30. *Scruparia ambigua*	15. *Smittoidea prolifica*
31. *Scrupocellaria bertholettii*	16. *Watersipora subovoidea*
III. Tropical Region	12. *Electra verticillata*
Cyclostomes	13. *Membranipora annae*
1. *Lichenopora intricata*	14. *Membranipora arborescens*
Ctenostomes	15. *Membranipora devinensis*
1. *Aeverrillia setigera*	16. *Membranipora hugliensis*
2. *Amathia convoluta*	17. *Membranipora savartii*
3. *Bowerbankia gracilis*	18. *Membranipora tenuis*
4. *Bowerbankia* sp. (Indian River sp.)	19. *Parellisina curvirostris*
5. *Nolella papuensis*	20. *Scrupocellaria scruposa(?)*
6. *Victorella pavida*	21. *Thalamoporella gothica*
7. *Zoobotryon verticillatum*	
Anascan Cheilostomes	**Ascophoran Cheilostomes**
1. *Antropora tincta*	1. *Cryptosula pallasiana*
2. *Beania intermedia*	2. *Hippopodina feegeensis*
3. *Bugula neritina*	3. *Hipporina verrilli*
4. *Bugula stolonifera*	4. *Hipporella gorgonensis*
5. *Conopeum reticulum*	5. *Microporella umbracula*
6. *Conopeum seurati*	6. *Parasmittina crosslandi*
7. *Conopeum tenuissimum*	7. *Rhynchozoon rostratum*
8. *Electra bellula*	8. *Savignyella lafontii*
9. *Electra bengalensis*	9. *Schizomavella linearis*
10. *Electra crustulenta(?)*	10. *Schizoporella unicornis*
11. *Electra monostachys*	11. *Watersipora subovoidea*

ual decrease to 0. Membraniporine anascans share dominance with ascophorans in euhaline water, but as the salinity becomes increasingly dilute, their share of the population rises, until at the most brackish stations one species of anascan usually makes up 100% of the ectoproct fauna.

Although Long Island Sound falls into the northern end of the warm temperate zone biogeographically, the distribution of the ectoproct fauna appears more characteristic of the boreal pattern, so it has been included in the boreal category (Fig. 3B).

Faunal gradients for the warm-temperate waters of the Chesapeake Bay area (Fig. 4A) show that cyclostomes appear to behave in the same manner as in boreal regions, increasing slightly in species number, then decreasing rapidly. Ascophorans also show the same rapid decrease in percent of fauna, but ctenostomes become increasingly important in the polyhaline and mesohaline regions and remain even in the oligohaline region. Anascans remain important. Continuing down the Atlantic coast, the pattern for Beaufort, N.C. (Fig. 4B) is similar to that for Chesapeake Bay, though cyclostomes decrease more sharply and ascophorans show less of a decline. In the northwest Florida region (Fig. 4C) the pattern for cyclostomes and ascophorans stays the same, but that for anascans and ctenostomes is somewhat different. Ctenostomes increase into the lowest salinity location surveyed, which however, is probably still in the polyhaline zone, and anascans appear to decline somewhat.

The pattern for the Plymouth, England area (Fig. 5A) in general seems similar to that for N.W. Florida, though numbers of cyclostomes decrease less abruptly.

Fig. 5B shows the change in composition of the ectoproct fauna from the Mediterranean (Adriatic) to the Pontocaspian region. While the climate in this area may be more extreme, the pattern from the Mediterranean through the Black Sea to the Caspian Sea fits that for the other warm-temperate areas, with ctenostome proportions rising above those of the anascans, while the number of cyclostomes declines rapidly. Ascophorans appear to decline abruptly also, though Black Sea populations of *Cryptosula pallasiana* can survive salinities as low as 12‰. In this gradient the salinity not only decreases, but the composition of the salt content changes (especially in the Caspian and Aral Seas), perhaps also affecting the distribution pattern.

Data on changes of composition of ectoproct faunas in a tropical area (Fig. 5C) also indicate the decrease in abundance of cyclostomes and ascophorans and the joint dominance of ctenostomes and anascans at the lowest salinities encountered.

