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A Recent Shallow-water Brachiopod Community from the Bay of Fundy*

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Introduction

The genus *Terebratulina* is one of the commonest brachiopods in present-day seas. Records compiled from Du Bois (1916), Hatai (1936), Hyman (1959), Paine (1959) and Foster (1969) indicate that there are at least 16 living species, of which 9 live in the waters around Japan. *Terebratulina* has also been found off South Australia, South Africa, South America and the Philippines; in the West Indies, and off the west coast of North America, from California to Alaska. Two species occur in the North Atlantic, of which *Terebratulina septentrionalis* (Couthouy), reported from New England to Nova Scotia, Norway and Scotland, is the subject of this study.

Although a number of detailed studies have been made on the embryology of *T. septentrionalis* (Morse 1871, 1873; Conklin, 1902) and on the physiology (McCammon, 1971), little is known of the ecology of this species, in spite of the fact that it appears to be an abundant component of a distinctive nearshore community. Part of the reason for this may be the fact that it is very difficult to sample adequately this rocky sub-tidal habitat where normal grab-sampling or dredge-sampling methods are totally inadequate, and one has to rely largely on divers to bring up adequate samples. This paper reports on preliminary investigations by the authors on the ecology of the *T. septentrionalis* community in the Bay of Fundy area of New Brunswick, and is part of a larger study using Recent marine benthonic ecosystems as models in the interpretation of fossil communities, particularly fossil brachiopod communities.

Habitat

Terebratulina septentrionalis occurs abundantly in the rocky shallow sub-tidal zone around the shores of the Gulf of Maine and the Bay of Fundy (Fig. 1). Within this area it has been found mainly from low water down to depths of 400 fathoms (about 750 m) in occasional dredgings (Paine, 1959), but most occurrences of abundant populations are present in the shallowest part of this range. In our investigations in the Bay of Fundy the optimum depth seems to be 0 to 120 (about 35 m) feet below low water, but this may be partly a reflection of the maximum depth explorable by diving. These brachiopods have also been found intertidally in the Eastport area of Maine (Paine, *op. cit.).*

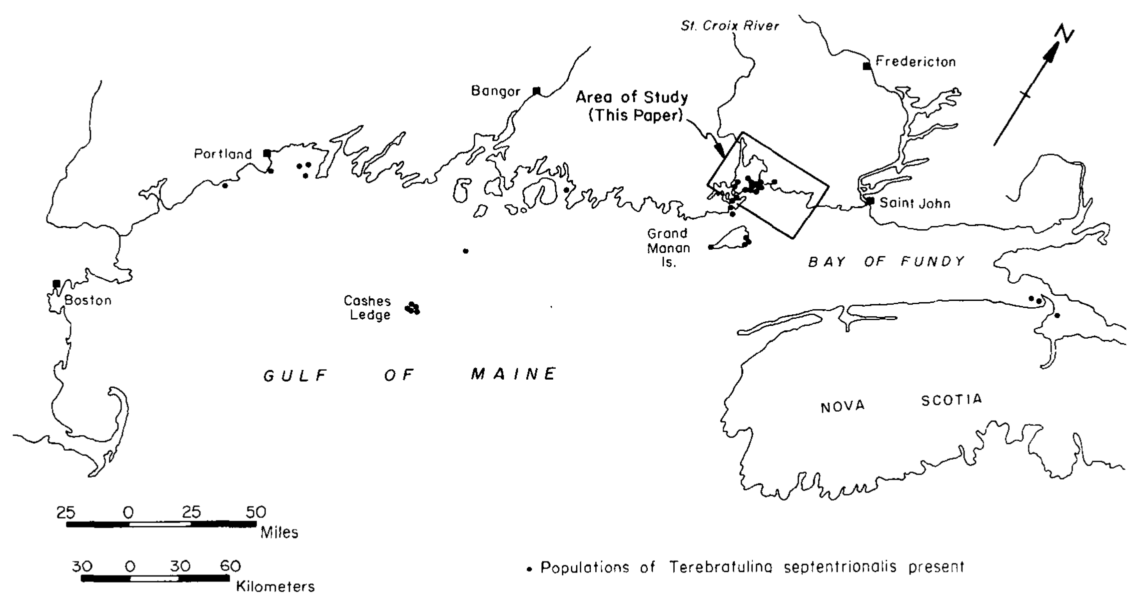

Figure 1 - Occurrence of *T. septentrionalis* in the Bay of Fundy and Gulf of Maine, based on Paine (1959), Bousfield and Leim (1960 and the authors' own collecting.)

