^{87}Sr/^{86}Sr and Sr/Ca Investigation of Jurassic molluscs from Scotland: Implications for Paleosalinities and the Sr/Ca Ratio of Seawater

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ABSTRACT

Measurements of ^{87}Sr/^{86}Sr, Sr/Ca, δ^{18}O, and δ^{13}C were performed on molluscan fossils from the Great Estuarine Group, Scotland, to deduce paleosalinity patterns and hydrodynamic environments in this classic Jurassic marginal marine succession. Fossils are found as winnowed accumulations in shell beds that bear low-diversity assemblages, consistent with deposition in a lagoonal paleoenvironment. Previous studies have concluded that estuarine mixing of seawater and freshwater took place based on correlated trends in δ^{18}O and δ^{13}C, most notably in the mussel *Praemytilus strathairdensis* from the Kildonnan Member. This interpretation is shown to be incorrect based on ^{87}Sr/^{86}Sr ratios, which reveal negligible amounts of seawater-derived strontium in the shells of *Praemytilus*. Furthermore, the ^{87}Sr/^{86}Sr ratios are remarkably uniform between specimens of *Praemytilus* from the same shell bed despite large changes in δ^{18}O, δ^{13}C, and the Sr/Ca ratio. This is consistent with a lagoonal hydrology controlled more by seasonal changes in evaporation, precipitation, and flooding than by direct inputs of seawater or riverine water transported over large distances. Lagoons containing the oyster *Praeexogyra* in the Duntulm Formation have similar inferred O and C isotope characteristics, but based on their ^{87}Sr/^{86}Sr ratios, they have a higher proportion of seawater than the *Praemytilus* lagoons of the Kildonnan Member.

The data thus far suggest that many of the lagoonal environments in the Great Estuarine Group were nearly hydrologically closed, at least over the interval representing the molluscan invasion of these habitats, rendering O and C isotopes unreliable proxies of paleosalinity. Because strontium isotopes are not directly affected by evaporation of the lagoons, knowledge of marine and freshwater ^{87}Sr/^{86}Sr ratios, along with estimates of Sr concentration, are used to calculate the proportion of seawater in the brackish water mixture. *Unio* is nearly always the most radiogenic taxon compared to other genera in closely adjacent sedimentary strata, confirming its freshwater affinity. The purported marine-brackish bivalve *Tancredia* yields a low paleosalinity of 4‰, only slightly more saline than *Unio* and *Praemytilus* at 1–3‰. The oyster *Praeexogyra hebridica* yields paleosalinities between 2‰ and 26‰, attesting to the wide salinity tolerance of this species.

Thus far, only *Neomiodon* from the Duntulm and Staffin Bay formations show covariant relationships between ^{87}Sr/^{86}Sr and Ca/Sr ratio that can be reconciled with a dynamic response to seawater–freshwater mixing. The slopes of these trends converge at 0.7068, which is close to the early Callovian seawater composition of 0.7069. Using values of D_{Sr} from modern aragonite secreting molluscs, the Sr/Ca ratio of middle Jurassic seawater is constrained from the best correlated mixing line to be 5.4 ± 0.6 millimoles/mole. In contrast, Sr/Ca ratios in the Great Estuarine Group lagoons and continental watershed range from 5.4 to 19.0. These are much higher than the average value of 2.3 for modern rivers but typical of Sr/Ca ratios in rivers draining arid climate regions. The semirestricted hydrodynamic regime inferred from the high seawater-like δ^{18}O values and high but uniform Sr/Ca ratios in many of the Great Estuarine Group molluscs is consistent with a seasonally dry, Mediterranean-style climate for the Middle Jurassic of Britain.

Keywords: paleoclimate, paleoenvironment, ^{87}Sr/^{86}Sr, Sr/Ca, mollusca, Jurassic.

INTRODUCTION

The Jurassic Great Estuarine Group of the Inner Hebrides, Scotland (Fig. 1), was interpreted by Hudson (1963, 1980) to represent a clear example of salinity-controlled ecological diversity among a benthic molluscan fauna; it has been cited in many reviews of this phenomenon (e.g., Raup and Stanley, 1978; Brenchley and Harper 1998; Fürsich, 1994). Although the 19th century name of the group suggests an estuarine paleoenvironment, the scale (280 m thick; at least 100 km lateral extent) and sedimentology are more compatible with wide, shallow, muddy lagoons in which fluvial deltas accumulated (Fig. 2). Nevertheless, it is widely believed that a connection to the sea existed over most of the Great Estuarine Group stratigraphic interval and that salinity was controlled by seawater-freshwater mixing, as is the case for the Texas Coast Bays, which were used as a modern analogue by Hudson (1963). Detailed sedimentological and faunal studies have been made of the most fossiliferous units within the Great Estuarine Group, including the Duntulm Formation, which is regarded as mainly marine-brackish (Andrews and Walton, 1990), and the Kildonnan Member of the Lealt Shale Formation, which is considered to have been deposited in waters of widely varying salinity with substantial freshwater input (Hudson et al., 1995;
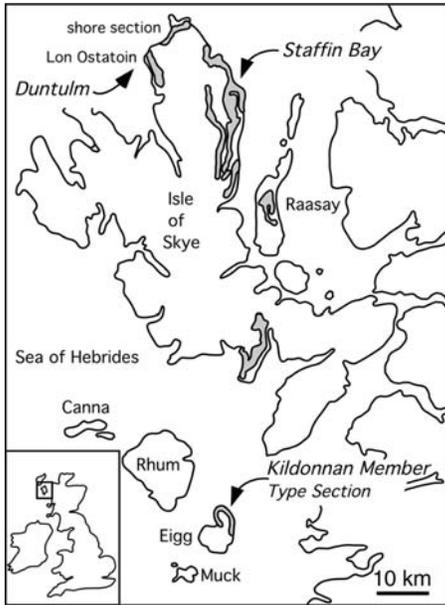
Figure 1. Location map of Inner Hebrides, Scotland, showing outcrop exposure of Great Estuarine Group. Modified from Hudson et al. (1995).
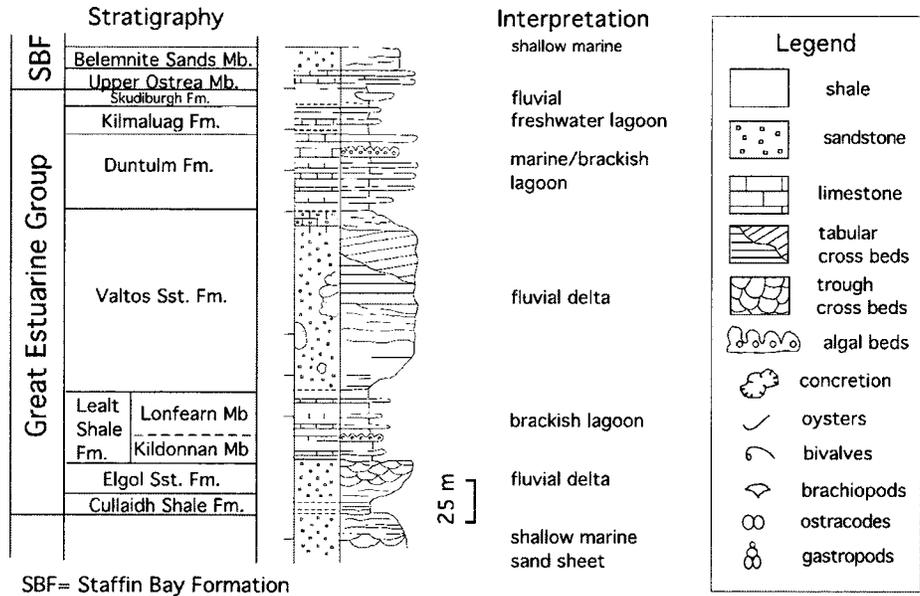

Figure 2. Stratigraphy and previous interpretations for sedimentary rocks of Great Estuarine Group and overlying Staffin Bay Formation, Scotland. Fm. = formation; Mb. = member; Sst = sandstone. Modified from Andrews (1985).

