OXYGEN AND CARBON ISOTOPE RATIOS RELATED TO GROWTH LINE PATTERNS IN SKELETONS OF *LOPHELIA PERTUSA* (L) (ANTHOZOA, SCLERACTINIA): IMPLICATIONS FOR DETERMINATION OF LINEAR EXTENSION RATES

Pål Buhl Mortensen & Hans Tore Rapp

SARSIA

Mortensen, P.B. & H.T. Rapp 1998 11 30. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L) (Anthozoa, Scleractinia): Implications for determination of linear extension rates. – *Sarsia* 83:433-446. Bergen. ISSN 0036-4827.

Patterns of growth lines and the composition of stable oxygen and carbon isotopes were studied in skeletons of the deep-water scleractinian *Lophelia pertusa* in longitudinal and transverse sections of corallites. $\delta^{18}O$ showed a significant, positive linear correlation with $\delta^{13}C$. A gradual depletion of ^{18}O and ^{13}C was found in the theca, both towards the corallite edge within single growth layers, and across growth layers from the theca surface. $\delta^{18}O$ was negatively correlated with the rate of linear extension. These results indicated that isotopic fractionation in *Lophelia* is controlled by kinetic isotope effects. The range of $\delta^{18}O$ was 3.5 times larger than expected for aragonite precipitating in isotopic equilibrium with ambient sea water. However, the shape of the $\delta^{18}O$ curve along the growth axis in the septa was almost parallel with the curve of sea water temperatures. This correspondence may be caused by a relation between growth rate and temperature or other environmental variables correlated with temperature. The $\delta^{18}O$ curve fitted best with the temperature curve when the pronounced growth lines were assigned to the first quarter of the year. A 6 year growth line chronology was established for corallites in one colony. Between 10 and 14 fine lines were counted between pairs of the more pronounced annual lines in the septa. An average linear extension rate of 5.5 mm/yr was suggested based on measured distances between distal ends of adjacent growth layers in the theca. Colonies of *Lophelia* from one locality were kept alive in aquarium for 18 months before analysis. Direct measurements on these corallites showed that the linear extension decreased to 2.6 mm/yr.

Pål Buhl Mortensen, Institute of Marine Research, P.O. Box 1870 Nordnes, N-5024 Bergen, Norway. E-mail: paal.buhl.mortensen@imr.no – Hans Tore Rapp, Trondhjem Biological Station, Norwegian University of Science and Technology, N-7018 Trondheim, Norway. E-mail: hansrap@stud.ntnu.no

Keywords: Ahermatypic corals; *Lophelia*; skeleton; linear extension; growth lines; isotopes.

INTRODUCTION

The deep-water scleractinian *Lophelia pertusa* (L) has been recorded from most seas except for the polar regions (Jungersen 1917; Zibrowius 1980; Cairns 1994). The colonies of this species often build large framework constructions, called banks, bioherms or reefs. In the northeast Atlantic *Lophelia* is often found near the continental shelf edges at depths between 200 and 400 m (Wilson 1979a; Frederiksen & al. 1992; Mortensen & al. 1995) with temperatures generally between 4 and 8 °C and salinities between 33.5 and 35.2 (Dons 1944; Strømgren 1971; Eide 1979). In the fjords of western Norway and on the Swedish west coast *Lophelia* occurs in shallower water but within the same temperature range (Dons 1944; Carlgren 1945; Burdon-Jones & Tambs-Lyche 1960; Strømgren 1971). The highest densities of *Lophelia* banks have been recorded off mid-Norway (Hovland & al. 1994, 1997) and around the Faroe Islands (Frederiksen & al. 1992).

Lophelia pertusa has a branching skeleton with cylindrical to conical shaped corallites having septa arranged in 3 cycles. As is common for most scleractinians, the skeleton is formed of aragonite crystals arranged into fan shape structures known as trabeculae. The centres of calcification occur along the axis of the trabeculae. The trabeculae have zones with a high density of aragonite crystals which appear white or opaque in polarised light (Wainwright 1964) and correspond to the density bands described in massive coral genera such as *Porites* and *Montastrea* (Emiliani & al. 1978; Le-Tissier & al. 1994). In the 1930's, Carl Dons photographed and studied the growth lines in transverse sections of *Lophelia* from the Norwegian coast and fjords. Unfortunately he never published any results on this topic. One example of his photographs is shown in Fig. 1.

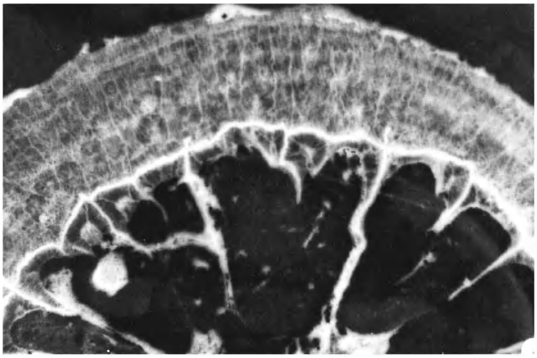

Fig. 1. Transverse section of a corallite of *Lophelia pertusa* from Røberg (station F), photographed by Carl Dons. Published with permission of the Gunnerus Library, Trondheim.

Wainwright (1964) described the shape and orientation of aragonite crystals in growth layers of *Lophelia*, but did not discuss the timing of growth line formation. Patterns of skeletal density banding in massive forms of tropical hermatypic scleractinians (e.g. *Porites* spp., *Montastrea annularis*, and *Pavona* spp.) have been described by several authors (e.g. Knutson & al. 1972; Buddemeier & Maragos 1974; Buddemeier & Kinzie 1975; Wellington & Glynn 1983; Barnes & Devereux 1988; Barnes & Lough 1989 & 1993; Dodge & al. 1992; Taylor & al. 1993; Le-Tissier & al. 1994; Lough & Barnes 1996). However, growth and formation of growth lines in deep-water ahermatypic corals have been little studied (Duncan 1877; Wainwright 1964; Emiliani & al. 1978; Wilson 1979b; Nagelkerken & al. 1997; Freiwald & al. 1997). The formation of high-density bands in massive hermatypic corals is generally accepted to represent an annual phenomenon, generated by changes in the dimensions of individual skeletal elements (Emiliani & al 1978; Barnes & Devereux 1988). Banding patterns in scleractinians are considered to have the potential to provide a marine analogue to dendrochronology and dendroclimatology (Le-Tissier & al. 1994) and have proved to be reliable proxy climate recorders in species where the growth mechanisms are well known (Lough & al. 1997).

The isotopic composition of scleractinian skeletons is a result of mixing between dissolved marine (inorganic) carbonate and metabolic, or respiratory CO_2 which is relatively depleted in both ^{13}C and ^{18}O. Varying isotopic compositions in scleractinian skeletons reflect variations in temperature, coral geometry, growth rates and local isotopic regimes (Swart 1983). For many hermatypic scleractinians the composition of oxygen isotopes is mainly controlled by the temperature of the water in which the corals live. Coral skeletons are not deposited in isotopic equilibrium with sea water bicarbonate (Weber & Woodhead 1970), but the oxygen isotope composition of skeletal aragonite shows an overall correlation with ambient temperature. This suggests a more or less constant offset of the skeletons isotopic composition from equilibrium values (Weber 1973). However, internal skeletal differences and varying 'vital' effects have complicated the interpretation of the stable isotope records in many scleractinians. A wide range of variation in isotopic compositions have previously been documented in *Lophelia pertusa* with $\delta^{18}O$ values from –2.9 ‰ to 2.7 ‰ vs. PDB and $\delta^{13}C$ values from –9.7 ‰ to –1.4 ‰ vs. PDB (Weber 1973; Mikkelsen & al. 1982; Swart 1983; Freiwald & al. 1997). The isotopic fractionation processes in *Lophelia* are poorly understood.