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Salinity variations within the area studied are minor. Nine measurements made in close proximity to the *T. septentrionalis* population of Passamaquoddy Bay and Deer Island all fell between 31 and 32 $^{o}/oo$ and Bousfield and Leim (1960) give salinity values of the same range for the Minas Channel and Basin where they observed *T. septentrionalis* populations. Ketchum and Keen (1951) made a large number of salinity measurements for the Bay of Fundy and found they varied from 31.9 $^{o}/oo$ to 32.9 $^{o}/oo$.

Water temperatures are predictably slightly out of phase with air temperatures; thus the mean monthly surface water temperatures near St. Andrews, New Brunswick, range from 0.2°C in March to 11.8°C in August and September (see records of Fisheries Research Board, St. Andrews, N.B., Prince Station 6, 1967) and it may be assumed that this range is close to that prevailing in adjacent waters in this part of the Bay of Fundy.

Substrate

T. septentrionalis is a pedunculate attached filter feeder and needs a relatively hard surface for attachment. In most cases, therefore, populations of *T. septentrionalis* are found attached to rocks; either rock outcrops or boulders or, more rarely, small pebbles and shell material. Most individuals occur predominantly on the undersides of boulders (Fig. 2, Fig. 3A), rock ledges or in the spaces and crevices between them. They, therefore, occupy what has been called the cryptic habitat (Jackson *et al.*, 1971) with reference to the many dark, shaded, semi-enclosed surfaces found in bouldery sediments or in areas of submarine outcrop. We observed, however, that with increasing depth there was an increasing tendency for individuals of *T. septentrionalis* to occupy the upper surfaces of rocks and ledges.

Figure 2 - Typical rocky substrate in about fifteen feet of water, station 1, west coast of Deer Island, Bay of Fundy. The elongate boulder in the centre, turned over to reveal *T. septentrionalis* on its under-surface, is about two feet long.