Wakefield, 1995). Although the faunas of the Great Estuarine Group were regarded as principally brackish water, both the Kidonnan Member and the Duntulm Formation contain algal stromatolites with pseudomorphs after gypsum, indicating evaporation of the lagoons or their margins (Hudson, 1970; Andrews and Walton, 1990). The Great Estuarine Group is succeeded by the early Callovian Staffin Bay Formation, which records first a lagoonal transgression (the Upper Ostrea Member) and then a return to fully marine deposition (the Belemnite Sands Member).

The exquisite preservation of the Great Estuarine Group molluscs (which are 100% aragonite at favorable localities) enables isotope and chemical signatures preserved within the shells to be used to reconstruct the Great Estuarine Group paleohydrology for the purpose of estimating relative paleosalinities. Tan and Hudson (1974) carried out a C and O isotope survey of Great Estuarine Group molluscs and compared the isotopic results with paleontological indicators of salinity. They found a good correlation between $\delta^{18}O$ and $\delta^{13}C$ in the mytilid bivalve *Praemytilus strathairdensis* from Bed 5e of the Kildonnan Member on the Isle of Eigg (Fig. 3). This result, discussed in detail by Hudson et al. (1995), is consistent with a seawater-freshwater mixing origin as documented for modern estuarine bivalves by Mook (1970). Using a $\delta^{18}O$ of $-1‰$ standard mean ocean water (SMOW) for Jurassic sea-
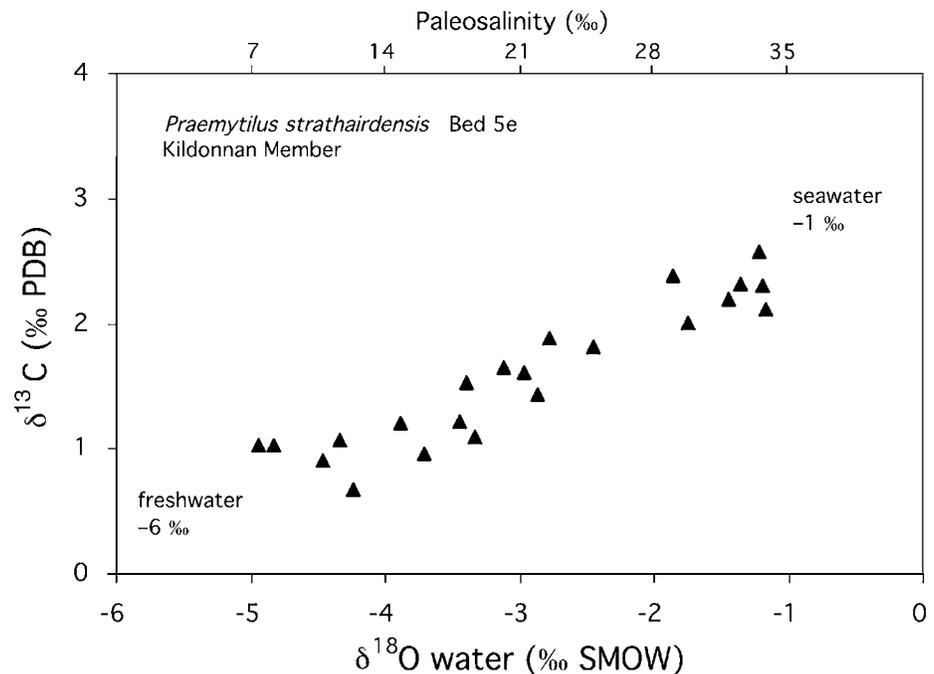

Figure 3. Carbon and oxygen isotope measurements of individual specimens of *Praemytilus strathairdensis* from Bed 5e of Kildonnan Member, reproduced from data in Tan and Hudson (1974). Shell $\delta^{18}O$ data (PDB) have been converted to equivalent water $\delta^{18}O$ (SMOW) using Grossman and Ku's (1986) aragonite paleotemperature equation for a temperature of 25 °C. Co-variant relationship was interpreted by Hudson et al. (1995) to reflect seawater–freshwater mixing in lagoon represented by Bed 5e. Assuming $-1‰$ for Middle Jurassic seawater, $-6‰$ for meteoric water, and assuming $\delta^{18}O$ and salinity were linearly correlated, paleosalinities between 8 and 34‰ were determined.

water, −6‰ for freshwater input, a temperature of 25°C, and assuming that $\delta^{18}O$ and salinity were linearly correlated, Hudson et al. (1995) concluded that calcification of *Praemytilus* occurred in waters varying from 8 to 34‰ salinity (Fig. 3), a result which agrees with paleoecology.

This paleohydrological approach to paleosalinity determination depends on the assumption that the molluscan fauna inhabited waters with salinities controlled by seawater-freshwater mixing and that O and C isotopes behaved conservatively in the estuarine mixing zone. Tan and Hudson (1974) recognized that other factors, such as evaporation within the lagoons, could complicate the salinity-isotope correlation. The problem is compounded in some Great Estuarine Group fossils, such as the oyster *Praeexogyra hebridica*, which did not show good correlations between $\delta^{18}O$ and $\delta^{13}C$, and some $\delta^{18}O$ values were unexpectedly high. In a study of the same species of oyster from stratigraphically equivalent deposits in England, Hendry and Kalin (1997) found $\delta^{18}O$ values as high as 2.3‰ Peedee belemnite (PDB), which yield equivalent water $\delta^{18}O$ values up to 3.5‰ (SMOW) for a Bathonian paleotemperature of 25°C. Such high $\delta^{18}O$ values are clear evidence that evaporation enriched lagoonal waters in ^{18}O, casting suspicion on the reliability of O isotopes as a proxy for paleosalinity in the seawater–freshwater mixing zone. The $\delta^{13}C$ of dissolved inorganic carbon (DIC) is also susceptible to nonconservative behavior in the seawater–freshwater mixing zone. Although DIC in marine and freshwaters generally contrasts in C isotope values, mixed brackish waters may be enriched in ^{13}C by CO_2 gas exchange across the air-sea interface or enriched in ^{12}C by oxidized sedimentary organic carbon.

Strontium isotopes have also been used for paleosalinity estimation in Holocene (Andersson et al., 1992; Ingram and Sloan, 1992; Ingram and DePaolo, 1993; Reinhardt et al., 1998) and Cretaceous paleoenvironments (Holmden et al., 1997a, 1997b) and are more likely than O and C isotopes to remain conservative in the seawater–freshwater mixing zone because the $^{87}Sr/^{86}Sr$ ratio in mixed (brackish) waters is not affected by evaporation. In this paper, we test the original oxygen isotope calibration of Great Estuarine Group paleosalinities against analyses of Sr isotopes performed on the same fossils. We show that $^{87}Sr/^{86}Sr$ ratios in *Praemytilus* cannot be reconciled with simple seawater–freshwater mixing and conclude that the previously calculated paleosalinities are erroneous because of the influence of nonconservative isotope effects

on $\delta^{18}O$ and $\delta^{13}C$ values in depositional waters of the Great Estuarine Group. Using Sr material balance calculations, we present a $^{87}Sr/^{86}Sr$ paleosalinity scale that measures seawater contributions (or minimum paleosalinities) in Great Estuarine Group depositional waters. We also report high precision measurements of Sr/Ca ratios in the Great Estuarine Group molluscs, which yield inferred Sr/Ca ratios in Great Estuarine Group lagoons as high as 19.0 millimoles/mole, for reasonable estimates of molluscan D_{Sr}. We discuss the significance of this result and estimate the Sr/Ca ratio of middle Jurassic seawater, which is found to be substantially lower than modern seawater.