Ahermatypic corals have no symbiotic algae support-

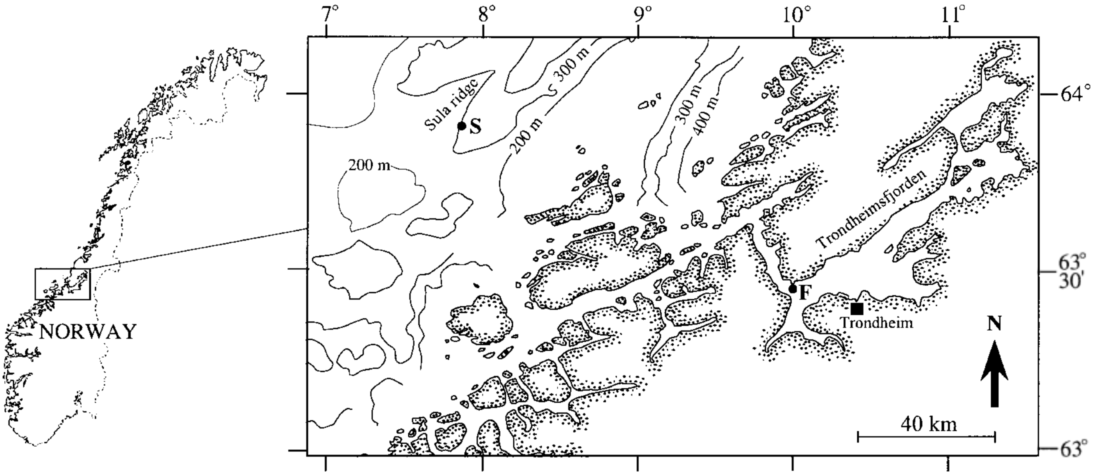

Fig. 2. Map of the study area showing the fjord (F) and shelf (S) sampling locations as filled circles.

ing the growth. One should therefore expect *Lophelia* to have a low growth rate when compared with branching hermatypic corals. However, previous studies of *Lophelia pertusa* in the northeast Atlantic have reported rates of linear extension between 4 and 25 mm/yr (Duncan 1877; Wilson 1979b; Mikkelsen & al. 1982; Freiwald & al. 1997).

The aim of this study is to describe the relation between patterns of growth lines and variation in oxygen isotope composition in the skeleton of *Lophelia pertusa* and to determine rates of linear extension for corallites. The results will hopefully help us to explain the great variation of previously published extension rates for *Lophelia pertusa.*

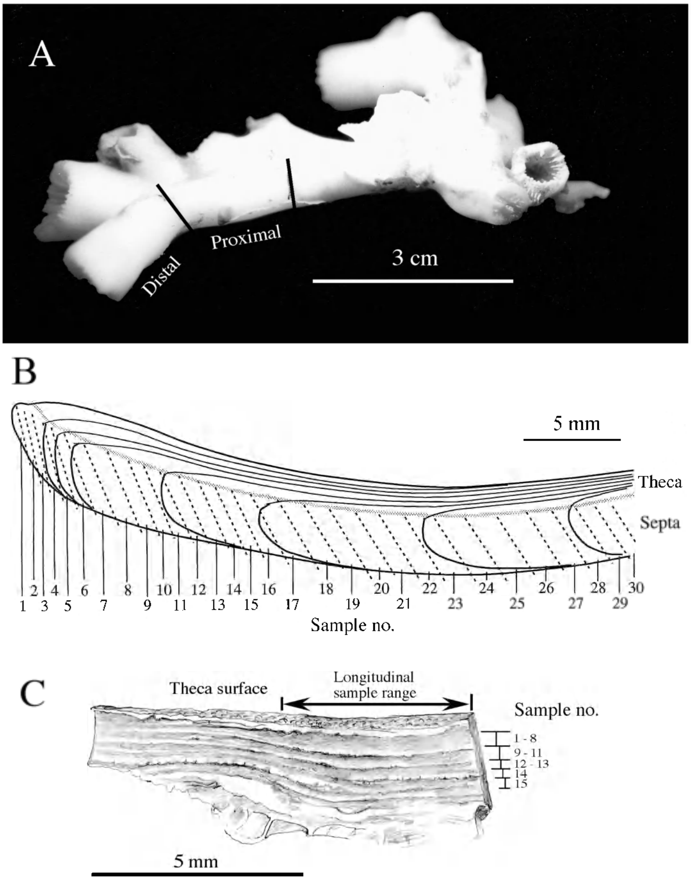

Fig. 3. Sampling sites in longitudinal sections of *Lophelia* corallites. A: Skeleton from station F used for sampling of septal aragonite, showing the division of corallite F1 into a distal and a proximal part. B: Schematic drawing of the longitudinal section of corallite F1 showing the pronounced growth lines and the sampling sites of series F1b. C: Drawing of a longitudinal section of the theca of corallite S1 from the shelf showing pronounced growth lines and sampling sites.

MATERIAL AND METHODS

Sampling of Lophelia

Living *Lophelia* was sampled at one shelf and one fjord locality in mid-Norway (Fig. 2). Station S (63°55'55" N, 07°53'50" E) is situated on the shelf, at the southern part of the Sula Ridge. At this location *Lophelia* was collected in September 1993, at a depth of 275 m, near the summit of a *Lophelia* bank. The sampling was performed by Statoil (the Norwegian state oil company) as part of the Haltenpipe Development Project. *Lophelia* were collected with a ROV (Remote Operated Vehicle) equipped with a manipulator arm. At station F, outside Røberg (63°30'17" N, 10°00'15" E), in Trondheimsfjorden, *Lophelia* was sampled in August 1995, from depths between 200 and 350 m with a triangular dredge. Colonies from the two localities are later referred to as shelf and fjord corals. The fjord corals were kept alive in an aquarium at Trondhjem Biological Station (Norwegian University of Science and Technology) with constantly flowing sea water from a depth of approximately 100 m. Skeleton for analysis was broken from one of the colonies after 18 months in the aquarium (March 1997). Monthly records of temperature and salinity, back to 1964 at 200 m depth outside Røberg, were provided by Jon-Arne Sneli of Trondhjem Biological Station.

Examination of growth layers and lines

Examination of growth lines and layers and analyses of oxygen and carbon isotopes were carried out on corallites closest to the terminal corallites of branches. In this study 'growth line' is equivalent to the high density zone in the trabeculae, and 'growth layer' refers to a distinct group of growth lines. All studied corallites were approximately the same size, extending about 1.5 cm out from the main branch. Longitudinal and transverse sections, about 3 mm thick, were cut with a rotating diamond saw and embedded in polyester resin. Sections were made both of the primary septa with connected theca, and of the theca between the septa. The sections were ground with coarse emery paper (grade 150) to a thickness of ca 1 mm, and attached to a slide with resin. The sections were then honed on successively finer emery paper (grades 200, 400, 500, and 700) to a thickness of about 80 µm, and polished. Sections of seven corallites were examined under a binocular microscope with transmitted and polarised light, and photographed or drawn. Distances between the distal ends of adjacent pronounced growth layers in the theca were measured. Some of the live corallites in the fjord coral were damaged by the dredging. One broken corallite was used as an approximate marker of the sampling date. The remains of this corallite were covered with new skeleton laid down by the

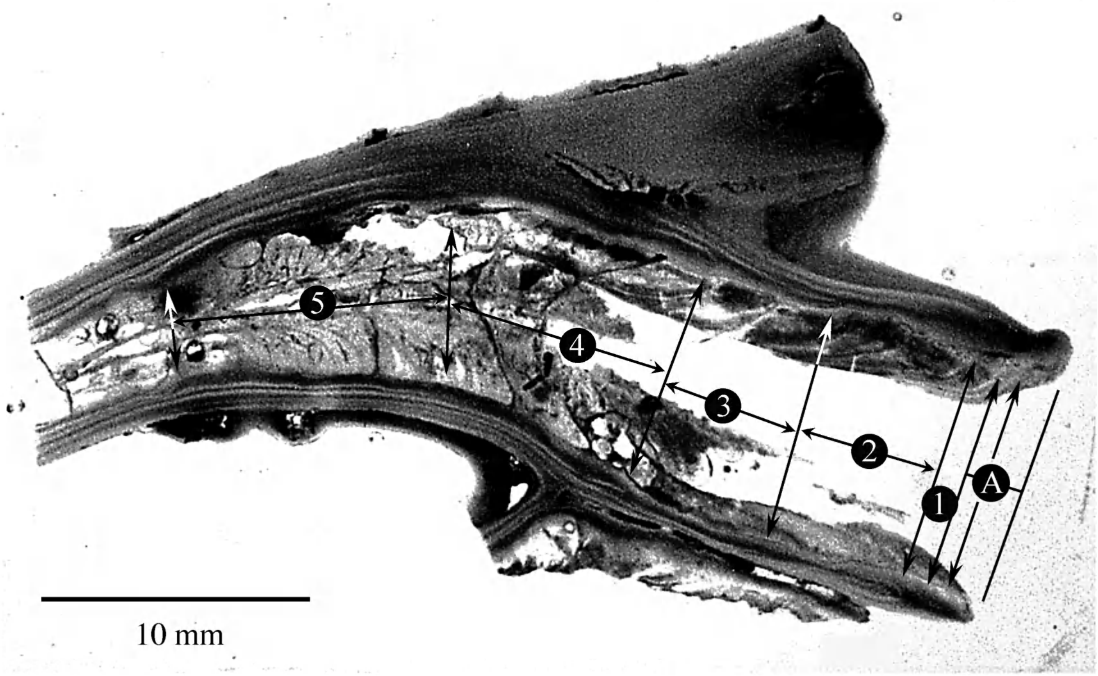

Fig. 4. Photograph of longitudinal section of corallite F3 from Trondheimsfjorden. The arrows point to the distal ends of growth layers. A, and numbers 1 to 5 refer to the extension intervals in Table 1.

adjacent corallite during the time in the aquarium, and its outer broken growth layer continued into its living neighbour. Linear extension in the aquarium could, therefore, be measured from this mark on some of the slides. Linear extension of two corallites was also measured directly in the aquarium as the distance between the corallite edge and a reference point on the skeleton. Measurements were made in mid-October 1995, 18 December 1996 and 26 May 1997.

