

Life history and environmental inference through retrospective morphometric analysis of bryozoans: a preliminary study

Aaron O'Dea* and Beth Okamura^{†‡}

*School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG. E-mail: aaronodea@yahoo.com

[†]School of Animal and Microbial Sciences, The University of Reading, Whiteknights, PO Box 228, Reading, RG6 6AJ.

[‡]Corresponding author: e-mail: b.okamura@reading.ac.uk

A preliminary comparative analysis of colony growth and zooid size in the perennial bryozoan *Flustra foliacea* (Bryozoa: Cheilostomatida) reveals reduced colony growth in the Bay of Fundy relative to growth in the Menai Straits and the Skagerrak, while seasonal fluctuations in zooid size are in synchrony with temperature regimes. Such retrospective morphometric analyses may allow inferences of primary productivity and thermal regimes and provide insights into the life histories of both Recent and fossil bryozoans.

The cold temperate and boreal bryozoan, *Flustra foliacea* (Linnaeus), produces large bushy colonies in sublittoral habitats subject to strong currents (Hayward & Ryland, 1998). Colony growth occurs between March and September and winter cessation results in clearly defined annual growth-check lines (GCLs) (Stebbing, 1971). Such GCLs are used in the present study to investigate seasonal patterns of colony growth and zooid size in *F. foliacea* from three widely-separated localities and to investigate the potential of such retrospective analysis for life history and environmental inference.

Colonies of *F. foliacea* were collected from the Menai Straits (Wales) (N=10), the Skagerrak (Denmark) (N=8), and the Minas Basin (Bay of Fundy, Nova Scotia) (N=10). Colonies were selected for analysis on the basis of length and quality of preservation of fronds and clarity of GCLs. Mean annual incremental growth (IG) within colonies was estimated by measuring the distances between GCLs on a given frond. As growth measurements were replicated within colonies at each locality, data were appropriate to an unbalanced repeated measures General Linear Model to examine the separate effects of locality and colony on IG by ANOVA. Heterogeneous variances required ln-transformations prior to analysis. The total number of yearly growth increments measured was 21 from the Menai Straits, 17 from the Skagerrak, and 61 from the Minas Basin.

Colonies from the Menai Strait and the Skagerrak revealed similar mean \pm SD IG values (26.5 \pm 6.13 mm; and 22.81 \pm 4.69 mm, respectively) while those from the Minas Basin showed a much lower IG value (13.8 \pm 3.21 mm). Locality had a highly significant effect on growth, accounting for 95% of the variation while colony (genotype) had no significant effect (locality: $F=23.93$, $P<0.001$; colony: $F=0.31$, $P=0.58$).

As increased food availability significantly increases growth in cheilostome bryozoans (see O'Dea & Okamura, 1999), reduced growth in the Minas Basin may reflect the relatively low primary productivity that results from the continual mixing of water in the Bay of Fundy (e.g. Gordon, 1994). However, low annual growth in the Minas Basin may also be explained by factors such as genetic variation, parasitism, or differential allocation to growth vs reproduction.

Stebbing (1971) found IG in *F. foliacea* from South Wales to be only 16.9 \pm 3.6 mm over the years 1969 and 1970. Despite our limited understanding of the factors influencing growth, our data suggest a substantial increase in the annual growth of *F. foliacea* in western Europe since 1970. Gradual eutrophication of many

coastal regions of western Europe due to increased organic pollution over the last 40 y is coincident with a significant rise in phytoplankton biomass in British coastal waters (e.g. Allen et al., 1998). Thus, the increase in annual growth in *F. foliacea* since 1970 may reflect increased primary productivity levels.

Patterns of seasonal variation in zooid size were investigated through frond profiles established by making transects starting at the distal end (growing tip). Zooid density, at 2 mm intervals along profiles, was measured as the number of zooids contained within an area of 3.2 mm², and provided an indirect means of retrospectively tracking mean zooid frontal areas. Figure 1 illustrates a typical zooid density profile for a single frond. To summarize overall zooid density trends and allow comparisons between localities, data from all fronds were standardized for each locality as follows. Firstly, zooid density data for each year's growth were standardized to a mean density of zero with variation from the mean represented as relative deviations. Secondly, due to variable annual growth within and between colonies, annual zooid density data (between GCLs) were interpolated to 20 regularly spaced 'pseudopoints' within one standardized year. A third order polynomial curve was fitted to the data to show the general trend. This approach is standard when illustrating trends of this nature (e.g. Andreasson et al., 1999).

Figure 2A,B show that the lowest zooid density, and therefore the largest zooids, occur during the times of coolest temperatures. There is no apparent correlation with patterns of primary productivity which, in the Menai Strait and the Skagerrak, is characterized by spring and autumn phytoplankton blooms (Figure 2C). These temporal changes in zooid size are likely to be a direct response to seasonal temperature variation since numerous studies have shown that temperature inversely affects zooid size while factors, such as rate of growth, reproductive state and food availability, do not (see O'Dea & Okamura, 1999 and references therein).

The isotope profiling technique has been used increasingly to investigate life histories and seasonal environments of many shell secreting taxa (e.g. Jones, 1998), including bryozoans (e.g. Brey et al., 1998). However, the technique entails certain assumptions that may be problematic while some studies have revealed potentially serious flaws or inconsistencies in the approach (e.g. Marshall et al., 1996). In addition, life history studies that employ the isotope profiling technique generally lack replicate data due to the expensive and time consuming nature of the approach.