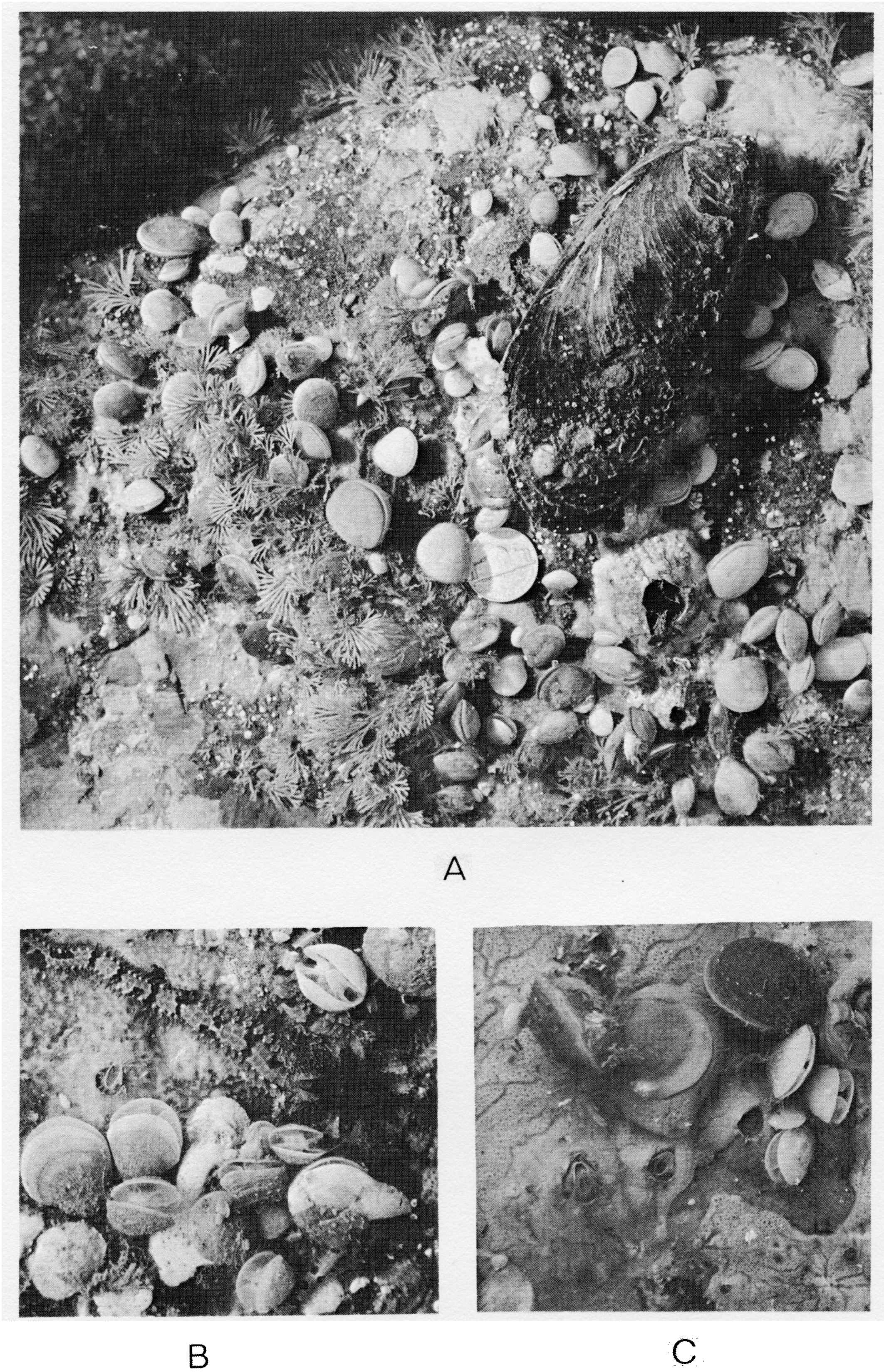

Figure 3 - A. Dense cluster of *T. septentrionalis* on underside of boulder, station 5, Bay of Fundy x 2/3.
B. Brachiopods filter feeding, lophophore well shown, x1.
C. *T. septentrionalis* heavily encursted and surrounded by the yellow sponge *Prosuberites spiphytum.* This is a common association. Note brachiopod anterior margins thrust well clear of the aponge tissue. x1. (B and C from station 2, Bay of Fundy).

Table 2 gives an indication of the actual brachiopod abundances in those habitats where boulders and rocks were dominant. At localities 1, 3 and 5 (Fig. 4) seventeen large boulders were sampled and the brachiopods removed and counted in the laboratory. 1,438 brachiopods from a total surface area of about $3m.^2$ gives a mean density of $479/m.^2$. As the mean proportion of boulders which have brachiopods is 35 per cent, the overall sea floor density is 479 x .35 = 168 individuals of *T. septentrionalis* per square metre for those areas of the sea floor where populations of *T. septentrionalis* exist.

Table 2 - Brachiopod density/m^2

STATION	1	3	5
Depth (in feet)	4-20	20-45	20-40
No. of boulders sampled	3	8	6
Boulder surface area sampled	$0.6m^2$	$1.5m^2$	$0.9m^2$
No. of brachiopods collected	122	776	540
Brachiopod density/m^2	203	517	600)Mean brachiopod)density = $479/m^2$

Actual densities, however, are considerably greater than this because brachiopod individuals tend to occur in clumps (Fig. 3A, B). This patchy distribution, probably the result initially of the very short planktonic larval stage, tends to promote increased efficiency in the fertilization process.

Population Dynamics

Although details of the embryologic stages of *T. septentrionalis* are well known, almost nothing is known of the post-larval rates and periods of recruitment, rates and duration of growth and rates of mortality of the species.

Percival (1944), in his studies of *Terebratella inconspicua* from New Zealand, determined a breeding season from early April to late May, but Morse (1873) found for *T. septentrionalis* in the Gulf of Maine that females ripe with eggs could be obtained at least as late as August, although May and early June were optimum spawning periods.