Table 1. Distance (mm) between distal ends of adjacent growth lines in seven corallites of *Lophelia pertusa*. F1-F3: corallites from Trondheimsfjorden. S1-S4: corallites from the shelf. Extension interval A represents growth in the aquarium. Extension interval number 1 starts from the August 1995 layer in the fjord coral, and from the corallite edge in the shelf corals.

Specimen	A	1	2	3	4	5
F1	3.3	0.8	5.2	6.9	9.5	9.9
F2	3.3	1.0	4.9	4.6	7.4	-
F3	3.7	1.1	4.6	5.1	8.6	10.6
Average	3.4	1.0	4.9	5.5	8.5	10.3
S1	-	1.3	5.3	3.6	7.1	6.2
S2	-	1.3	3.9	3.5	5.6	-
S3	-	1.5	3.9	3.0	4.3	5.2
S4	-	1.1	2.6	1.7	5.2	3.9
Average	-	1.3	3.9	3.0	5.6	5.1

Sampling of skeletal aragonite and analysis of oxygen and carbon isotopes

Three series of samples of skeletal aragonite were ground out from the theca (S1, S4a and F1a) and two from the septa (S4b and F1b) using a dental grinder.

Sampling of aragonite in the septa. Before sampling of aragonite in the septa, the outer 35 mm of corallite was divided into a distal (youngest), and a proximal (oldest) part with lengths of 15 and 20 mm, respectively (Fig. 3A). Remains of animal tissue were removed by soaking the corallite parts in 'Klorin' (10 % NaClO) for 15 h. Prior to sampling, the corallite parts were washed in distilled water and dried. A series of 30 samples from the fjord coral (F1b) was taken from the septa starting at the distal end, proceeding down to 35 mm below the corallite edge. Samples were taken from corresponding areas in several septa to get sufficient aragonite for isotope analysis. To avoid breakage while sampling, a longitudinal section containing five septa was cut out from the distal part (F1b, sample 1-15) and embedded in resin. Each sample represented between 0.6-1.5 mm in longitudinal direction and 2-3 mm in transverse direction (Fig. 3B and Table 3). To check for possible effects of the resin on the isotope analysis, a control sample of septa without resin was ground out from between 5 and 6 mm below the corallite edge. The proximal corallite part (F1b, sample 16-30) was too narrow to be sectioned longitudinally without destroying the septa. Instead, the theca were partly removed by grinding to expose the septa. The septa in this corallite part

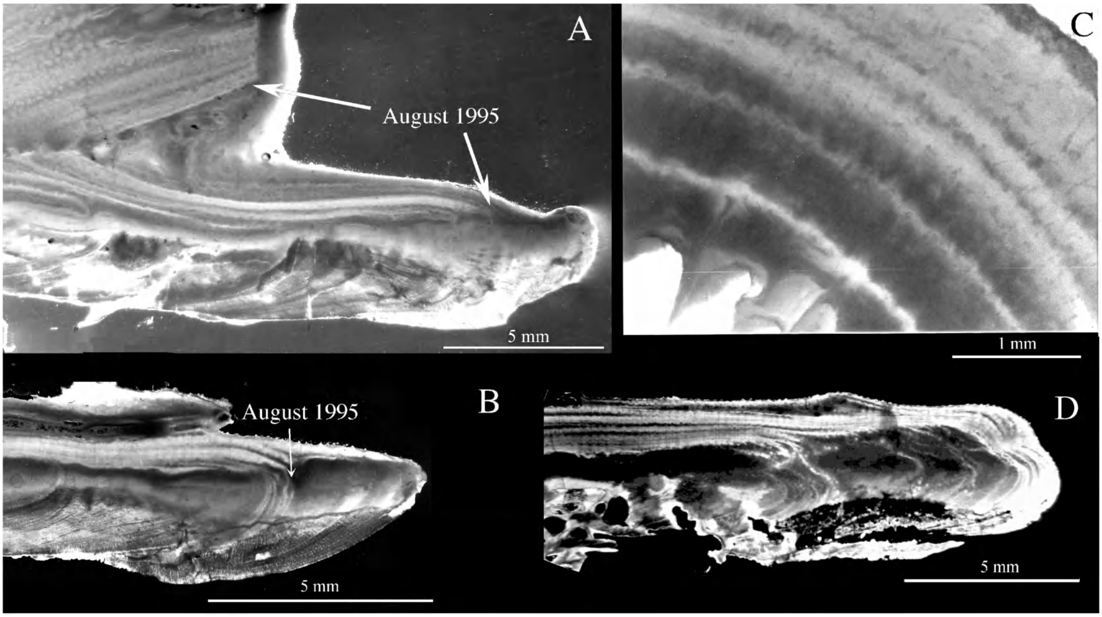

Fig. 5. Photographs of *Lophelia* skeleton sections. A and B: Longitudinal sections of the theca of corallite F3. C: Transverse section of corrallite S1 taken 3 cm below the corallite edge. D: Longitudinal section of the theca of corallite S1. a, b, and were photographed with polarised light.

were not embedded in resin. Sample series S4b consisted of four samples successively ground out from the corallite edge down to 4 mm below.

Sampling of aragonite in the theca. A series of 15 samples was ground out successively across the theca wall 1.5-2.0 cm below the corallite edge in the shelf coral (S1) (Fig. 3C). A section, 2 mm thick, was cut out before sampling. Each sample of this series was 5 mm long, and 0.2-0.5 mm wide. The sample series F1a, and S1a consisted of 4 samples, each ground out at different distances from the edge of the corallite (Table 2). These samples were taken from the outer growth layer and were about 1 mm long, and 0.5 mm wide.

Analysis of oxygen and carbon isotope ratios

The samples were analysed at the Department of Geology, University of Bergen, with a Finnigan MAT 251 mass spectrometer with automatic carbonate preparation line for small sample measurements. Carbonate samples (down to ca 20 µg) were reacted with 100 % phosphoric acid, and evolved CO_2 gas was collected and purified in cryogenic traps prior to ^{13}C and ^{18}O analysis. The $^{18}O/^{16}O$ ratio was expressed using the standard δ notation:

$$\delta^{18}O = \frac{{}^{18}O/{}^{16}O_{sample} - {}^{18}O/{}^{16}O_{standard}}{{}^{18}O/{}^{16}O_{standard}} \times 1000\ (‰)$$

where positive values indicate enrichment in the heavier isotope. The $^{18}O/^{16}O_{standard}$ refers to the value obtained from standard Peedee Belemnite (PDB) for carbonate samples, and Standard Mean Ocean Water (SMOW) for water samples. The $^{13}C/^{12}C$ ratio was expressed using the same standard δ notation.

Determination of temperature and oxygen isotope ratios in carbonates precipitating in isotopic equilibrium with ambient sea water. Assuming that coral carbonate precipitates in isotopic equilibrium with ambient sea water, temperature can be estimated from skeletal $\delta^{18}O$ values by applying the palaeotemperature equation developed by Epstein & al. (1953) and later rewritten by Shackleton (1974):

$$t = 16.9 - 4.38\,(\delta_c - \delta_w) + 0.10\,(\delta_c - \delta_w)^2$$

where δ_c is the $\delta^{18}O$ value of aragonite and δ_w is the $\delta^{18}O$ of the ambient water. δ_w values were calculated using the relationship: $\delta_w = (0.235 \cdot S) - 8.0$, derived from Israelson & Buchard (1991). This relationship gives δ_w values of –8.0 ‰, and 0.25 ‰ vs. PDB for salinities of 0 and 35.4, respectively. Calendar age was assigned to the samples from the fjord coral septa based on their position relative to the pronounced growth lines. Equilibrium values for δ_c were calculated from the palaeotemperature equation by applying measured temperatures and salinities from station F.