Biogeography

From Table 3 it appears that cyclostomes are more diverse in brackish waters of the boreal region, while higher numbers of species of ctenostomes are known in the warm-temperate region. It is not known if this change in composition is just characteristic of the estuarine fauna, or if it occurs in the euhaline region as well. The ratios of anascans and ascophorans show no important differences between the two regions. Because of the limited amount of information available on ectoproct faunas of tropical brackish water it is difficult to make any statements about the distribution of the different groups compared to boreal and warm-temperate regions. The lack of cyclostomes is apparently real; it is difficult to ascertain whether the more restricted numbers of species of the other groups represents a true ecological limitation or is merely an effect of lack of sampling.

Factors Influencing Distribution

Salinity

Poor tolerance of reduced salinity is apparently the chief factor responsible for the distributions reported above, with cyclostomes and ascophoran cheilostomes being least tolerant and membraniporine anascan cheilostomes and ctenostomes most tolerant. These differences in tolerance may be related to differences in morphology and physiology between the groups.

Ectoprocts, with their microscopic body size, have no excretory systems (Hyman 1959), and presumably, any active osmoregulation (homiosmotic behavior) must be carried out by the body surfaces (body wall, tentacles, etc.). According to Schlieper (1971) those organisms which show only a slight degree of euryhalinity (probably those which do not penetrate beyond the polyhaline region) generally are passively poikilosmotic (their internal salt concentration will passively adjust to the concentration of the external medium). The truly brackish water species (those which can live in water of low salinity without reductions of size or loss of activity) are homiosmotic.

Cyclostome morphology may help to explain their poor tolerance of lowered salinities. The zooids are long and tubular with a rigidly calcified wall which prevents expansion with increasing volume when the salinity of the external medium is reduced. On the other hand, the terminal membrane which closes the distal end of the zooid, may be more permeable than the operculum closing the orifice of cheilostomes, thus making it impossible for them to escape short term salinity fluctuations (such as those found in harbors) merely by closing up tightly as a mussel or an ascophoran cheilostome might. *Crisia eburnea* (reported from 8 localities) appears to be the most euryhaline cyclostome.

The ascophorans are second poorest in tolerance of brackish water. While an ascophoran, with its calcified wall structure and calcareous operculum has some protection from the short term fluctuations that might occur in harbors or estuary mouths, their strong calcification apparently prohibits most of them from making the changes in volume, and perhaps the regulation of volume that would permit them to survive brackish water conditions. Only 3 ascophorans (Table 2) occur in water of the pleiomesohaline region (18–8‰); *Schizoporella errata*, *Cryptosula pallasiana* and *Celleporella hyalina*. It should be noted that of these, *Celleporella* has a simple primary wall (holocyst) uncovered by any secondary thickening (Ryland 1970). The other two species possess the type of secondary calcification known as a tremocyst in which the pseudopores (plugs of tissue from the underlying cell layers whose epithelium spreads over the primary wall to lay down the secondary layer) cover the frontal surface in a more or less regular manner (Ryland 1970). It may be that this regular distribution of tissue plugs makes it easier for the zooid to sustain volume changes.

Like the ascophorans the weakly euryhaline anascans appear to be poikilosmotic, perhaps functioning in the same manner as the mussel *Mytilus edulis*, in which internal and external salt concentrations are the same, and in brackish water, ciliary activity, size, and activity of shell-producing tissue (especially $CaCO_3$ secretion) are reduced (Schlieper 1971). When environmental conditions become too stressful the organism closes up to await their amelioration. This type of behavior would seem to explain the occurrence of the euryhaline harbor species discussed by Gautier (1962), which included some cellularine anascans (e.g., *Bugula* spp), ctenostomes and a few ascophorans, living in environments which were characterized by sudden, sharp, but short-term variations in salinity and temperature. According to Gautier, these shallow water species (often important as fouling organisms) can survive short duration variations in salinity of not greater than 10‰, and can live at least temporarily in waters where the salinity is in the range of 28‰.

The membraniporine cheilostome *Electra pilosa*, and the carnose ctenostome *Farrella repens* probably fall into a more euryhaline category. Using specimens of those species collected on the North Sea where the salinity was about 35‰, Marcus (1926) subjected them by gradual stages to increased and decreased salinities. The reactions of the zooids to reduced salinity were indicated by reduced response to mechanical stimulation of the tentacles. *Farrella repens* first showed reduction of sensitivity at 28‰; and at 21‰ the tentacles which at first showed no response to mechanical stimulation, became adapted to that salinity and regained their irritability within one hour. *Electra pilosa* appeared to be less tolerant of salinity reduction, with most zooids of the *Electra* colonies being able to adapt to 20‰, but dying at 17.5‰.