In the following discussions about estuarine and lagoonal waters, it is important to distinguish between three distinct but commonly related quantities. Salinity, equivalent to total dissolved solids, is dominated by NaCl in seawater and in simple mixtures with river waters that contain essentially no salts, as are found in temperate estuaries. In enclosed lagoons, reactions involving the dissolution or precipitation of salts may modify the ionic ratio of seawater or of mixtures of seawater and freshwater; this is particularly characteristic of lagoons in arid environments where input waters from the land may be saline. In such cases, the salinity of the lagoon and the proportion of seawater in it will not be correlated linearly because evaporation enriches the residual water in ^{18}O. In cases discussed below, salinity is the major control on the nature of the lagoonal fauna. The Sr isotope method estimates a maximum seawater contribution, which represents a minimum salinity if evaporation has occurred. Thus, the inferred $\delta^{18}O$ of the water, calculated from the measured $\delta^{18}O$ of the shell by assuming a reasonable temperature, provides a measure of the degree of evaporation suffered by a particular lagoon.

STRATIGRAPHY AND SAMPLING STRATEGY

We sampled some of the most abundant and ecologically significant bivalves from the Great Estuarine Group, of latest Bajocian to late Bathonian age, concentrating on discrete shell beds; each was characterized by a molluscan assemblage of monotypic to low species diversity from which numerous shells of the same species could be collected. From the type section of the Kildonnan Member, Isle of Eigg (Figs. 1 and 4), the mussel *Praemytilus strathairdensis* was re-sampled from hand samples already studied by Tan and Hudson (1974) and Hudson et al. (1995), and from new collections. The samples were collected

from several horizons within Bed 5e and were believed to represent a wide range of salinities. The freshwater bivalve *Unio andersoni* was sampled from Beds 3h and 7b; a heterodont bivalve, *Tancredia gibbosa*, believed to be of marine affinity, was sampled from Bed 6b; and the small heterodont bivalve *Neomiodon* sp. was sampled from bed 6f. *Neomiodon* appears to have been an opportunistic colonizer of unstable environments and often of lowered salinity in the Middle Jurassic to Lower Cretaceous of Europe (e.g., Hudson, 1980; Morter, 1984). Other biota support the salinity assignments in each case (Hudson et al., 1995).

Samples of the oyster *Praeexogyra hebridica* were also taken from two beds within the Duntulm Formation at the type locality, Isle of Skye (Andrews and Walton, 1990; Figs. 1 and 5). This species is regarded as the first oyster to have inhabited waters of reduced-marine salinity (Hudson and Palmer, 1976). The two *Praeexogyra* samples are separated stratigraphically by a freshwater intercalation within the Duntulm Formation, from which we sampled shell-beds with populations of *Unio andersoni* and *Neomiodon*. Finally, we sampled *Neomiodon* from two shell beds within the transgressive, Upper Ostrea Member of the Staffin Bay Formation of early Callovian age (Riding and Thomas, 1997). We also sampled a belemnite from the top of the Belemnite Sands Member of the Staffin Bay Formation that represented a fully marine environment a little younger than the lagoonal molluscs we studied (Fig. 2). The oysters and the belemnite are primary calcite; the other shells are primary aragonite. In our discussions we simplify the nomenclature of the bivalves by using generic names: *Unio* (in a wide sense; freshwater clam), *Praemytilus* (mussel), *Tancredia* (heterodont), *Neomiodon* (heterodont), *Praeexogyra* (oyster). For documentation of taxonomic affinities, see Hudson et al. (1995) and Hudson and Palmer (1976).

We chose to analyze shells of the same species collected from the same shell bed for two reasons: (1) the bulk D_{Sr} value between individual fossils of the same species is likely to be nearly constant, and (2) the hydrodynamic setting of lagoons represented by individual shell beds was likely to have been characterized by relatively constant $^{87}Sr/^{86}Sr$ and Sr/Ca ratios for marine and freshwater inputs. Studies of modern rivers have shown that both the concentration and $^{87}Sr/^{86}Sr$ ratio are somewhat variable within an individual river (Goldstein and Jacobsen, 1987). By limiting measurements to individual specimens from the same shell bed, the composition for the freshwater end-member is less likely to have varied wide-
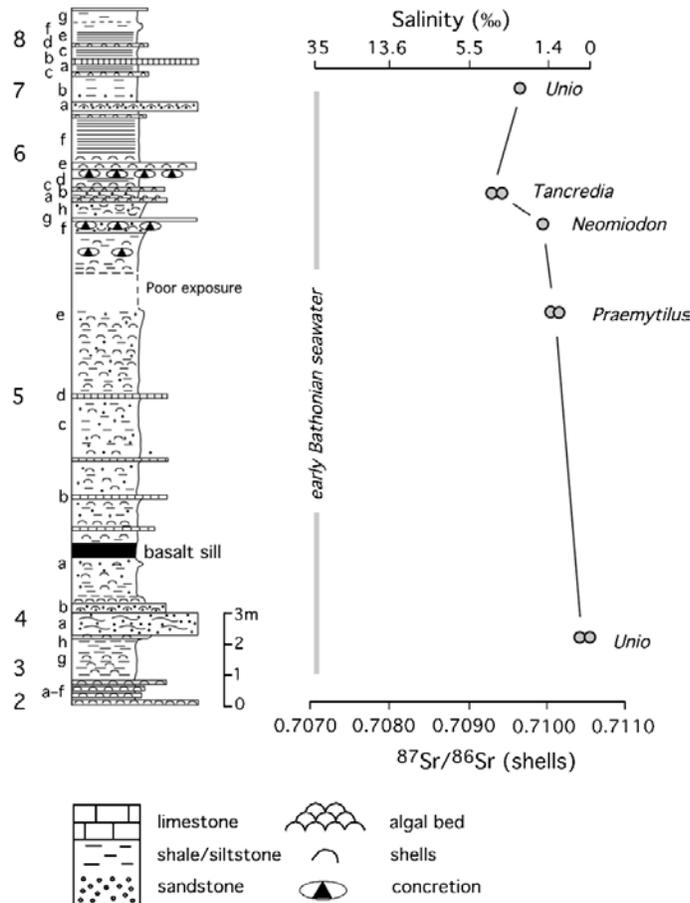
Figure 4. Detailed schematic log of type section of Kildonnan Member, Lealt Shale Formation, near Kildonnan, Eigg, showing fossil bed numbers and lithologies (modified from Hudson et al., 1995). Paleosalinities are calculated from Sr material balance considerations as described in text.

ly. Therefore, any correlated trends in $^{87}Sr/^{86}Sr$ and Sr/Ca ratio in brackish water shells should represent degrees of mixing between seawater and freshwater rather than changes in the composition of the freshwater end-member independent of changes in degree of mixing.

The long residence times for Sr (ca. 5 Ma) and Ca (ca. 1 Ma) in the oceans means that the seawater Sr/Ca and $^{87}Sr/^{86}Sr$ ratios can be considered constant over the time-scale that a shell bed would have accumulated. Over the depositional interval represented by the Great Estuarine Group and Staffin Bay Formation, there is evidence that the $^{87}Sr/^{86}Sr$ ratio of seawater decreased (Fig. 6). For the purpose of comparison, and to provide a seawater composition for material balance calculations, we assign each of the major sedimentary units a marine $^{87}Sr/^{86}Sr$ ratio based on the seawater $^{87}Sr/^{86}Sr$ secular curve. These are 0.70708 for the Kildonnan Member, 0.70698 for the Duntulm Formation, and 0.70690 for the Staffin

Bay Formation. Seawater at the time of deposition of the Belemnite Sands Member is 0.70688 (Table 1).

ANALYTICAL PROCEDURES AND MASS SPECTROMETRY

Whole fossil shells or fragments of individual specimens were separated from fist-sized hand samples and cleaned of adhering detritus and any calcite overgrowths by scraping with dental tools. Specimens of *Praeoxgyra* and *Neomiodon* were separated from single hand samples taken from individual shell beds, whereas specimens of *Praemytilus*, *Unio*, and *Tancredia* were collected from individual shell beds but not from individual hand samples. Quantitative X-ray diffraction analysis on selected specimens of *Praemytilus*, *Neomiodon*, *Tancredia*, and *Unio* confirm that the specimens retained their original aragonite mineralogy. Strontium isotope analyses and

Sr/Ca ratios were determined on a single fragment of an individual shell. Additional fragments of the same shell were used for selected X-ray diffraction and O and C isotope analysis. Electron microscopy of the shell demonstrates excellent preservation of shell microstructure in *Praemytilus* from the Kildonnan Member (Hudson, 1968), of *Neomiodon* from shales within the Great Estuarine Group (Sandberg and Hudson, 1983), and of *Unio* (J.D. Hudson, unpubl. data). These aragonitic shells are preserved unaltered; thus, it can be assumed that calcitic *Praeexogyra* are also preserved.