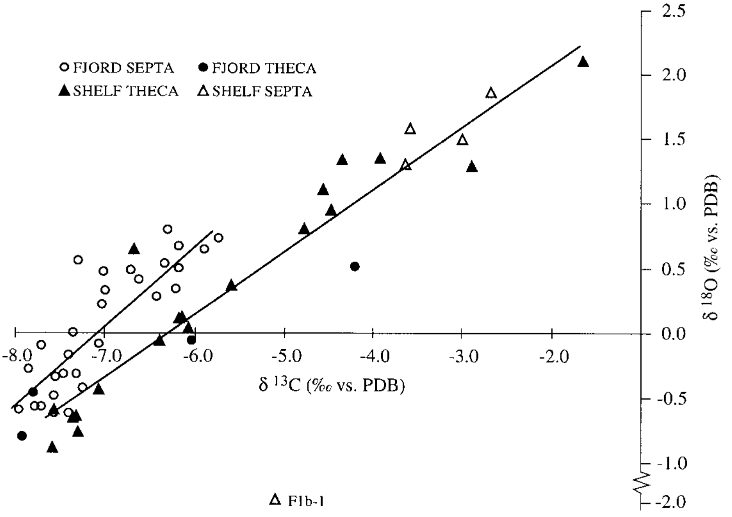

Fig. 6. Relationship between $\delta^{18}O$ and $\delta^{13}C$ in the septa and the theca from the shelf and the fjord corals.

RESULTS

Description of growth line patterns

Alternating white and dark lines were observed in both the transverse and the longitudinal sections of the theca and the septa (Figs 4 & 5). Growth lines appeared clearest in polarised light with a white or opaque colour (Fig. 5B, D). The growth layers in the theca were about 0.5 mm wide, parallel, and separated laterally by 0.2-0.5 mm. The resolution of growth layers and lines was clearest in sections less than 100 μm thick. Growth layers and lines terminated distally with a sharper curvature in the theca than in the septa (Fig. 5B, 5d). The number of growth layers in the theca increased from 1 near the corallite edge up to 5, at ca 2 cm below the edge. The length of the growth layers was difficult to measure since they appeared less pronounced near their proximal end. However, in two specimens (F3 and S1) the outer growth lines were clearly visible, and measured 2.5 cm and 1.7 cm respectively. The growth lines in the theca were continuous with the growth lines in the septa (Fig. 5B, 5D). Examination under polarised light of thin longitudinal sections of septa revealed that the pronounced growth lines in the septa consisted of 2-6 finer lines, ca 0.1 mm thick. The extension interval (distance between the distal ends of growth layers) consisted of between 9 and 14 fine growth lines (Fig. 5B, 5D). These fine lines were best observed in the septa but were also present in the theca (Fig. 5D). Fig. 5B shows that fine lines were also formed in the corals growing in the aquarium, but pronounced growth lines were less developed. However, the fine lines were difficult to discriminate in most sections of septa from both the shelf and the fjord coral.

Five pronounced growth layers were found proximal to the 'stress'-related layer representing the sampling date line in the theca of fjord corallite F1. One pronounced line was found distally to the 'stress' line (Figs 4; 5A, B). The distance between the distal ends of adjacent pronounced growth lines (extension intervals) suspected to represent yearly linear extension, varied between 1.7 and 10.6 mm in the sea (interval 2-5, Table 1), with an average of 5.5 mm. The distal extension interval (A) in the fjord coral (F1-F3) represented two extension sequences formed during the 18 months in the aquarium. The length of this interval was about 3.4 mm (Table 1). Direct measured linear extension of two corallites in the aquarium was 3.1 and 3.3 mm between mid-October 1995 and 18 December 1996, and 0.8 and 0.5 mm between 18 December 1996 and 26 May 1997. This gave a total linear extension of 3.9 mm for the period in the aquarium. Extension interval 1 represented the growth sequence interrupted by the sampling. In the shelf coral (S1-S4) this interval was the most recent and incomplete growth sequence. The length of interval 1 was almost equal for the shelf and the fjord coral, and varied between 0.8 and 1.5 mm. The suspected yearly linear extension was, on average, 4.3 mm in the shelf coral and 7.0 mm in the fjord coral. The length of extension intervals decreased towards the corallite edge in all corallites.

Composition of stable oxygen and carbon isotopes

The $\delta^{18}O$ values in the skeleton varied between –0.89 and 2.10 ‰ vs. PDB (Tables 2, 3), with an average of 0.21 ‰. The $\delta^{13}C$ values varied between –7.95 and –1.64 ‰, with an average of –6.27 ä. $\delta^{18}O$ showed a significant, positive linear correlation with $\delta^{13}C$ ($R^2 = 0.83$, $p < 0.0001$, $n = 57$). Average values were calculated without the distal sample from the septa of the fjord coral (F1b-1, Table 3), which had a low $\delta^{18}O$ value (–1.93 vs. PDB), and a high $\delta^{13}C$ value (–5.05 ‰ vs. PDB), lying far outside the range of the other samples of septa (Fig. 6). This was most probably due to a sampling artefact, maybe caused by too low content of aragonite in the sample. This sample was, therefore, not included in the discussions. Highest correlation between $\delta^{18}O$ and $\delta^{13}C$ was found for samples from the theca of the shelf coral ($R^2 = 0.91$, $p < 0.0001$, $n = 19$). On average, ^{13}C was enriched by 0.74 ‰ in the septa compared with the theca, while ^{18}O was only 0.03 ‰ enriched. The average oxygen and carbon isotope ratios in the shelf coral were 0.56 ‰ and 1.75 ‰ respectively, enriched compared with the fjord coral. ^{18}O and ^{13}C in sample series F1a and S4a, from the outer growth layer in the theca, were gradually depleted towards the corallite edge (Table 2). The sample series across the corallite wall showed a marked decrease in δ^{18}O towards the inner layer of the theca with steps associated with the border lines between growth layers (Fig. 7). Fig. 10 shows the relation between δ^{18}O in the septa and the length of linear extension intervals. Extension interval A and 1 are not included in this figure, since these do not represent natural conditions or full extension intervals. ^{18}O was more enriched in samples from the short extension interval (2 and 3) than in the long growth sequences (4 and 5). δ^{18}O approached the equilibrium value when the rate of linear extension decreased.

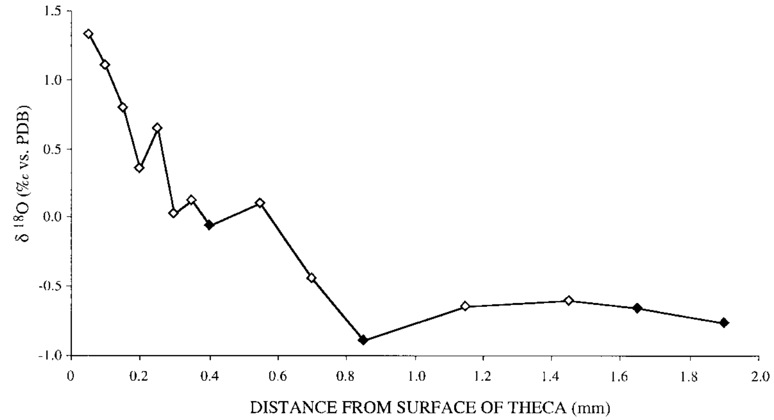

Fig. 7. δ^{18}O values in the theca of corallite S1 vs. distance from the theca wall surface in samples taken 1.5-2.0 cm behind the corallite edge. Samples covering the border line between growth layers are indicated with filled rectangles.

Table 2. δ^{13}C, and δ^{18}O (‰ vs. PDB) in successive samples across the growth lines in theca of a corallite from the shelf coral (S1-1 - S1-15), and in samples taken at different intervals in the outer growth layer in the theca of the fjord coral (F1a), and the shelf coral (S1 and S4).