The reactions of these two species approach those described for many euryhaline organisms. The body volume first increases more or less markedly (indicated by insensitivity of the tentacles), then the volume slowly returns to its original level, and the individuals are able to move normally (e.g., the return to irritability of the tentacles) with no or only slight injury. In many cases, this kind of volume regulation has been shown to be an active process.

Still greater adaptability is shown by a truly brackish water species such as *Conopeum tenuissimum*. Experimental work carried out by the author showed that zooids were capable of adapting to a drop in salinity more rapid than they would be likely to experience in nature. Colonies which had been maintained in the laboratory for several weeks at 15–16‰ were placed in 8‰ filtered seawater. A few polypides expanded immediately and then quickly retracted. Thirteen minutes later polypides expanded again and were able to move their tentacles, but ciliary activity had slowed so that the waves could clearly be seen. Within 22 minutes other polypides had emerged, but tentacles looked misshapen and bent, especially near their free ends (apparently the "Ekelstellung" or "attitude of aversion" described by Marcus [1926] for the tentacles of *Farrella repens* when the salinity change was too drastic). In 47 minutes time the expanded polypides began to look more nearly normal. Tentacles were still bent, but were no longer twisted. After 60 minutes, most polypides appeared normal, and when observed 90 minutes later, the ciliary activity had increased again so that it was no longer possible to see the waves clearly. Measurements made on 6 polypides of one colony before and after the salinity drop showed no significant difference in tentacle width, tentacle length, zooid width, lophophore diameter, or mouth diameter, indicating that the original volume had been regained. The colonies were followed for a week thereafter while being maintained at the low salinity, without noting any degeneration of the polypides.

The greatest tolerance to lowered salinities is shown by the ctenostomes, a group lacking in calcification of the body wall. This feature apparently gives the zooids the flexibility to adapt to widely varying osmotic conditions. *Victorella pavida* is one of the most euryhaline of the brackish water forms, having been collected in salinities ranging from fresh water to 28–30‰. In Chesapeake Bay Osburn (1944) found it occurring between 3 and 27‰, but growing best between 10 and 12‰. In Cochin Harbor, India, a tropical estuary where the water ranges from euhaline salinities in the premonsoon period to almost fresh during the monsoon, Menon and Nair (1967a and b, 1971) found *Victorella pavida* colonies apparently adapted to the ambient salinities at the time they settle and grow. Specimens collected at the same locality during the low salinity period (September) and the medium salinity period (December) had different optimal and lethal limits. The specimens collected in September were all able to survive in salinities of 0, 2, and 5‰, while tolerance decreased with increasing salinity until only 5% could survive 30‰. However, the specimens collected in December could not survive fresh water for 24 hours; 22% survived 32‰, and their optimal salinity lay between 16 and 24‰.

Carrada and Sacchi (1964) found that lagoonal (Lago Fusaro, Naples, Italy) populations of *Victorella pavida* occurring in different environmental situations formed a chain of physiological subpopulations, each adapted to certain conditions ranging from fresh water to almost fully marine conditions. This type of physiological differentiation in space may explain the occurrence of *Victorella pavida* under different conditions in an area like Chesapeake Bay; however, in the Cochin area with its dramatic environmental changes during the year, physiological races would appear to replace each other in time rather than in space.

Temperature

Next to salinity, temperature is probably the most important factor influencing the distribution of estuarine ectoprocts. As Gautier (1962) points out, on a local scale, temperature controls the life cycle of ectoprocts. The spring rise in temperature stimulates the development of phytoplankton and thereby initiates simultaneously a process of active budding. In various degrees of intensity according to the species it also stimulates sexual reproduction. Ryland (1970) noted that temperature is especially important in the bathymetric distribution of ectoprocts in the Norwegian fjords, shallow water species seeming to require a high summer temperature for breeding, while deeper water species either do not need or cannot survive the higher summer temperature and/or the cold of the surface water in winter. Since estuarine and brackish water situations are usually characterized by both warmer (summer) and colder (winter) temperatures (Emery, Stevenson, Hedgpeth 1957), this is certain to affect the distribution of many ectoproct species.

Cyclostomes apparently are the most stenothermal as well as stenhaline of the living orders of ectoprocts, and many species appear to prefer cold water to warm. This may be another reason why the number of cyclostomes decreases so rapidly in estuarine areas. It may also help explain why the slight increase in percentage of cyclostomes found in the polyhaline zone in boreal areas does not occur in warm-temperate areas.