Shell fragments were dissolved in 1.5N HCl for $^{87}Sr/^{86}Sr$ and Sr/Ca analysis. An aliquot of the resulting stock solution was passed through cation ion exchange resin to purify Sr from Ca and other trace constituents and loaded onto single Ta filaments with a phosphoric acid Ta–gel or TaO_5 mixture to increase ionization efficiency. Isotopic measurements of Sr were performed on a Finnigan-MAT 261 instrument using a multidynamic peak-hopping routine and correction for instrumental mass fractionation using $^{88}Sr/^{86}Sr$ of 8.375209. ^{87}Rb interference on ^{87}Sr was monitored using ^{85}Rb but was always negligible. Reproducibility of $^{87}Sr/^{86}Sr$ analyses was better than 30 ppm (2RSD) based on numerous runs of SRM 987 performed throughout the course of this work yielding $^{87}Sr/^{86}Sr$ of 0.710248.

A second aliquot of the stock solution was diluted five to 25 times by weight. From this dilute solution, $\sim$10 µg of Ca was aliquoted and mixed with a ^{42}Ca–^{48}Ca–^{84}Sr tracer. The sample was dried, converted to the nitrate form, and loaded onto the Re side filament of a double Re filament assembly. Isotope dilution analysis of Ca isotopes was performed using a single collector peak-hopping routine for the cycle ^{40}Ca–^{42}Ca–^{44}Ca–^{48}Ca, whereas isotope dilution Sr analysis was performed by static multicollection. The isotope ratios of Sr and Ca in the tracer were determined by mass spectrometry, and concentrations of the tracer Sr and Ca isotopes determined by analysis of tracer–standard mixtures using gravimetrically prepared, isotopically normal CaF_2 and $SrCO_3$ standards. The isotope ratio of the CaF_2 standard was normalized to a $^{42}Ca/^{44}Ca$ of 0.33124 (Russell et al., 1978) to correct for instrumental mass fractionation. Analyses of our gravimetrically prepared Sr/Ca standard yields a reproducibility of better than ± 0.1% (2 RSD) on the ratio. All Sr/Ca ratios are reported in millimoles/mole.

Oxygen and carbon isotope analyses were performed by the method of McCrea (1950) on an F-MAT Delta E instrument. Reproduc-
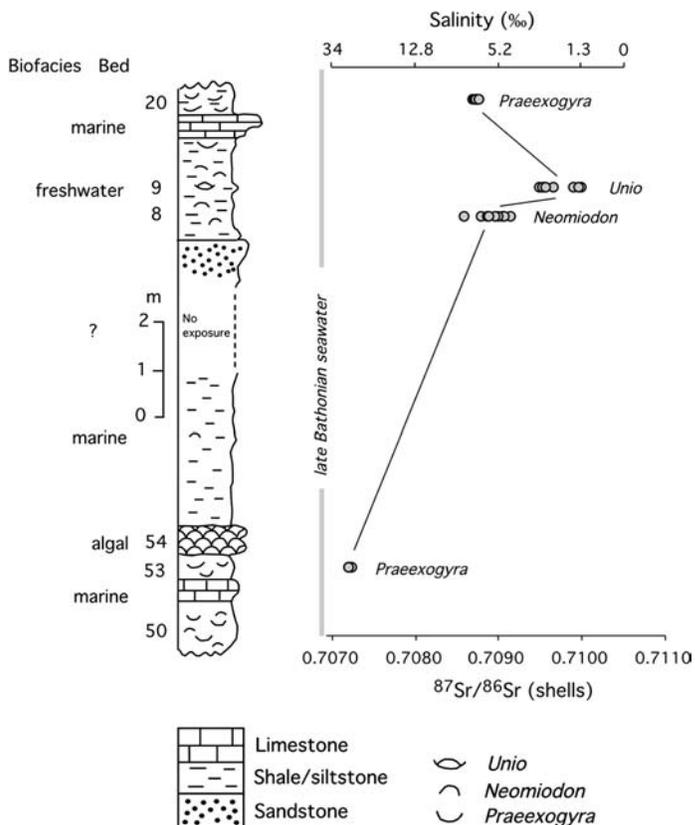
Figure 5. Detailed schematic log of Duntulm Formation showing bed numbers and lithologies (based on Andrews and Walton, 1990). Paleosalinities are calculated from Sr material balance considerations as described in text.

ibility is equal to or better than ± 0.2‰ (2σ) for both $\delta^{18}O$ and $\delta^{13}C$ based on long-term reproducibility of SRM 19, which, relative to PDB, yielded values of −2.20 ± 0.2‰ and 1.95 ± 0.14‰, respectively.

STRONTIUM ISOTOPE RATIOS AND PALEOSALINITIES

Results of the Sr isotope analyses are the least equivocal of the analytical data collected in this study (presented in Table 1, Figs. 4 and 5) because the $^{87}Sr/^{86}Sr$ ratio is not dependent on taxon or mineralogy. We also discuss their correlation with previous results on stable isotopes and the implications for paleoecology. Later, more quantitative assessments of paleohydrology and paleosalinity are presented, taking into account our results on Sr/Ca ratios in the molluscs. This involves consideration of distribution coefficients that depend on analogy with modern molluscs.

Unio: Characterizing the Freshwater End-Member

Modern Unionid bivalves are exclusively freshwater with a low tolerance for elevated salinity. This dominantly freshwater habitat appears to be a long-lived feature of the group based on interpretations of the sedimentary environments from which they have been found in the rock record. The species *Unio andersoni* was thus sampled from three horizons to gain insight into the freshwater end of the Great Estuarine Group salinity spectrum; samples were taken from two beds from the Kildonnan Member, generally regarded as one of the most freshwater-influenced parts of the Great Estuarine Group, and from one bed from a freshwater intercalation within the marine-brackish Duntulm Formation. Our analyses of *Unio andersoni* confirmed the expectation that the *Unio* hosted beds were formed under influence of freshwater. When it is possible to compare $\delta^{18}O$, $\delta^{13}C$, and $^{87}Sr/^{86}Sr$ ratios between *Unio* and contemporaneous taxa from the same bed or adjacent beds, *Unio* usually displays one or more of the following features: lower $\delta^{18}O$, lower $\delta^{13}C$, and higher $^{87}Sr/^{86}Sr$. For example, specimens of *Unio* from the Kildonnan Member (Bed 3h) have the highest $^{87}Sr/^{86}Sr$ ratios measured thus far in the Great Estuarine Group (0.71052;

Fig. 4) and relatively low $\delta^{13}C$ and $\delta^{18}O$ (Table 1). In the Duntulm Formation, the freshwater intercalation yields relatively radiogenic $^{87}Sr/^{86}Sr$ from 0.7095–0.7099, compared to an underlying bed of the oyster *Praeexogyra* (Beds 50–53) yielding 0.7072 (Fig. 5), which is close to the composition of late Bathonian seawater at 0.70698 (Fig. 6). In general, this pattern in the isotopes of O, C, and Sr is to be expected because, compared to seawater, meteoric waters tend to have lower $\delta^{18}O$ values and increased contribution of oxidized organic carbon with lower $\delta^{13}C$ values and radiogenic strontium derived from the continental crust. The high $^{87}Sr/^{86}Sr$ in *Unio* from the Great Estuarine Group requires a Middle Jurassic continental drainage system developed on silicate basement rocks of Precambrian age, with paleohighlands most likely located in the present-day Scottish mainland (Harris, 1989, 1992; Thomson et al., 1999). The fact that the two *Unio* shell-beds in the Kildonnan Member (Beds 3h, 7b) have different $^{87}Sr/^{86}Sr$ ratios indicates variation in the freshwater composition over time. Indeed, it seems that the ratio became slightly less radiogenic with time, possibly due to changes in the riverine source and the position of the lagoons relative to the sea (Fig. 4).