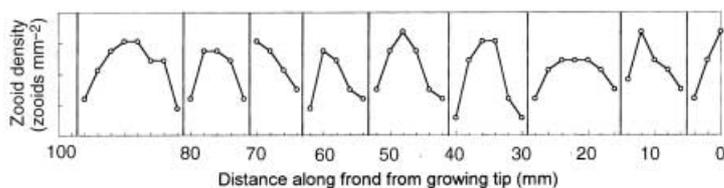


Figure 1. Zooid density profile along a frond of *Flustra foliacea* from the Minas Basin, Bay of Fundy. Vertical lines represent position of GCLs.

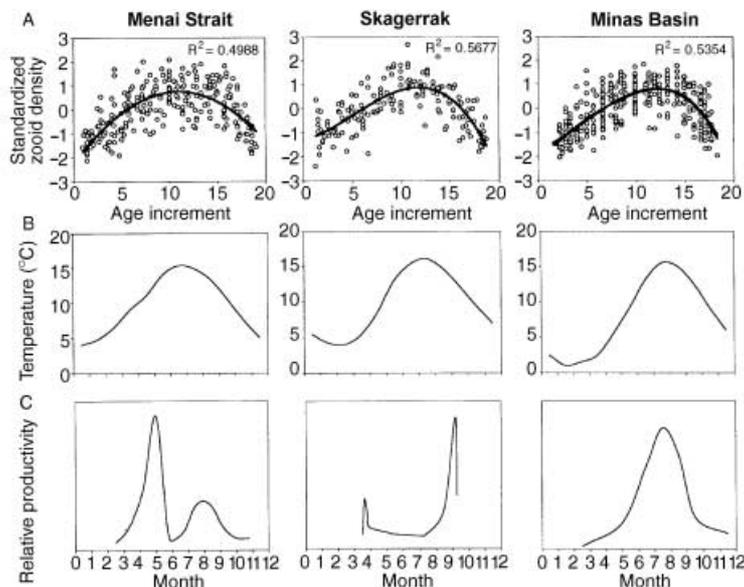


Figure 2. Annual variations in standardized zooid density in *Flustra foliacea* and environmental variables in the Menai Straits (left), the Skagerrak (centre) and the Minas Basin (right). (A) Standardized zooid density plotted against interpolated pseudo-distance representing one year's growth. A third order polynomial is fitted to each plot. (B) Typical temperature data for the three localities (compiled from data over a number of years from various sources). (C) Typical patterns of annual primary productivity for the three localities (derived from chlorophyll-*a* data from various sources). Note that primary productivity data are represented as relative within but not between sites.

We suggest that the retrospective morphometric analyses described here provide a means of gaining insights into the ecology of Recent, historically-collected, and fossil bryozoans. For instance, seasonal growth cycles revealed by zooid size profiling could provide life history information, such as longevity and growth-rate in perennial bryozoans. Similarly, variation in zooid size and colony growth may be used to infer previous environmental regimes, providing a complementary approach to isotope profiling. In particular, evidence for inter-seasonal, interdecadal, and long-term changes in temperature could be obtained by zooid size profiling, while spatial and temporal variation in primary productivity may be identified through estimation of colony growth rates, assuming these mainly reflect a response to food levels.

In conclusion, our preliminary study highlights the potential of retrospective analyses of growth and zooid size in perennial bryozoans. Such analyses could provide both unique and important information on local and global environmental change as well as specific insights into bryozoan life histories.

We would like to thank Sherman Blakney, Mike Brylinsky and Howard Falcon-Lang for collecting *Flustra foliacea* colonies from the Bay of Fundy. This work was carried out during a tenure of a Biotechnology and Biological Sciences Research Council (BBSRC) research studentship to A.O.

REFERENCES

Allen, J.R., Slinn, D.J., Shammon, T.M., Hartnoll, R.G. & Hawkins, S.J., 1998. Evidence for eutrophication of the Irish Sea over four decades. *Limnology and Oceanography*, **43**, 1970–1974.

- Andreasson, F.P., Schmitz, B. & Jönsson, E., 1999. Surface-water seasonality from stable isotope profiles of *Littorina littorea* shells: implications for paleoenvironmental reconstructions of coastal areas. *PALAIOS*, **14**, 273–281.
- Brey, T., Gutt, J., Mackensen, A. & Starmens, A., 1998. Growth and productivity of the high Antarctic bryozoan *Melicerita obliqua*. *Marine Biology*, **132**, 327–333.
- Gordon, D.C., 1994. Intertidal ecology and potential power impacts, Bay of Fundy, Canada. *Biological Journal of the Linnean Society*, **51**, 17–23.
- Hayward, P.J. & Ryland, J.S., 1998. *Cheilostomatous Bryozoa. Part 1. Aeteoidea—Cribriloidea*. Shrewsbury: Field Studies Council. [Linnean Society of London.]
- Jones, D.S., 1998. Isotopic determination of growth and longevity in fossil and modern invertebrates. In *Isotope paleobiology and paleoecology*, vol. 4 (ed. R.D. Norris and R.M. Corfield), pp. 37–67. The Palaeontological Society Papers. [Palaeontological Society Special Publication.]
- Marshall, J.D., Pirrie, D., Clarke, A., Nolan, C.P. & Sharman, J., 1996. Stable-isotopic composition of skeletal carbonates from living Antarctic marine invertebrates. *Lethaia*, **29**, 203–212.
- O'Dea, A. & Okamura, B., 1999. Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*. *Marine Biology*, **135**, 581–588.
- Stebbing, A.R.D., 1971. Growth of *Flustra foliacea* (Bryozoa). *Marine Biology*, **9**, 267–273.

Submitted 6 December 1999. Accepted 17 June 2000.