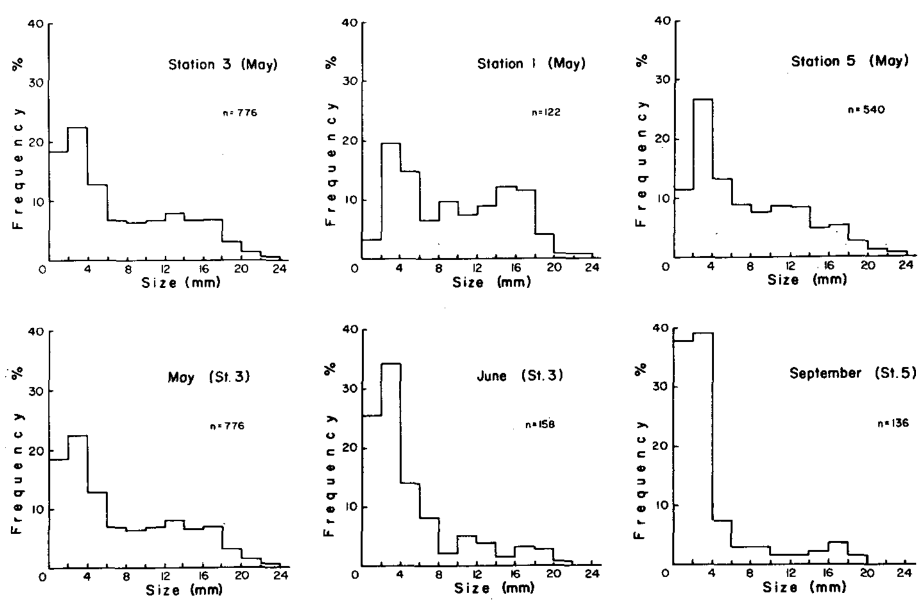

Figure 4 - Size frequency histograms for pedicle valves of *T. septentrionalis*.