Among the ctenostomes one group in particular—the suborder Carnosa—may be more sensitive either to temperature or to the combination of high temperature and decreased salinity. This group is very common in polyhaline and meiomesohaline brackish water of boreal areas, occurs in warm-temperate brackish water areas, but is increasingly replaced by members of the other groups of ctenostomes, and does not seem to have been recorded from brackish water in the tropical region.

Seasonal rhythms in ectoproct life cycles may help them tolerate extreme temperature conditions. For example, Carrada, Sacchi, and Rigillo (1966) studied the life cycles of extoprocts living in a littoral lagoon to the west of Naples, Italy. They found the life cycles of the species occurring there, particularly *Victorella pavida* and *Bowerbankia gracilis*, to be closely attuned to the seasonal variations. In spring, when environmental conditions are relatively mild (O_2 high, salinity relatively low, temperature mild) rapid asexual growth and development occur, while in summer, when the conditions are much more rigorous than those found in the sea (high temperature and lack of O_2 in places) sexual reproduction occurs, allowing adaptation to unfavorable conditions by means of planktonic larvae which can settle elsewhere; populations are reduced, or special resistant stages, e.g., the hiburnacula of *Victorella pavida*, are produced. In the fall when environmental conditions again become mild, the populations recover and grow until partially blocked by low winter temperatures.

Physiologically the importance of temperature to brackish water animals can be explained by its effect on osmoregulation. The permeability of living membranes generally increases with increasing temperature, and as Schlieper (1971) states, "Apparently not all temperate brackish water species are able to perform the required higher osmoregulatory work in brackish water of a low salinity and at a higher temperature." This factor may explain why some of the less euryhaline species are unable to survive in brackish water, or are only present during the colder months, or (like the cyclostomes) seem only to be found in brackish water in cold-water regions.

Substrate

Substrate is also extremely important in determining the distribution of brackish water ectoprocts, as most species cannot live without some type of firm support, and many seem to prefer a certain type of support: rock, shell, algae, etc. Rocky, algae-covered bottoms generally support diverse ectoproct populations in coastal areas, but this biotope seldom occurs in brackish water except near river mouths. Day (1951) has summarized the importance of substrate in estuarine areas:

> There is no doubt that the substratum has a very profound effect on the constitution of the fauna and the distribution of the component species. Rocky areas are commonest at the mouth, and rock-loving species are largely limited to this section of an estuary, although they will also occur on the poles of bridges and wharves, buoys and in tropical countries on the roots and trunks of mangroves. . . . But even in these situations the fauna is scanty, possibly because . . . the surfaces are covered with a thin film of mud . . . . The richest parts of the estuary are the banks of muddy sand, particularly those overgrown by *Zostera* which provides shelter for small surface forms. . . .

The euryhaline species which preferred rocky areas in the coastal region generally make a transition to the phytal zone: brackish water algae, and aquatic flowering plants, *Ruppia, Zostera, Potamogeton,* etc. (Remane 1971). In addition some species from hard substrates start to live epizooically on other organisms to a great extent, e.g., *Alcyonidium polyoum* in the Baltic lives on the gastropods *Littorina* and *Zippora* (Remane 1971), and, in San Francisco Bay lives on *Nassarius obsoletus* (Filice 1958).

Larval Distribution

Hutchins (1941) has pointed out the importance of the larva in determining survival of estuarine ectoprocts. During transplantation experiments with one species of ectoproct he found that adults of other species also living on the oysters used as a substrate were able to live and in some cases grow in conditions more severe than those in which they ordinarily existed. He therefore concluded that it was the larval physiology that limited the distribution of these species. However, at that time, little was known about the larval biology of the ectoproct groups, and he thought that the two groups most characteristic of brackish water, the ctenostomes and the membraniporine cheilostomes, were alike in having very primitive larvae. The actual situation is more complicated and the patterns of larval distribution have not yet been fully described. The membraniporine cheilostomes, are characterized by the production of many small eggs which develop into cyphonautes larvae able to feed and live in the plankton for an extended period of time. However, it appears that among the estuarine members of the group there is a trend toward reduction of the planktotrophic cyphonautes larva into short-lived and probably more bottom-dwelling forms. The ctenostomes which produce cyphonautes-like larvae, moreover, do not penetrate deeply into brackish water. Though *Flustrellidra hispida*, a carnose ctenostome found in brackish water to 10–12‰, has a larva which is externally rather similar to a cyphonautes, this larva lacks an alimentary tract and can have only a very short planktonic life. The ctenostome genera which are most characteristic of brackish water, *Victorella* and *Bowerbankia*, have a very short-lived larva also.