The contrast between seawater and freshwater ratios makes $^{87}Sr/^{86}Sr$ a very sensitive indicator of the seawater contribution to the Great Estuarine Group lagoons. Although $\delta^{18}O$ and $\delta^{13}C$ may be used for this purpose in favorable circumstances where estuarine mixing occurs, these isotopes become nonconservative tracers of water source in lagoons characterized by long water residence times. A case in point is $\delta^{18}O$ values in *Unio* from the Duntulm Formation (−0.3 to 1.3‰), which overlap with those of the brackish oyster *Praeexogyra* (−2.9 to 0.7). Differences in the proportion of seawater show up clearly, however, in the different $^{87}Sr/^{86}Sr$ ratios exhibited by *Unio* (~0.7097) and *Praeexogyra* (~0.7072). The lack of sensitivity in the tracer potential of the stable isotopes of C and O is most likely due to differing degrees of evaporation in the lagoons, which increases water $\delta^{18}O$ values and also promotes ^{13}C–exchange with CO_2 in the atmosphere, thus increasing lagoonal $\delta^{13}C$ values. A modern example of these effects is found in the Florida Everglades, where long water residence times and high evaporation rates cause freshwater to attain seawater-like $\delta^{18}O$ values. Lloyd (1964) noted that such effects could confound paleoenvironmental interpretations of $\delta^{18}O$ values in fossil molluscs from transitional environments with dry paleoclimates if it were

assumed that freshwater molluscs should exhibit lower δ18O values compared to both marine and brackish water molluscs. Molluscan δ18O systematics in the Great Estuarine Group appear to confirm Lloyd's prediction. Likewise, δ13C values in nearby Florida Bay can be significantly lower than open seawater values while salinity is higher (Patterson and Walter, 1994).

Kildonnan Member; *Praemytilus*, *Tancredia*, and *Neomiodon*

Specimens of the bivalve *Praemytilus strathairdensis* from Bed 5e of the Kildonnan Member, originally used to calibrate a δ18O paleosalinity scale (Tan and Hudson, 1974; Hudson et al., 1995), were reanalyzed for δ18O and δ13C along with analyses of new specimens of 87Sr/86Sr and Sr/Ca (Fig. 7A). The relatively high paleosalinities predicted using the δ18O calibration (up to 34‰) are not compatible with the very radiogenic 87Sr/86Sr ratios of 0.71004 to 0.71014 measured on new specimens from the same suite of fossils, relative to an early Bathonian seawater composition of 0.70708 (Fig. 6). These 87Sr/86Sr ratios are similar to those of *Unio* from the Kildonnan Member (0.70963, 0.71052; Fig. 4), which supports the interpretation that *Praemytilus* inhabited lagoons dominated by freshwater inputs. Ruling out different proportions of seawater as an explanation for the δ18O variance, and recognizing that the 4‰ range in δ18O, which translates to an environmental temperature range of ~16°C, makes a temperature effect unlikely. The environmental cause of the 4‰ range in δ18O must be tied to the local water balance of the lagoon, in particular to the evaporation–precipitation ratio. A lagoonal-scale hydrodynamic explanation is supported by the positive co-variance between δ18O and δ13C observed among sequential microsamples of aragonite analyzed parallel to growth axes of individual *Praemytilus* shells; this emphasizes the importance of changing lagoonal water balances over the lifetime of a single organism (Hartman et al., 2001).

The radiogenic 87Sr/86Sr ratios in *Neomiodon* are compatible with previous interpretations of its low-salinity habitat (Hudson et al., 1995). More surprisingly, the supposedly marine-brackish bivalve *Tancredia* also has a radiogenic Sr isotope signature, though to a lesser extent than the other bivalves from the Kildonnan Member (Fig. 4), which indicates that it was also living in lagoonal waters with negligible seawater input. The *Praemytilus* and *Tancredia* results have implications for paleoecology. A freshwater environment for

TABLE 1. (??)

Sample	Taxon	δ18O (PDB)	δ13C (PDB)	Sr (ppm)	87Sr/86Sr	Sr/Ca (shell)	D_Sr[†]	Sr/Ca[†] (water)
Staffin Bay Formation, Staffin Bay, Skye (Bed numbers from Morton and Hudson, 1995)								
<u>Belemnite Sands Member</u>								
Bed BS 8								
TR 397D	*Cylindroteuthis*	−1.18	3.01	1135	0.706878 (9)	1.306	0.24	5.4
<u>Upper Ostrea Member</u>								
Bed UO 5c								
TR 664-1	*Neomiodon*	0.68	−0.64	1462	0.707726 (17)	1.786	0.28	6.4
TR 664-2	*Neomiodon*	1.73	1.16	1427	0.707684 (16)	1.679	0.28	6.0
TR 664-3	*Neomiodon*	0.38	−0.56	1561	0.707737 (12)	1.844	0.28	6.6
TR 664-4	*Neomiodon*	0.45	−0.12	1145	0.707578 (13)	1.655	0.28	5.9
TR 664-5	*Neomiodon*	2.08	0.72	1487	0.707696 (22)	1.831	0.28	6.5
TR 664-6	*Neomiodon*	0.68	−1.05	1368	0.707655 (10)	1.671	0.28	6.0
TR 664-7	*Neomiodon*	0.92	−0.66	1205	0.707713 (7)	1.663	0.28	5.9
TR 664-8	*Neomiodon*	0.60	−0.18	1469	0.707682 (11)	1.794	0.28	6.4
TR 664-9	*Neomiodon*	−0.22	−0.09	1512	0.707741 (11)	1.817	0.28	6.5
Bed UO 5b (0.9 m below top)								
TR 638 E-1	Neomiodon	−2.19	0.70	2497	0.708099 (8)	3.189	0.28	11.4
TR 638 E-2	*Neomiodon*	−2.05	−0.20	1801	0.707700 (7)	2.286	0.28	8.2
TR 638 E-3	*Neomiodon*	−1.49	1.89	2376	0.708066 (9)	3.101	0.28	11.1
TR 638 E-4	*Neomiodon*	−2.34	1.46	2484	0.708176 (6)	3.227	0.28	11.5
TR 638 E-6	*Neomiodon*	−2.13	1.69	2270	0.707937 (8)	2.771	0.28	9.9
TR 638 E-7	*Neomiodon*	−1.85	1.31	2085	0.707864 (14)	2.784	0.28	9.9
TR 638 E-8	*Neomiodon*	−2.19	0.07	2548	0.708004 (8)	3.004	0.28	10.7
Great Estuarine Group								
<u>Duntulm Formation, Duntulm, Skye (bed numbers from Andrews and Walton, 1990)</u>								
Lon Ostatoin section								
Bed 20								
TR 337A-1	*Praeexogyra*	−2.07	2.05	1291	0.708677 (7)	1.565	0.12	13.0
TR 337A-2	*Praeexogyra*	0.27	2.51	1109	0.708692 (8)	1.343	0.12	11.2
TR 337A-3	*Praeexogyra*	−2.37	1.23	1304	0.708693 (11)	1.557	0.12	13.0
TR 337A-4	*Praeexogyra*			1338	0.708698 (7)	1.629	0.12	13.6
TR 337A-5	*Praeexogyra*	1.86	3.30	1067	0.708713 (10)	1.367	0.12	11.4
TR 337B-1	*Praeexogyra*			1274	0.708736 (10)	1.574	0.12	13.1
TR 337B-2	*Praeexogyra*			1338		1.640	0.12	13.7
TR 337B-3	*Praeexogyra*			1314	0.708718 (9)	1.638	0.12	13.7
TR 337B-4	*Praeexogyra*	−1.07	3.23	1221	0.708745 (11)	1.504	0.12	12.5
Bed 9								
TR321 A-1	*Neomiodon*			2487	0.708782 (8)	2.883	0.28	10.3
TR 321 A-2	*Neomiodon*			2989	0.709004 (7)	3.407	0.28	12.2
TR 321 A-3	*Neomiodon*			2888	0.709047 (14)	3.639	0.28	13.0
TR 321 A-4	*Neomiodon*			2948	0.709137 (9)	3.508	0.28	12.5
TR 321 A-5	*Neomiodon*			2554	0.709044 (10)	3.290	0.28	11.8
TR 321 A-6	*Neomiodon*				0.709068 (7)	3.986	0.28	14.2
TR 321 A-7	*Neomiodon*			2538	0.708581 (10)	2.971	0.28	10.6
TR 321 A-8	*Neomiodon*			2506	0.708985 (8)	3.477	0.28	12.4
TR 321 A-9	*Neomiodon*			3429	0.708959 (8)	3.987	0.28	14.2
TR 321 A-10	*Neomiodon*			2527	0.708682 (11)	3.048	0.28	10.9
TR 321 A-11	*Neomiodon*				0.708885 (14)	3.573	0.28	12.8
Bed 8								
TR 322 B	Unio	−0.97	1.55	1085	0.709962 (11)	1.373	0.20	6.9
TR 322 C	Unio	−0.98	1.34	2514	0.709513 (13)	3.052	0.20	15.3
TR 322 E	Unio	−0.22	2.13	1649	0.709860 (8)	2.115	0.20	10.6
TR 322 F	Unio	−1.26	2.01	2538	0.709465 (14)	3.042	0.20	15.2
TR 322 G	Unio	−0.29	1.89	2725	0.709490 (11)	3.257	0.20	16.3
TR 322 I	Unio	−1.31	2.05	1674	0.709960 (8)	2.032	0.20	10.2
TR 322 J	Unio	−0.37	1.79	1808	0.709617 (8)	2.296	0.20	11.5
TR 322 K	Unio	−0.67	1.74	1647	0.709537 (19)	2.078	0.20	10.4
Duntulm Forshore south section								
Bed 50–53								
TR 1138-1	*Praeexogyra*	−2.42	2.42	757	0.707223 (7)	0.904	0.12	7.5
TR 1138-2	*Praeexogyra*	−1.28	2.53	713	0.707221 (13)	0.822	0.12	6.9
TR 1138-4	*Praeexogyra*	0.66	3.39	826	0.707203 (9)	0.968	0.12	8.1
TR 1138-6	*Praeexogyra*	−0.64	2.10	603	0.707206 (6)	0.701	0.12	5.8
TR 1138-8	*Praeexogyra*	−1.20	1.94	644	0.707233 (9)	0.746	0.12	6.2
TR 1138-9	*Praeexogyra*	−2.88	2.10	871	0.707210 (8)	1.034	0.12	8.6
Lealt Shales Formation								
<u>Kildonnan Member, Kildonnan, Eigg (bed numbers from Hudson, 1997)</u>								
Bed 7b								
E 7-2	Unio	−2.97	−1.84	1092	0.709634 (13)	1.253	0.20	6.3
Bed 6f								
E 6–1.1	*Neomiodon*	−1.93	2.90		0.709931 (11)	3.152	0.28	11.3
E 6–1.2	*Neomiodon*				0.709954 (11)	2.895	0.28	10.3
E 6–1.3	*Neomiodon*				0.709941 (9)	3.582	0.28	12.8