Sample no.	Distance from corallite edge (mm)	Distance from theca surface (mm)	δ^{13}C	δ^{18}O
S1-1	15 - 20	0.00 - 0.05	–4.33	1.33
S1-2	-	0.05 - 0.10	–4.56	1.10
S1-3	-	0.10 - 0.15	–4.77	0.80
S1-4	-	0.15 - 0.20	–5.58	0.36
S1-5	-	0.20 - 0.25	–6.67	0.64
S1-6	-	0.25 - 0.30	–6.07	0.03
S1-7	-	0.30 - 0.35	–6.13	0.12
S1-8	-	0.35 - 0.40	–6.39	–0.06
S1-9	-	0.40 - 0.55	–6.17	0.10
S1-10	-	0.55 - 0.70	–7.06	–0.44
S1-11	-	0.70 - 0.85	–7.58	–0.89
S1-12	-	0.85 - 1.15	–7.31	–0.65
S1-13	-	1.15 - 1.45	–7.55	–0.60
S1-14	-	1.45 - 1.65	–7.34	–0.66
S1-15	-	1.65 - 1.90	–7.28	–0.77
Average S1			–6.32	0.03
S4a-1	0.0 - 1.0	0.0 - 0.5	–3.91	1.34
S4a-2	3.0 - 4.0	-	–4.46	0.94
S4a-3	6.0 - 7.0	-	–1.64	2.10
S4a-4	9.0 - 10.0	-	–2.88	1.28
Average S4a			–3.22	1.42
F1a-1	0.0 - 1.0	0.0 - 0.5	–7.91	–0.81
F1a-2	5.0 - 6.0	-	–7.79	–0.47
F1a-3	10.0 - 11.0	-	–6.02	–0.07
F1a-4	20.0 - 21.0	-	–4.19	0.51
Average F1a			–6.48	–0.21
Average Theca			–5.81	0.23

Skeletal δ^{18}O correlated with ambient temperature and equilibrium δ^{18}O

Measured temperature and salinity at 200 m depth at station F are shown in Fig. 8, and estimated skeletal δ^{18}O in isotopic equilibrium with ambient sea water are shown in Fig. 9, together with measured δ^{18}O and δ^{13}C. The average measured skeletal ^{18}O was 2.44 ‰ depleted compared with equilibrium values for δ^{18}O expected from the observed temperatures and salinities (Fig. 9). The range of δ^{18}O values was 2.99 ‰ vs. PDB in the shelf coral and 1.54 ‰ in the fjord coral. These ranges were about 3.5 times larger than expected for precipitation in isotopic equilibrium with ambient temperature and salinity, and correspond to temperature ranges of 13 °C and 7 °C, respectively. However, there was a high degree of similarity between the shape of the δ^{18}O curve along the growth axis in the septa from the fjord coral and the sea water temperatures over the period 1990 to 1996 (Fig. 9). The δ^{18}O curve fitted best with the temperature curve when the pronounced growth lines were assigned to the first quarter of the year. This correspondence was found by standardising the lengths of the growth sequences. A pronounced temperature fall in spring 1993 was clearly reflected by a corresponding increase of δ^{18}O, and was used for assigning dates to the sample sites F1b-15 and F1b-16. No clear differ-

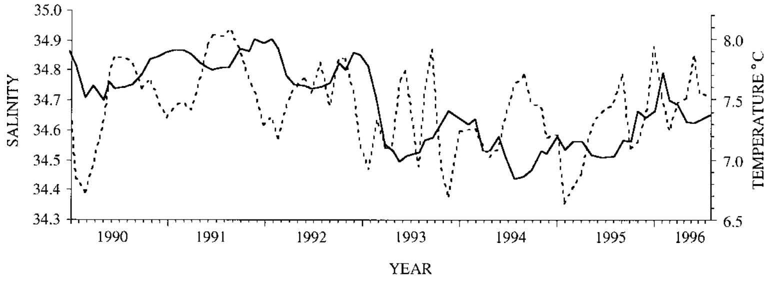

Fig. 8. Monthly temperature (solid line) and salinity (dashed line) data from 200 m depth at station F from January 1990 to July 1996.

ence was found between the δ^{18}O values in samples covering the pronounced growth lines and the other samples within the corresponding growth sequence (Fig. 9). The control sample of septa not embedded in resin had a δ^{18}O value of 0.78 ä and a δ^{13}C value of –6.34 ‰ vs. PDB which means an enrichment of 0.12 ‰ and a depletion of 0.17 ‰ of ^{18}O and ^{13}C respectively, compared with the corresponding sample with resin (Fig. 9). This was less than the variation between samples from growth sequence 1 and 2, between 4 and 14 mm from the edge of the corallite.

DISCUSSION

Methods

Accurate time-series profiles of skeletal δ^{13}C and δ^{18}O can be used to estimate yearly growth rates and confirm the presence of annual temperature cycles (DUNBAR & WELLINGTON 1981; DUNBAR & al. 1994; LEDER & al. 1996; WELLINGTON & al. 1996). High sampling resolution is crucial for the representation of cyclic variations in the δ^{18}O values along the skeleton's growth axis (FAIRBANKS & DODGE 1979; WINTER & al. 1991; LEDER & al. 1996; WELLINGTON & al. 1996). The highest possible number of samples per growth sequence depends on the rate of skeleton extension, and the size of samples that can be analysed. Sampling of skeletal aragonite from *Lophelia* was more difficult to perform within the narrow growth layers in the theca than in the septa where the growth lines were wider apart. Sampling with a drill provides samples larger than ca 0.5 mm, which includes the whole width of layers in the theca, or may lead to bulk sampling of several layers. Increased sampling resolution along the growth axis can be facilitated by grinding out aragonite across the septa parallel to the growth lines. The broad curvature of the distal termination of growth lines in the septa provides controlled sampling of corresponding parts of growth layers.

Knowing the year of formation of certain layers or lines in the skeleton is essential for comparison of environmental records from different coral colonies. The sampling rate and accuracy used in this investigation was too low for assigning dates of samples based on the typical small seasonal variation in the δ^{18}O value of the ambient water. In this study, a sudden change in temperature and salinity between January and March 1993 (Fig. 8) was used as a natural marker of the skeleton. Marking of density bands in skeletons of hermatypic scleractinians has previously been performed by staining techniques (BUDDEMEIER & KINZIE 1975; BARNES & LOUGH 1993) and inclusion of radiogenic isotopes (KNUTSON & al. 1972).

Carbon and oxygen isotope fractionation in Lophelia pertusa

The values of δ^{18}O and δ^{13}C in the skeletons of *Lophelia*, used in this study, varied within the range of previously published results (WEBER 1973; MIKKELSEN & al. 1982; SWART 1983; FREIWALD & al. 1997). Variations of δ^{18}O in *Lophelia* larger than expected from the variations of ambient sea water temperatures have been attributed to 'vital' effects or isotopic disequilibria (MIKKELSEN & al. 1982; FREIWALD & al. 1997). Isotopic disequilibria are classified according to the contribution of two patterns, designated 'metabolic' and 'kinetic' isotope effects (MCCONNAUGHEY 1989). The positive linear correlation between δ^{18}O and δ^{13}C found here was in agreement with previous studies on the isotopic composition of *Lophelia* skeletons by WEBER (1973), MIKKELSEN & al. (1982), SWART (1983), and FREIWALD & al. (1997). This pattern is commonly found in carbonates showing mainly the kinetic pattern (MCCONNAUGHEY 1989). MIKKELSEN & al. (1982) propose that the slope of δ^{13}C/δ^{18}O varies depending on the geographical origin of the specimen, and may reflect differences in the organism's growth response to various types of oceanic conditions. EMILIANI & al. (1978) report that the abundance of ^{13}C and ^{18}O is inversely related to growth rate in the solitary deep-water coral *Bathypsammia tintinnabulum* with both carbon and oxygen approaching equilibrium values with increasing age. SWART (1983) records extreme negative values of ^{18}O and ^{13}C at the edge of corallites in *Lophelia*, and proposes that this is due to variations in growth rate. In this study, the gradual depletion of ^{18}O and ^{13}C towards the corallite edge within a single growth layer in the theca indicated increasing kinetic effects towards the most rapidly growing areas within a polyp. This pattern probably also existed along the growth lines in the septa since the skeletal extension decreased significantly towards the proximal ends of a growth layer.

One main problem using deep-water corals as environmental recorders is that the isotopic fractionation can vary widely within a particular coral individual (Emiliani & al. 1978; Swart 1983; Smith & al. 1997), and between different skeletal elements (septa, thecae, and columella) (Land & al. 1977). Land & al. (1977) found variations of 3.1 ‰ in $\delta^{13}C$, and 0.4 ‰ in $\delta^{18}O$ between samples from the septa, thecae and columella in a colony of *Tubastrea aurea*. They also found that the septa of the caryophyllids *Caryophyllia* spp., and *Desmophyllum riisei,* are enriched in both ^{13}C and ^{18}O relative to their respective bulk corallites. Our results agreed with this only for ^{13}C, while the abundance of ^{18}O in the septa was not different from the theca. These variations are most probably due to the different geometry of the skeletal elements (Swart 1983).