Stability

According to students of ecosytem development (e.g., Odum 1969, 1971; Margalef 1968; Valentine 1971) estuaries can be thought of biologically as regions of instability both in time and in space. Such regions are often characterized by low species diversity, though often the species which are found occur in high densities.

The species able to live under estuarine conditions have often developed adaptations which enable them to survive changes in their environment: small zooid size, large populations (to counteract large mortality due to environmental fluctuation), short life cycles, rapid sexual development and high reproductive potential are among those mentioned (e.g., Pianka 1970). Many of these same characteristics had been considered by other authors to be distinctive to estuarine animals, but they now appear to be characteristic of unstable regions in general, rather than just estuarine regions *per se*.

The membraniporine cheilostome *Conopeum tenuissimum*, common to estuaries of the southeast coast of the United States, displays many of these characteristics: zooids and colonies are small, populations are large, the life cycle is short with rapid sexual development and high reproductive potential to take advantage of favorable conditions while they last. Colonies can grow and produce eggs in three weeks at summer temperatures, and the planktonic larvae seem to show some adaptations to estuarine conditions also, being small and perhaps somewhat benthonic in their habits (Dudley 1973a).

While not all brackish water species fit the generalist or opportunist category, as even in an unstable environment fractions of the trophic and habitat resources remain stable (Valentine 1972), most of the truly brackish water species of ectoprocts seem to have adopted this type of life strategy.

Among the brackish water ctenostomes, colony development appears to be quite rapid. For example Menon and Nair (1967) noted gonad formation in 20 days in *Victorella pavida* from the S.W. coast of India. Embryos of this species mature into non-feeding larvae with only a short (few hours) planktonic life before settlement and the formation of a new colony. It seems that life spans of ctenostomes such as *Victorella* and *Bowerbankia* are, at least under laboratory conditions, shorter than those of estuarine cheilostomes such as *Conopeum tenuissimum* or *Membranipora tenuis*. Unpublished laboratory studies made by the author showed that ctenostome colonies developed from pieces of stolons on experimental slides, grew for up to two months, but were not able to overgrow the experimental cheilostome colonies (*Membranipora tenuis*). Eventually the ctenostome colonies died and decayed while the cheilostomes flourished.

Schopf (1973) has developed a model of the relationship between the development of polymorphism in ectoproct colonies and environmental stability. His model predicts that specialization, with the various functions of the colony being divided among different types of zooids will be favored in stable environments, but that in unstable areas like estuaries polymorphism will be unrewarding to the colony. From his own experience and analysis of the literature he concludes that avicularian polymorphism does not occur in any of the true brackish water species, while among the avicularia-bearing marine species penetrating into the polyhaline region, there is some evidence to indicate reduction or loss of avicularia in brackish water habitats.

Thus, while polyhaline species may be characterized by long life spans, low reproductive rates, brooding of embryos in special chambers, and low population densities, most of the species which have the major part of their distributions in brackish water are of the opposite type with short life cycles, small zooid size, lack of polymorphism, large population numbers, and rapid reproduction.

This phenomenon may be less characteristic of stable brackish water regions such as parts of the Baltic where salinity, for instance, remains constant though lowered. It has already been noted that many species can survive lower salinities in the Baltic than in other estuarine regions, and many species which do not have the capabilities of surviving environmental change may be able to penetrate into lowered salinities in such stable brackish areas.

Suggestions for Future Research

The lack of basic research on the salinity tolerances of ectoprocts is obvious. Other than the work of Menon and Nair (1967) on *Victorella*, Simkina and Turpaeva (1961) on *Cryptosula pallasiana*, and Marcus (1926) for *Electra pilosa* and *Farrella repens*, there have been no salinity tolerance tests carried out. Nor has anyone attempted to determine the method of osmoregulation, which must occur in the truly brackish water species, though physiological techniques are certainly adequate.

While research on the tolerances of adults would be of interest, it would be even more interesting to test the resistance of the larvae of marine and estuarine species to heat and salinity stress.

Good studies of estuarine ectoproct faunas with respect to general stability and to the influence of substrate versus that of salinity are also lacking, and would be relevant both from the theoretical and biogeographic point of view.

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