(*Continued*)

TABLE 1. (*Continued*)

Sample	Taxon	$\delta^{18}O$ (PDB)	$\delta^{13}C$ (PDB)	Sr (ppm)	$^{87}Sr/^{86}Sr$	Sr/Ca (shell)	D_{Sr}[†]	Sr/Ca[†] (water)
Bed 6b								
E 5-1	*Tancredia*			3753	0.709389 (18)	4.413	0.28	15.8
E 5-2	*Tancredia*	−0.45	2.97	3627	0.709300 (15)	4.148	0.28	14.8
Bed 5e								
94E8-2	*Praemytilus*	−1.80	2.92	1917	0.710042 (8)	2.284	0.30	7.6
E 220 PR2	*Praemytilus*	−2.58	1.95	3834	0.710135 (8)	4.811	0.30	16.0
E 331	*Praemytilus*	−4.45	1.14		0.710142 (12)			
E 355	*Praemytilus*	−2.33	2.79	2353	0.710091 (13)	3.321	0.30	11.1
94E−7	*Praemytilus*	−1.81	2.54	1955	0.710026 (13)	2.661	0.30	8.9
E 218	*Praemytilus*	−4.78	0.85	4176	0.710122 (9)	5.696	0.30	19
Bed 3h								
E1-2	Unio	−2.12	−4.16	2727	0.710407 (16)	3.310	0.12	16.6
E329	Unio	−2.23	−2.70	2115	0.710523 (12)	2.498	0.12	12.5

[†]Estimated Sr distribution coeficients (D_{Sr}) were set: (1) to minimize the calculated Sr/Ca$_{water}$ compositions in *Praemytilus* and *Neomiodon*, (2) to maximize calculated Sr/Ca$_{water}$ compositions in oysters, and (3) to fall within the range of modern D_{Sr} for aragonite- and calcite-secreting molluscs (see text for details).
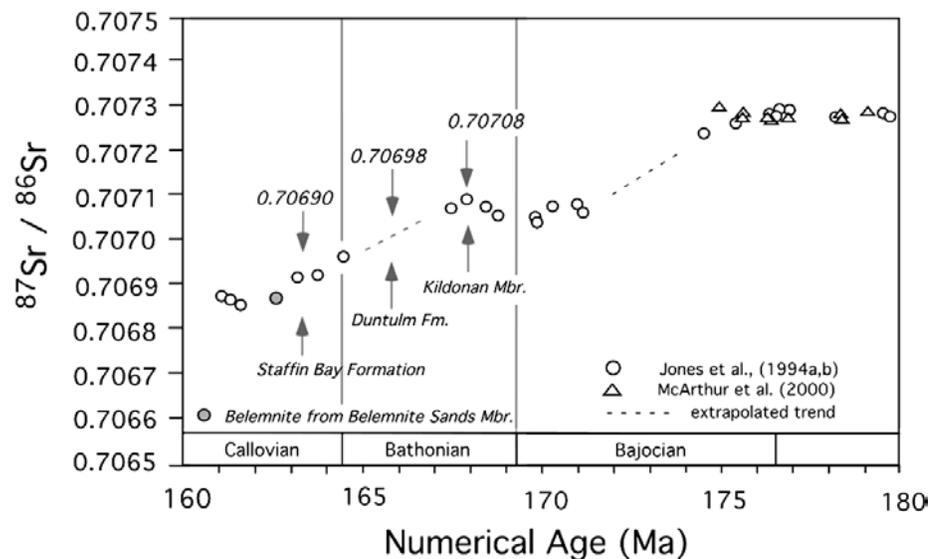

Figure 6. Strontium isotope evolution curve for Middle Jurassic seawater. A belemnite analyzed in this study from Belemnite Sands Member yielded 0.70688. This curve is used to determine $^{87}Sr/^{86}Sr$ ratio of seawater at time of deposition of Staffin Bay and Duntulm Formations and Kildonnan Member. Marine $^{87}Sr/^{86}Sr$ ratios are used as reference points for comparing molluscan $^{87}Sr/^{86}Sr$ ratios from Great Estuarine Group and for paleosalinity calculations based on Sr material balance considerations. Fm.—formation; Mbr.—member.

Praemytilus allows that this species was ecologically equivalent to the Chinese species *Modiolus yunnanensis* and possibly conspecific with it (cf. Hudson et al., 1995). As *Praemytilus* is unknown in Europe outside the Hebrides, no comparison can be made with the well-known faunas there. *Praemytilus* co-occurs with freshwater indicators such as *Botryococcus*, conchostracans, and *Viviparus* (though rarely with *Unio*), but also with molluscs generally regarded as near marine, including *Tancredia*, and with marine-derived microplankton (Hudson et al., 1995, Fig. 9). This indicates that a connection, however ten-

uous, existed at times between the Kildonnan lagoons and the sea. This is also required by Patterson's (1999) interpretation that stable isotopic compositions of otoliths from Bed 3g represent fish that were in part migratory. The results of Hudson et al. (1995) show a consistent co-occurrence of biota from a wide taxonomic range that is in line with expectations based on salinity control from modern and other fossil occurrences (e.g., Fürsich 1994), a fact that cannot be ignored. It is clear, however, that salinity variations within the lagoons were generated more by evaporation than by marine mixing. This is a significant result for

paleoecological studies that the response of the biota to evaporation-induced salinity variations simulated that expected from marine mixing, especially as the ionic proportions in the evaporated water need not have been the same as those in seawater.