What controls the oxygen isotope composition in *Lophelia*? It is well established that temperature, through normal equilibrium fractionation processes, affects the $\delta^{18}O$ value of coral skeleton (Weber & Woodhead 1970; Weber 1973; Swart 1983). Variation in sea water salinity also has an effect on the $\delta^{18}O$ value of coral skeleton since the $\delta^{18}O$ of sea water largely depends on the salinity. However, the variation in salinity at 200 m depth at the fjord locality was only 0.6 psu and contributed an additional expected variation of $\delta^{18}O$ of only 0.04 ‰ vs. PDB. Previously published values for $\delta^{18}O$ in *Lophelia* skeletons range from –2.85 to 2.53 ‰ vs. PDB (Weber 1973; Mikkelsen & al. 1982; Swart 1983; Freiwald & al. 1997), which according to the temperature-$\delta^{18}O$ relation described by Shackleton (1974) correspond to a temperature range of 23 °C. However, Weber (1973) found a range of average $\delta^{18}O$ values of 1.15 ‰ in *Lophelia* colonies from different localities. When corrected for a constant displacement of 2.5 ‰ these values correspond to a temperature range from 6 to 11 °C, which is in good agreement with measured sea water temperatures (Strømgren 1971; Eide 1979). The average $\delta^{18}O$ value presented in this study corresponded to a displacement from estimated temperatures of about 2.42 ‰, corresponding to 10.5 °C, which is in accordance with the results of Weber (1973). However, the range of $\delta^{18}O$ corresponded to a temperature range of approximately 13 °C, assuming precipitation in equilibrium with the sea water. This was 3.5 times larger than the measured temperature range. This large discrepancy was probably caused by kinetic isotopic effects as a result of varying growth rate. This conclusion was also supported by the correlation between average $\delta^{18}O$ and the length of extension intervals in the septa (Fig. 10).

Rates of linear extension for Lophelia pertusa

The presence of three pronounced growth lines in the fjord corallite F1, between the sampling site with a marked rise of $\delta^{18}O$ (F1b-17) and the 'stress' related line representing the sampling date (F1b-5), agreed with the number of years. The pronounced line between the 'stress' line and the end of the septa in this corallite was probably an annual line formed in 1996. These results strongly indicated that the pronounced growth lines

Table 3. Values (‰ vs. PDB) of $\delta^{13}C$, and $\delta^{18}O$ in successive samples across the growth lines in septa of a corallite from the fjord coral. Samples 16-30 were taken from septa embedded in polyester resin. ⊗: sample not included in calculation of average values, *: samples from pronounced growth lines.

Sample no	Distance from corallite edge (mm)	$\delta^{13}C$	$\delta^{18}O$
F1b-1 ⊗	0.0 - 0.7	–5.05	–1.93
F1b-2	0.7 - 1.3	–7.35	0.00
F1b-3	1.3 - 1.9	–6.98	0.32
F1b-4 *	1.9 - 2.7	–7.03	0.22
F1b-5 *	2.7 - 3.6	–6.71	0.48
F1b-6 *	3.6 - 4.6	–6.17	0.49
F1b-7	4.6 - 5.8	–6.17	0.66
F1b-8	5.8 - 7.2	–6.61	0.41
F1b-9	7.2 - 8.8	–5.73	0.73
F1b-10	8.8 - 9.9	–6.20	0.34
F1b-11 *	9.9 - 11.0	–6.33	0.53
F1b-12	11.0 - 12.1	–6.41	0.27
F1b-13	12.1 - 13.2	–5.89	0.64
F1b-14	13.2 - 14.2	–7.00	0.47
F1b-15	14.2 - 15.0	–7.29	0.56
F1b-16 *	15.0 - 16.3	–7.06	–0.09
F1b-17	16.3 - 17.6	–7.70	–0.10
F1b-18	17.6 - 18.9	–7.24	–0.43
F1b-19	18.9 - 20.2	–7.40	–0.17
F1b-20	20.2 - 21.5	–7.70	–0.57
F1b-21	21.5 - 22.8	–7.44	–0.32
F1b-22	22.8 - 24.1	–7.84	–0.28
F1b-23 *	24.1 - 25.5	–7.56	–0.62
F1b-24	25.5 - 27.0	–7.95	–0.60
F1b-25	27.0 - 28.5	–7.39	–0.62
F1b-26	28.5 - 30.0	–7.31	–0.32
F1b-27	30.0 - 31.4	–7.56	–0.49
F1b-28 *	31.4 - 32.8	–7.55	–0.62
F1b-29	32.8 - 33.9	–7.53	–0.34
F1b-30	33.9 - 35.0	–7.77	–0.57
Control	5.0 - 6.0	–6.34	0.78
Average F1b		–7.04	0.03
S4b-1	0.0 - 1.0	–2.67	1.83
S4b-2	1.0 - 2.0	–2.99	1.49
S4b-3	2.0 - 3.0	–3.62	1.30
S4b-4	3.0 - 4.0	–3.57	1.58
Average S4b		–3.62	1.55
Average Septa		–6.55	0.20

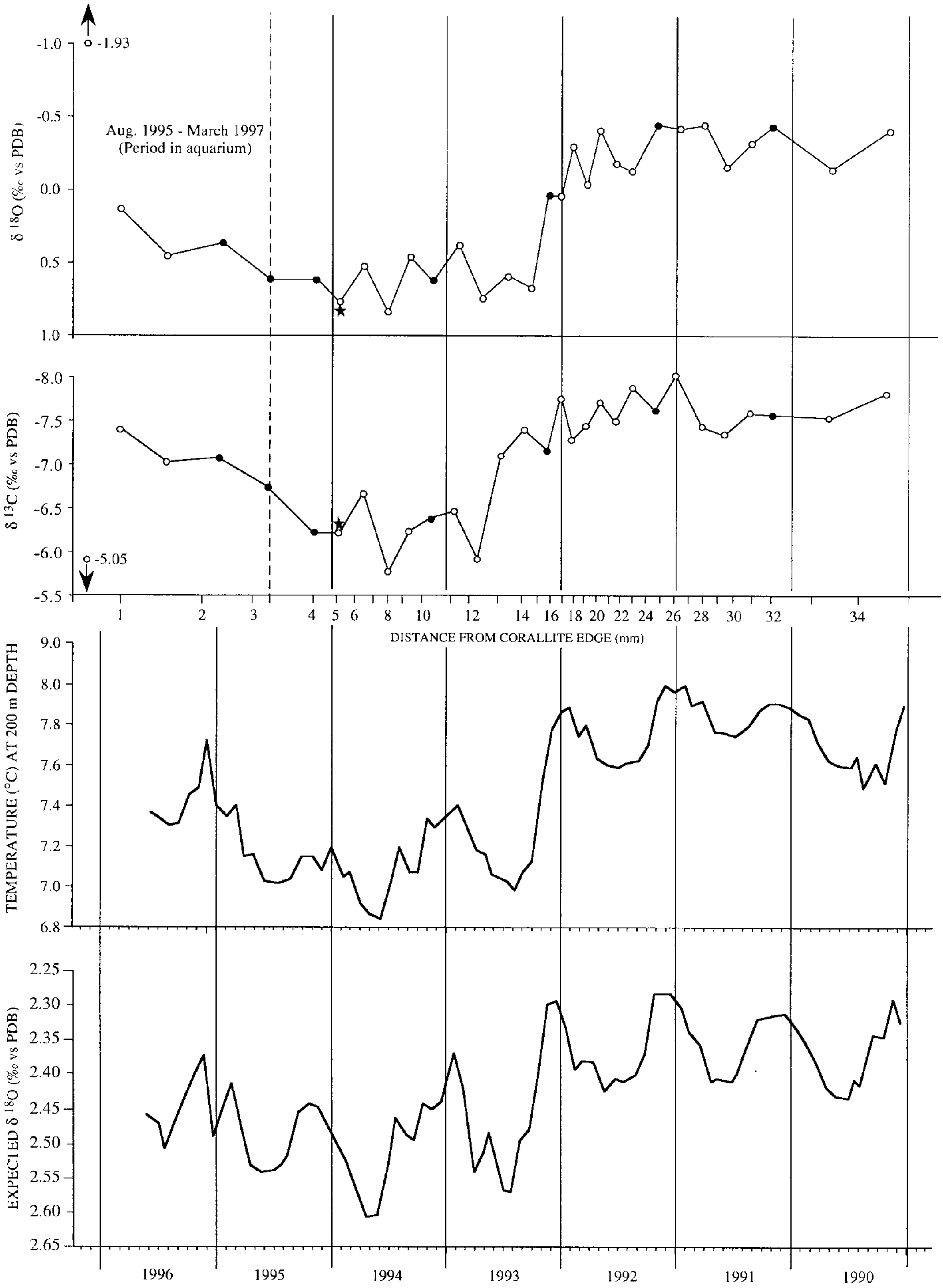

Fig. 9. $\delta^{18}O$ and $\delta^{13}C$ in the septa of corallite F1 from Trondheimsfjorden, measured temperatures at 200 m depth, and estimated $\delta^{18}O$ in isotopic equilibrium with ambient temperature and salinity. The control sample of septa without polyester resin is indicated by a star, and the samples of pronounced growth lines are indicated with a filled circle.