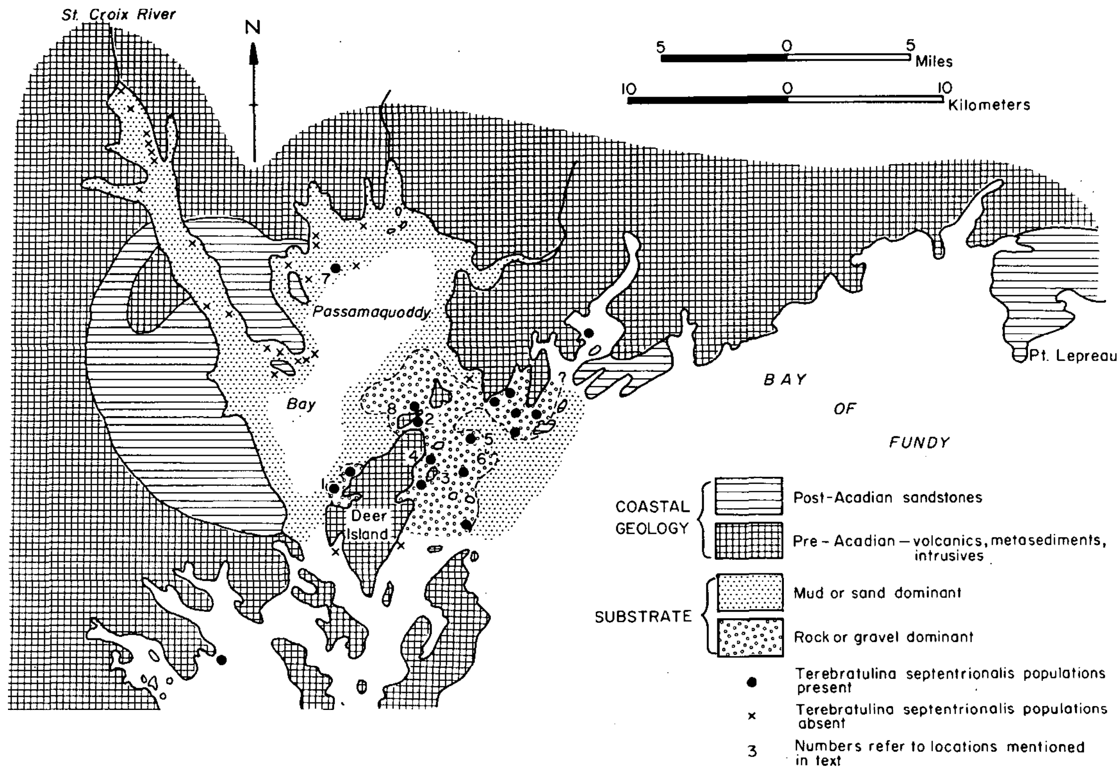

Figure 5 - Map showing the relationship between rock outcrop, sediment type and distribution of *T. septentrionalis* in the Bay of Fundy.

It is apparent from Figure 4 that the substrate type is the dominant controlling factor in the distribution, occurrence and abundance of *T. septentrionalis*. Table 1 shows this relationship by comparing the substrate type with brachiopod abundance as measured by the percentage of randomly selected boulders which had any brachiopods on their surfaces. Thus, with the exception of the shallower depths at station 6 all samples, for which boulders and rocks were the dominant substrate, had high brachiopod occurrences. On the other hand, wherever sediment was finer than pebble size (less than 2 mm in diameter, i.e. sand, silt or mud) the brachiopod occurrences were low. It is also apparent (Fig. 2) that coastline character is important in *T. septentrionalis* distribution, as populations are generally absent from coasts where easily-eroded post-Acadian rocks outcrop. Presumably this is related to the greater rates of sedimentation in those areas.

Table 1 - Brachiopod Abundance and Substrate Type

STATION	1	2	3	4	5	5	5	5	6	6	6	7	8
Depth (in feet)	4-20	15	20-45	50	15	20-40	60	80	20-30	50	75	20-45	30
Dominant substrate[1]	B	B+S	B+R	B+R	B+R	B+R	B+R	R+B	B+R	B+R	R+B	S+B	S+B
% Boulders with brachiopods[2]	45	10	68	-	82	56	60	41	0	28	71	16	0

B-boulders (> 2 mm) dominant

R-rock outcrop dominant

S-sand, silt or mud dominant

[2] Mean % of boulders with brachiopods = 35%

In an attempt to provide some data on the population dynamics of *T. septentrionalis* we collected random samples from a number of localities at different times of the year. In order not to miss the smaller individuals of the population, randomly-selected boulders were brought to the surface by divers. After transportation to the laboratory these boulders were stripped of their entire brachiopod populations, which were then counted and measured. From this data size frequency histograms (Fig. 5) were plotted.

Conclusions based only on frequency distributions are necessarily tentative but a study of the results allows the following deductions: 1) The 3 mm peaks in May and June appear to represent spat of the current year's recruitment, i.e. Spring 1971 recruitment. 2) The pronounced 3 mm peak in the September census must represent Fall recruitment and the fact that there appears to be no peak for the Spring 1971 recruitment indicates a high juvenile mortality during the summer. Until a winter census is taken it is impossible to make any further statement about mortality rates. Highly skewed curves are normal for marine invertebrates with planktonic larval stages (Deevey, 1947) because mortalities are high during the free-swimming larval stage due to predators and flushing out to sea (Ayers, 1956). It is clear, however, from the data for *T. septentrionalis* that high mortalities occur even after settling of the spat. Percival (1944) obtained a similar curve for *Terebratella inconspicua* and attributed it to high juvenile mortality due to overcrowding and starvation. At this stage such suggestions for our populations are merely speculative. 3) There is also a peak at about 17 mm in both the Spring and Fall censuses. This peak presumably represents the mean size for mature adults, and it would appear from the evidence of the September census that the growth to maturity takes only one year, as there are no intermediate peaks. On the other hand there is some evidence of a peak at about 8 to 13 mm in the Spring census and it may be that this is the 1970 recruitment and the 17 mm peak the 1969 recruitment, with a growth to maturity period of two years. This conflicting evidence cannot be resolved at this stage.