Duntulm Formation; *Praeexogyra, Unio, Neomiodon*

The Duntulm Formation is interpreted as mainly marginal-marine, based on faunas dominated by the oyster *Praeexogyra hebridica*, with a brief freshwater intercalation marked by *Unio* and *Neomiodon* assemblages (Andrews and Walton, 1990; Fig. 5). We sampled one population of *Praeexogyra* from the most marine part of the section, with pectinid bivalves and serpulids as well as oysters (Beds 50–53, south Duntulm shore, Fig. 1), *Unio* and *Neomiodon* from the freshwater intercalation in Lon Ostatoin, and *Praeexogyra* from the overlying beds where marine influence is resumed (Bed 20 Lon Ostatoin). The most marine *Praeexogyra* population shows a narrow range of values (0.70720–0.70723) only slightly more radiogenic than late Bathonian seawater at 0.70698 (Fig. 6). The other *Praeexogyra* population is more radiogenic (0.70868–0.70875), suggesting greater freshwater input consistent with its position just above the freshwater intercalation. The freshwater intercalation contains specimens of *Unio* with radiogenic $^{87}Sr/^{86}Sr$ ratios up to 0.70996, similar to those from the upper part of the Kildonnan Member.

The oyster $\delta^{18}O$ values are relatively high with one specimen yielding +1.9‰ PDB, indicating evaporation of the original lagoonal waters. Hendry and Kalin (1997) also found *Praeexogyra* with high $\delta^{18}O$ values in correlative strata from England, which they attributed to evaporation effects. Stable isotope values in *Unio* from the freshwater intercalation are similar to the oysters (Table 1). This can be explained as a consequence of carbon and oxygen isotope exchange between the lagoons and the atmosphere as suggested above and by Tan and Hudson (1974). It is interesting to note that the evaporatively increased salinities in these lagoons must have remained less than a few permil within the salinity tolerance of *Unio*.

Neomiodon: Duntulm and Staffin Bay Formations

Specimens of *Neomiodon* from the Duntulm Formation (Bed 9) and Upper Ostrea Member of the Staffin Bay Formation (Beds
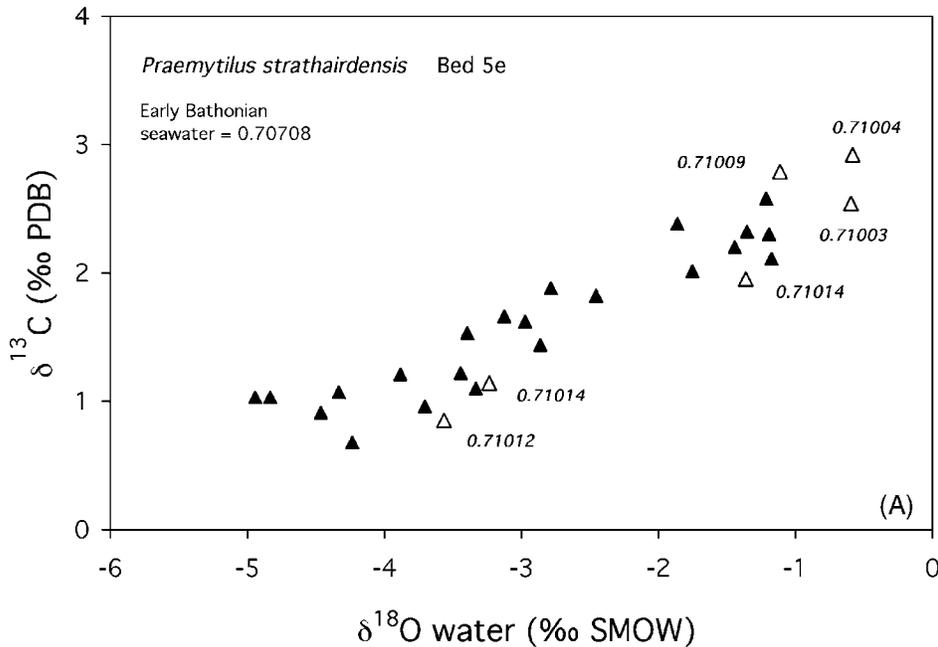
Figure 7. (A) Same covariant relationship between C and O isotopes in *Praemytilus* from Bed 5e as in Figure 3, with additional samples analyzed for [87]Sr/[86]Sr. Very radiogenic [87]Sr/[86]Sr ratios reveal negligible seawater contributions to depositional waters represented by Bed 5e, contrary to interpretation of estuarine-style mixing made on the basis of stable isotope data. Alternatively, we interpret seawater-like δ^{18}O values in *Praemytilus* to reflect various degrees of evaporation of a freshwater-dominated lagoon, and correlation with δ^{13}C to reflect increased CO_2 exchange between atmosphere and lagoon during desiccation of lagoon. During wet season, flooding lowers δ^{18}O values of lagoons and decreases δ^{13}C due to increased inputs of oxidized organic carbon from peripheral marsh runoff. (B) Similar covariant relationship between δ^{18}O and δ^{13}C in oyster *Praeexogyra* from Beds 50–53 and 20 of Duntulm Formation. High δ^{18}O values clearly indicate evaporation effects.

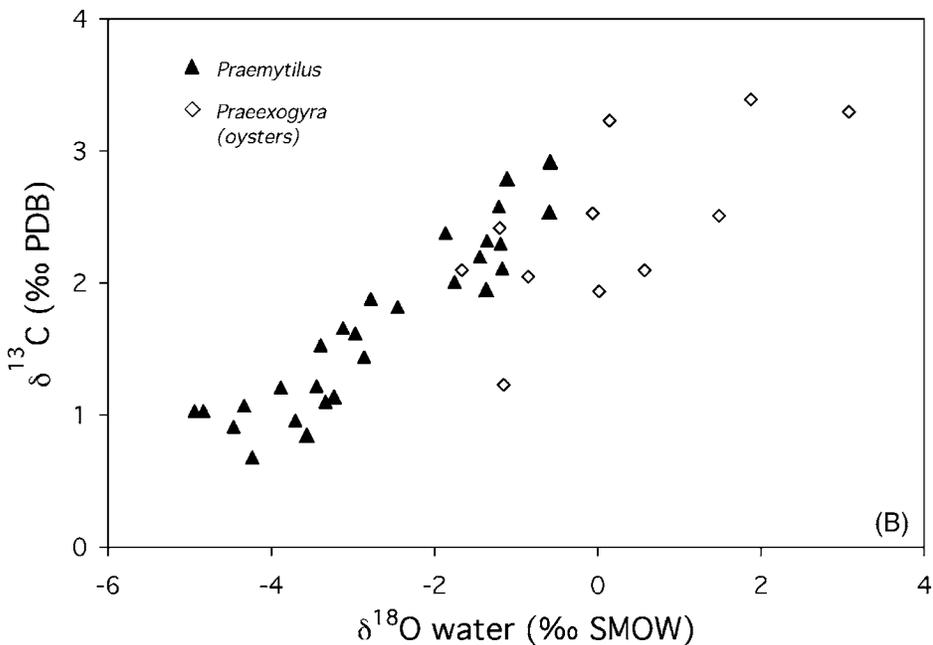**Figure 7. (*Continued.*)**

UO5b, 5c) are also radiogenic but display a strong correlation between [87]Sr/[86]Sr and Ca/Sr ratio (Fig. 9A).