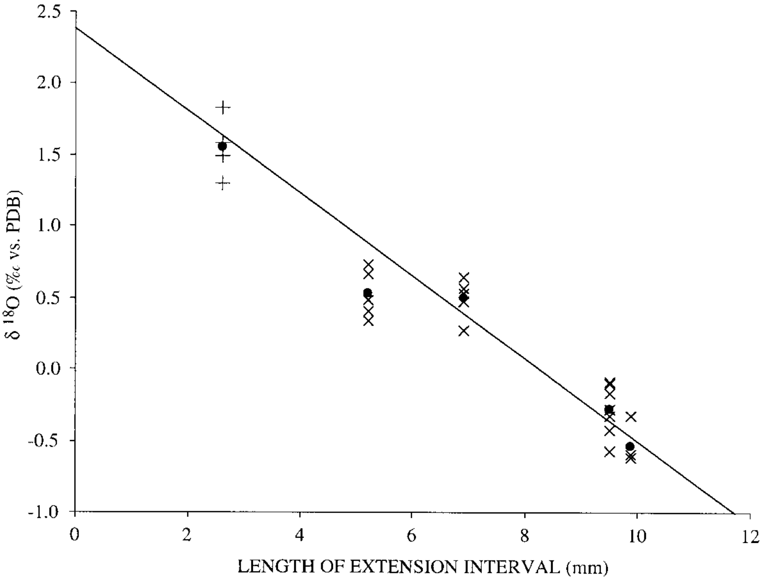

Fig. 10. Values of $\delta^{18}O$ for linear extension intervals in the septa vs. rates of linear extension. ×: samples from series F1b, +: samples from series S4b, ●: average $\delta^{18}O$ for extension intervals. The line crosses the $\delta^{18}O$ axis at ca 2.40 ‰ vs. PDB, which is the estimated oxygen isotope ratio for carbonate precipitating in isotopic equilibrium with the surrounding water.

were formed annually, and that the distances between adjacent distal tips represented yearly linear extension. All examined corallites from the same localities showed more or less similar patterns with approximately the same distances between equivalent growth lines. The average linear extension rate of 5.5 mm/yr was close to the value of 6 mm suggested by Wilson (1979b), based on his own observations together with earlier observations of young specimens on cables. The isotopic studies by Mikkelsen & al. (1982) and Freiwald & al. (1997) however, indicate extension rates of up to 25 mm/yr. This is surprisingly high and comparable to many tropical hermatypic corals. The estimates presented by these authors are based on sampling of the theca, and are most probably caused by bulk sampling of more than one layer. Moreover, Freiwald & al. (1997) sampled at intervals of about 4-6 mm, which cannot detect oscillations in the $\delta^{18}O$ signal within intervals as short as 5-10 mm. Mikkelsen & al. (1982) report an extension rate of 25 mm/yr for a specimen from Røberg. Their results are based on 28 samples taken at 1 mm intervals. However, these samples do not represent a true time series since the distance between the thecae surface and the drilling hole, varied without control on which layer (or layers) the samples represent.

The rate of linear extension decreased gradually towards the corallite edge (Table 1). This growth pattern is similar to what has been found for other ahermatypic scleractinian (Emiliani & al. 1978; Nagelkerken & al. 1997) and is probably a common ontogenetic feature for many corals.

The range of $\delta^{18}O$ was larger in the shelf coral (2.99 ‰ vs. PDB) than in the fjord coral (1.54 ‰ vs. PDB). A similar pattern was found by Mikkelsen & al. (1982) with a range of 5.5 ‰ vs. PDB in corals from the mid-Norwegian shelf and 1.5 ‰ in corals from Trondheimsfjorden (station F). This suggests that corals from the mid-Norwegian shelf have more variable linear extension rates than corals from Trondheimsfjorden. However, this pattern was not reflected in the variation of extension interval-lengths.

Possible causes of growth-line formation in Lophelia

The annual high-density bands in massive hermatypic scleractinians bands are generally depleted in ^{18}O, and are believed to be formed in the period of highest water temperature (Emiliani & al. 1978; Fairbanks & Dodge 1979; Winter & al. 1991, and many others). In our study, comparison of the $\delta^{18}O$ curve with a rescaled growth axis and temperature curve indicated that the pronounced growth lines were formed during the first quarter of the year. This was the time of year when temperature at 200 m depth at station F was falling and salinity was rising (Fig. 8). Assuming that the fine lines were formed regularly, reduced distances between the fine lines within the pronounced growth lines indicated that formation of these annual lines was related to reduced growth. Consequently, the $\delta^{18}O$ should be relatively high in the skeleton associated with these lines. However, we did not find this pattern in our results, but too low sampling resolution (around 1 mm) probably masked the true $\delta^{18}O$ values. More sophisticated sampling techniques may provide measurements of the isotopic composition of the fine lines. In addition to temperature, reproduction and variations in food-supply have also been linked to high density bands in tropical scleractinians (Wellington & Glynn 1983). Unfortunately, almost nothing is known about the reproductive biology and food preferences of *Lophelia*.

The causes of formation of fine growth lines in *Lophelia* are not known, but Scrutton (1965) and Clarkson (1979) report that the number of septal growth ridges (fine lines) was correlated with the lunar cycle. Fine bands within the seasonal bands have been described in many hermatypic scleractinians e.g. *Porites* and *Hydnophora* (Buddemeier & Kinzie 1975; Barnes & Lough 1989; Barnes & Lough 1993). Better techniques for examination of growth lines and experimental use of markers in the skeleton are required for drawing conclusions on the number and possible causes of the formation of fine lines in the skeleton of *Lophelia.*

Implications for description of environmental conditions in the past

Skeletons of many hermatypic scleractinians have proved to be reliable paleothermometers by means of oxygen isotope ratios, and extension rates, and have been successfully used as a tool for describing both paleohistoric and recent environmental changes (Aharon 1983; Dunbar & al. 1994; Lough & Barnes 1996).

Earlier studies of banding patterns in tropical coral skeletons have covered time series ranging up to 507 years (Lough & Barnes 1996). Living *Lophelia* banks on the Norwegian shelf have existed for the last 8 000 years (Mikkelsen & al. 1982; Hovland & al. 1996). The branched colonies of *Lophelia* are easily broken when sampling, and growth sequences longer than around 30 cm (corresponding to ca 40-60 years) are difficult to find. Therefore, long continuous time series of environmental data will be very difficult using *Lophelia,* but subfossil skeletons may provide 'windows' into the past. However, the interpretation of carbon- and oxygen-isotope ratios in *Lophelia* skeletons still seems to be an ambiguous task. More data are needed to provide a basis for distinguishing the effects of temperature from the effect of varying calcification rates on the isotopic composition.

ACKNOWLEDGEMENTS

This work was carried out with financial support from the Haltenpipe Project, Statoil, and the Directorate for Nature Management. We want to acknowledge Jon-Arne Sneli (Trondhjem Biological Station) for providing the long time series of hydrographical data from Trondheimsfjorden. Thanks to the Gunnerus Library and Harald Nissen senior for their kind help. Martin Hovland (Statoil) who initiated this study, is thanked for providing skeletons from the Sula Ridge. Thanks are given to Eystein Jansen (University of Bergen), David J. Barnes (Australian Institute of Marine Science), Lene Buhl-Mortensen (University of Bergen), Murray Roberts (Dunstaffnage Marine Laboratory), and Jan Helge Fosså (Institute of Marine Research) for fruitful discussions and constructive critique. Matilde S. Chauton and Anne Sophie Klaveness (Trondhjem Biological Station) are thanked for help with practical problems.

REFERENCES

Aharon, P. 1983. 140,000 Yr isotope climatic record from raised coral reefs in New Guinea. – *Nature* 304:720-723.

Barnes, D.J. & M.J. Devereux 1988. Variations in skeletal architecture associated with density banding in the hard coral *Porites.* – *Journal of Experimental Marine Biology and Ecology* 121:37-54.

Barnes, D.J. & J.M. Lough 1989. The nature of skeletal density banding in scleractinian corals: Fine banding and seasonal patterns. – *Journal of Experimental Marine Biology and Ecology* 126:119-134.

— 1993. On the nature and causes of density banding in massive coral skeletons. – *Journal of Experimental Marine Biology and Ecology* 167:91-108.

Buddemeier, R.W. & R.A. Kinzie 1975. The chronometric reliability of contemporary corals. – Pp. 135-147 in: Rosenberg, G.D. & S.K. Runcorn (eds). *Growth rhythms and the history of the earth's rotation.* John Wiley & Sons, London.

Buddemeier, R.W. & J.E. Maragos 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. – *Journal of Experimental Marine Biology and Ecology* 14:179-200.

Burdon-Jones, C. & H. Tambs-Lyche 1960. Observations on the fauna of the North Brattholmen stone-coral reef near Bergen. – *Årbok for Universitetet i Bergen, Matematisk-naturvitenskapelig Serie* 1960 (4):1-24.