The *Terebratulina septentrionalis* Community

T. septentrionalis is frequently associated with a number of other organisms in the shallow rocky sub-tidal cryptic habitat. These include: the sponge *Prosuberites epiphytum*, the bryozoan *Bugula* sp., the amphineuran *Chiton* sp. and pelecypods *Anomia aculeata*, *A. simplex*, *Hiatella arctica*, *Modiolus modiolus*, *Musculus discors* and *Mytilus* sp., plus various gastropods, the barnacle *Balanus* sp., the asteroid *Henricia sanguinolenta* and echinoid *Strongylocentrotus drobachiensis*, the polychache worms *Lepidonotus* sp., *Myxicola* sp. and *Spirorbis* sp., the ascidians *Boltenia ovifera*, *Botryllus* sp., *Dendrodoa carnea* and *Halocynthia pyriformis* and the calcareous alga *Lithothamnion* sp. The dominant elements of this community are brachiopods, encrusting sponges, encrusting algae and bryozoa. It is apparent that this is an environment where competition for space is high, as every boulder and rock is covered with these organisms. The fact that *T. septentrionalis* usually occurs on the underside of boulders and ledges may be a consequence of this competition; for instance the prolific algae often dominate the upper surfaces but are less abundant on the lower surfaces where there is less light. On the other hand, it is possible that the undersurfaces provide better protection from the clogging effects of sedimentation and from predators. The fact that *T. septentrionalis* appears more frequently on the upper surfaces in deeper water than it does in shallow water tends to support the competition hypothesis because several organisms, and algae in particular, thin out appreciably with increasing depth, whereas the *T. septentrionalis* populations maintain and even increase their abundance with depth.

T. septentrionalis is often encrusted by a sponge *Prosuberites epiphytum* (ident. by Dr. M.L.H. Thomas, University of New Brunswick) but the exact relationship between these species is not yet known (Fig. 3C).

This community appears to be very similar in its dominant elements, i.e. brachiopods, sponges, bryozoa and encrusting algae, to the community described by Jackson *et al* (1971) from the cryptic habitat of coral reefs, although genera and species are different. This similarity of association of higher taxa occurs in spite of the considerably different environmental situation and is clearly related to the cryptic habitat, and to the mode of life and particular mode of attachment of these organisms.

Distribution and Migration of *T. septentrionalis*

T. septentrionalis is known only from the Recent and only from the northern Atlantic region. We know that it is an abundant species of the shallow-water rocky sub-tidal habitat but it may also occur in deeper water, and in fact has been dredged from depths of 400 fathoms (750 m) in the Gulf of Maine. It remains a problem to know what happened to this species during and prior to the Pleistocene.

During the Pleistocene the rapid sea-level changes associated with the waxing and waning of continental glaciers must have been accompanied by rapid advances and retreats of the shoreline. If depth was the controlling factor in the maintenance of *T. septentrionalis* communities, then these communities would have migrated with the shoreline. It is evident, however, (Fig. 4 and Table 1) that the substrate type and coastline character are at least as important, and *T. septentrionalis* populations will tend to be inhibited off shores where the coastal rocks are easily eroded, such as the Carboniferous, Triassic and Tertiary clastics. On the other hand *T. septentrionalis* populations will tend to flourish where the shoreline is dominated by the resistant pre-Acadian volcanics, metasediments and granites such as those dominating the shoreline of most of this northwestern Atlantic region today.

During periods of lower sea level the coastline character must have been very different from that of today. For instance, about 16,000 years ago sea level was apparently about 130 metres below the present sea level (Milliman and Emery, 1968) and much of the coastline then must have been dominated by easily-eroded Tertiary and Mesozoic rocks. In such a situation the shallow rocky sub-tidal cryptic habitat may have been quite rare in this region, and shallow-water populations of *T. septentrionalis* would also have been rare. This means that unless *T. septentrionalis* is a very recent migrant into this region, populations of these brachiopods (and possibly also the entire *T. septentrionalis* community) must have been maintained in relatively deep waters during the periods of lower sea level. When sea level rose these populations migrated into the shallow-water zones where a favourable habitat now existed. In other words, *T. septentrionalis*, while having a total depth range of very shallow to deep, is at times predominantly a shallow-water species and at times a predominantly deeper water species. Because of the obvious paleoecologic significance of this conclusion we hope to reduce its admittedly still speculative nature by further work on this community and on the associated sediments in the Bay of Fundy and other areas.

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