Cairns, S.D. 1994. Scleractinia of the Temperate North Pacific. – *Smithsonian Contributions to Zoology* 557. 150 pp.

Carlgren, O. 1945. Polypdyr III. Koraldyr – *Danmarks fauna* Vol. 51. 167 pp.

Clarkson, E.N.K. 1979. *Invertebrate palaeontology and evolution.* – George Allen & Unwin, London. 94 pp.

Dodge, R.E., A.M. Szmant, R. Garcia, P.K. Swart, A. Forester & J.J. Leder 1992. Skeletal Structural Basis of Density Banding in the Reef Coral *Montastrea annularis.* – *Proceedings of the Seventh International Coral Reef Symposium, Guam, 1992* 1:186-195.

Dons, C. 1944. Norges korallrev. – *Det Kongelige Norske Videnskabers Selskabs Forhandlinger* 16:37-82.

Dunbar, R.B & G.M. Wellington 1981. Stable isotopes in a branching coral monitor seasonal temperature variation. – *Nature* 293:453-455.

Dunbar, R.B, G.M. Wellington, M.W. Colgan & P.W. Glynn 1994. Eastern Pacific sea surface temperature since 1600 AD: the $\delta^{18}O$ record of climate variability in Galapagos corals. – *Paleoceanography* 9:291-315.

Duncan, P.M. 1877. On the rapidity of growth and variability of some Madreporaria on an Atlantic Cable with remarks upon the rate of Foraminiferal Deposits. – *Annals and Magazine of Natural History* 20:361-365.

Eide, L.I. 1979. Evidence of a topographically trapped vortex on the Norwegian continental shelf. – *Deep-Sea Research* 26:601-622.

Emiliani, C., J.H. Hudson, E.A. Shinn & R.Y. George 1978. Oxygen and carbon isotopic growth record in a reef coral from the Florida Keys and a deep-sea coral from Blake Plateau. – *Science* 202:627-629.

Epstein, S., R. Buchsbaum, H.A. Lowenstam & H.C. Urey 1953. Revised carbonate-water isotopic temperature scale. – *Geological Society of America Bulletin* 64:1315-1326.

Fairbanks, R.G. & R.E. Dodge 1979. Annual periodicity of the $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios in the coral *Montastrea annularis*. – *Geochimica et Cosmochimica Acta* 43:1009-1020.

Frederiksen, R., A. Jensen & H. Westerberg 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe islands and the relation to internal mixing. – *Sarsia* 77:157-171.

Freiwald, A., R. Heinrich & J. Pätzold 1997. Anatomy of a deep-water coral reef mound from Stjernsund, west Finnmark, northern Norway. – Pp. 141-161 in: James, N.P. & J.A.D. Clarke (eds). *Cool-water carbonates.* Society for Sedimentary Geology, Special Volume 56.

Hovland, M., R. Farestveit & P.B. Mortensen 1994. Large cold-water coral reefs off mid-Norway - a problem for pipe-laying? – *Conference Proceedings (3), Oceanology International, 8. - 11. March, 1994, Brighton.*

Hovland, M., P.B. Mortensen, E. Thomsen & T. Brattegard 1997. Substratum-related ahermatypic corals on the Norwegian continental shelf. – *Proceedings of the Eighth International Coral Reef Symposium, Panama, 1996.* Vol. 2:1203-1206.

Israelson, C. & B. Buchard 1991. The isotopic composition of oxygen and carbon in some fossil and recent bivalve shells from East Greenland. – *Lundqua* 33:117-123.

Jungersen, H.F.E. 1917. Alcyonarian and Madreporarian Corals in the Museum of Bergen, collected by Fram-Expedition 1898 - 1900 and by the "Michael Sars" 1900 - 1906. – *Bergen museums aarbok 1915 - 16. Naturvidenskabelig Række* 6. 44 pp.

Knutson, D.W., R.W. Buddemeier & S.V. Smith 1972. Coral Chronometers: Seasonal Growth Bands in Reef Corals. – *Science* 177:270-272.

Land, L.S., J.C. Lang & D.J. Barnes 1977. On the stable carbon and oxygen isotopic composition of some shallow water, ahermatypic, scleractinian coral skeletons. – *Geochimica et Cosmochimica Acta* 41:169-172.

Leder, J.J., P.K. Swart, A.M. Szmant & R.E. Dodge 1996. The origin of variations in the isotopic record of scleractinian corals: I. Oxygen. – *Geochimica et Cosmochimica Acta* 60:2857-2870.

Le-Tissier, M.D.A.A., B. Clayton, B.E. Brown & P.S. Davis 1994. Skeletal correlates of coral density banding and an evaluation of radiography as used in sclerochronology. – *Marine Ecology Progress Series* 110:29-44.

Lough, J.M. & D.J. Barnes 1996. Several centuries of variation in skeletal extension, density and calcification in massive Porites colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability against which to identify unnatural change. – *Journal of Experimental Marine Biology and Ecology* 211:29-67.

Lough, J.M., D.J. Barnes & R.B. Taylor 1997. Understanding growth mechanisms: The key to successful extraction of proxy climate records from corals. – *Proceedings of the Eighth International Coral Reef Symposium, Panama, 1996.* Vol. 2:1697-1700.

McConnaughey, T. 1989. ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates: I. Patterns. – *Geochimica et Cosmochimica Acta* 53:151-162.

Mikkelsen, N., H. Erlenkauser, J.S. Killingley & W.H. Berger 1982. Norwegian corals: Radiocarbon and stable isotopes in *Lophelia pertusa*. – *Boreas* 5:163-171.

Mortensen, P.B., M. Hovland, T. Brattegard & R. Farestveit 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian shelf: structure and associated megafauna. – *Sarsia* 80:145-158.

Nagelkerken, I., G. van der Velde & P.H. van Avesaath 1997. A description of the skeletal development of the temperate coral *Caryophyllia smithi* based on internal growth lines. – *Journal of the Marine Biological Association of the United Kingdom* 77:375-387.

Scrutton, C.T. 1965. Periodicity in Devonian coral growth. – *Palaeontology* 7:552-558.

Shackleton, N.J. 1974. Attainment of isotopic equilibrium between ocean water and the benthonic foraminifera genus *Uvigerina*: isotopic changes in the ocean during the last glacial. – *Collegues Internationaux de CNRS* 219:203-209.

Smith, J.E., M.J. Risk, H.P. Schwarcz & T.E. McConnaughey 1997. Rapid climate change in the North Atlantic during the Younger Dryas recorded by deep-sea corals. – *Nature* 386:818-820.

Strømgren, T. 1971. Vertical and horizontal distribution of *Lophelia pertusa* (Linne) in Trondheimsfjorden on the west coast of Norway. – *Det Kongelige Norske Videnskabers Selskabs Skrifter* 6:1-9.

Swart, P.K. 1983. Carbon and Oxygen Isotope Fractionation in Scleractinian corals: a Review. – *Earth-Science Reviews* 19:51-80.

Taylor, R.B., D.J. Barnes & J.M. Lough 1993. Simple models of density band formation in massive corals. – *Journal of Experimental Marine Biology and Ecology* 167:109-125.

Wainwright, S.A. 1964. Studies of the mineral phase of coral skeleton. – *Experimental Cell Research* 34:213-230.

Weber, J.N. 1973. Deep-sea ahermatypic scleractinian corals: isotopic composition of the skeleton. – *Deep-Sea Research* 20:901-909.

Weber, J.N. & P.M.J. Woodhead 1970. Carbon and oxygen isotope fractionation in the skeletal carbonate of reef-building corals. – *Chemical Geology* 6:93-117.

Wellington, G.M., Dunbar, R.B. & G. Merlen 1996. Calibration of stable oxygen isotope signatures in Galapagos corals. – *Paleoceanography* 11:467-480.

Wellington, G.M. & P.W. Glynn 1983. Environmental influences on skeletal banding in eastern Pacific corals. – *Coral Reefs* 1:215-222.

Wilson, J.B. 1979a. The distribution of the coral *Lophelia pertusa* (L.) (*L. prolifera* (Pallas)) in the north-east Atlantic. – *Journal of the Marine Biological Association of the United Kingdom* 59:149-164.

— 1979b. 'Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall bank. – *Journal of the Marine Biological Association of the United Kingdom* 59:165-177.

Winter, A., C. Goenaga & G.A. Maul 1991. Carbon and Oxygen Isotope Time series From an 18-Year Caribbean Coral. – *Journal of Geophysical Research* 96:16,673-16,678.

Zibrowius, H. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. – *Memoires de l'Institut oceanographique.* Vol. 11. 226 pp.

Accepted 26 May 1998
Editorial responsibility: Ulf Båmstedt