The Staffin Bay Formation represents the beginning of a return to fully marine conditions after the regressive upper part of the Great Estuarine Group. The Upper Ostrea Member is interpreted as lagoonal but with greater connection to the open sea than in the Great Estuarine Group (Hudson and Trewin, 2003). The shell-beds containing *Neomiodon* were sampled close to the upper contact with the Belemnite Sands Member (Fig. 2). Thus far, the [87]Sr/[86]Sr and Sr/Ca ratios of all *Neomiodon* sampled indicate seawater-freshwater mixing with the freshwater input dominant, as detailed below. They are in good agreement with previous inference that *Neomiodon* was one of the more freshwater-tolerant members of the brackish molluscan fauna in the Great Estuarine Group.

Sr/Ca RATIOS IN MOLLUSCAN SHELLS, PALEO–LAGOONS, AND THE JURASSIC OCEAN

Further insights into the paleohydrology of the Great Estuarine Group lagoons may be gleaned from the Sr/Ca ratios in the molluscan shells. The interpretation of these ratios is less straightforward than for the [87]Sr/[86]Sr ratios because the distribution coefficient (D_{Sr}) that relates the shell Sr/Ca ratio to the Sr/Ca ratio in the original habitat waters, defined as

$$D_{Sr} = \frac{\left(\dfrac{Sr}{Ca}\right)_{shell}}{\left(\dfrac{Sr}{Ca}\right)_{water}} \qquad (1)$$

is influenced by mineralogy, physiology, temperature, growth rate and ontogeny, some of which are not easily constrained. Based on a literature survey, we have determined that D_{Sr} values for molluscs may be accommodated by the following means and ranges: 0.24 ± 0.07 for aragonite and 0.16 ± 0.04 for calcite (Thompson and Chow, 1955; Odum, 1951; Odum, 1957b; Turekian and Armstrong, 1960; Rucker and Valentine, 1961; Lerman, 1965; Faure et al., 1967; Thompson and Bowen, 1969; Bender et al., 1975; Buchardt and Fritz, 1978; Lorens and Bender, 1980; Dodd and Crisp, 1982; Graham et al., 1982; Rosenthal and Katz, 1989; Palacios et al., 1994; Klein et al., 1996; Purton et al., 1999).

One modern molluscan group, the cephalopods, does not fit into the above range for aragonite-secreting organisms, as cephalopods

tend to have higher Sr/Ca ratios and therefore higher inferred D_{Sr} values (Mann, 1992). It is not known whether this pattern extends to the extinct, calcite-secreting belemnites, but our analysis below suggests that it may.

Kildonnan Member

We have established from the rather uniform and radiogenic $^{87}Sr/^{86}Sr$ ratios within the Bed 5e lagoon that the hydrodynamic setting of the Kildonnan Member was dominated by freshwater inflow with negligible seawater mixing and that positively correlated variations of $\delta^{18}O$ and $\delta^{13}C$ in *Praemytilus* were caused by changes in the lagoonal water balance driven by evaporation, precipitation, and local runoff.

Other notable features of the strontium systematics in *Praemytilus* are their relatively high and widely ranging Sr/Ca shell ratios (2.3–5.7) and a negative covariant relationship between Sr/Ca and $\delta^{18}O$ (Fig. 8A). Sr/Ca ratios up to 3.3 were also obtained from analyses of *Unio* in Bed 3h and even higher ratios from *Tancredia* in Bed 6b (Table 1). Knowing that molluscs discriminate against Sr during calcification, it would appear that for Bed 5e, and probably other parts of the Kildonnan succession, depositional waters had Sr/Ca ratios ranging from 6.0 to 19.0 (using $D_{Sr} = 0.3$). Although unusual, this is not an unprecedented feature of the distribution of Sr/Ca ratios in modern rivers and lakes. Holmden et al. (1997a) compiled riverine and lake Sr and Ca data from the literature but only considered surface waters with concentrations of less than 1 ppm and 30 ppm, respectively, graphically determining a median Sr/Ca for world lakes and rivers of 2.3. Skougstad and Horr (1963) reported high Sr/Ca ratios in rivers draining the arid southwestern regions of the United States (6.5–16.0), emphasizing that climate, in addition to bedrock type, is an important determinant of the Sr/Ca ratio in continental freshwaters. Dry climate rivers also have higher total dissolved solids than the riverine world average (Sr = 0.071 ppm and Ca = 19.65 ppm; cf. Holmden et al., 1997a), with Sr and Ca concentrations of ~0.9 ± 0.5 and 55 ± 15 ppm, respectively (n = 11; Skoug-stad and Horr, 1963). The relationship between aridity and high Sr/Ca ratios in continental freshwaters was also noted by Odum (1957a, 1957b). Although neither author provided a detailed mechanism to explain the relationship between dry climate and high Sr/Ca ratios in rivers, calcite precipitation in the riverine watershed is likely the main contributing factor. In addition, the water budget for rivers
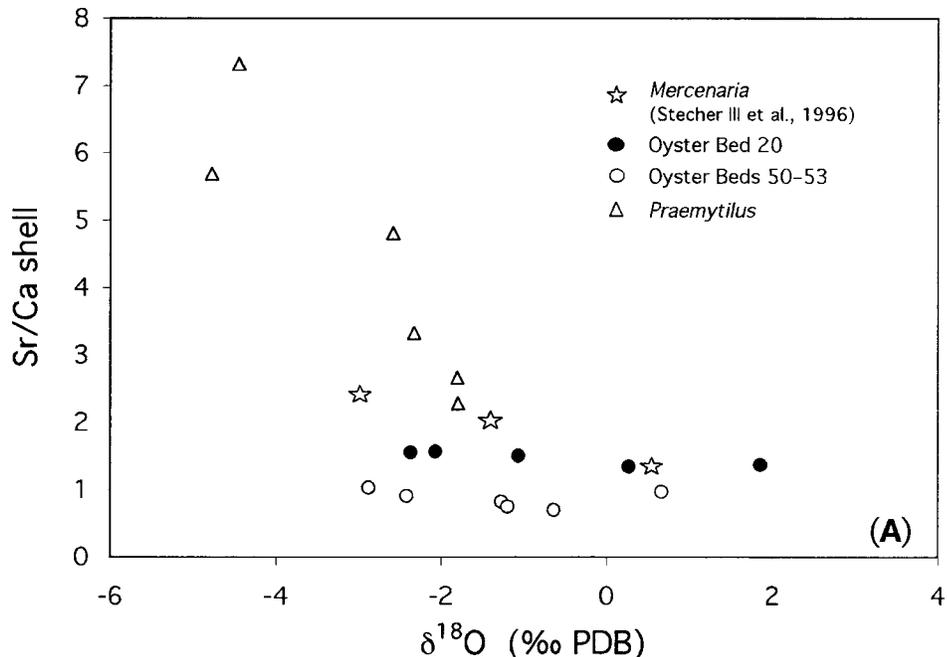

Figure 8. (A) Negative covariant relationship between Sr/Ca and ^{18}O in *Praemytilus* from Kildonnan Member and *Praeexogyra* (oysters) from Duntulm Formation. Range in oyster Sr/Ca and $\delta^{18}O$ is small enough that it could be explained by a temperature effect, as in modern mollusc *Mercenaria mercenaria* (Stecher III et al., 1996), which records sinusoidal variations in Sr/Ca and $\delta^{18}O$ within a single shell: high Sr/C, low $\delta^{18}O$ values in summer months and low Sr/Ca, high $\delta^{18}O$ values in winter months. Three points taken from summer and winter extrema in *Mercenaria mercenaria* time series are shown for comparison. By analogy, if temperature caused negative covariant relationship between Sr/Ca and $\delta^{18}O$ in Great Estuarine Group oysters, analyzed fragments of individual oysters could represent different seasons of growth and, therefore, different Sr/Ca and $\delta^{18}O$ values. This is not our preferred interpretation because pattern displayed by *Mercenaria mercenaria* is not universally observed in molluscs and does not explain covariance with $\delta^{13}C$ (especially large in *Praemytilus*). Furthermore, $\delta^{18}O$ variance in *Praemytilus* (4‰) is too large to be explained by environmental temperature change alone (~16 °C). (B) A hydrodynamic explanation for observed negative covariance between Sr/Ca and $\delta^{18}O$ involves cyclic seasonal aridity and flooding affecting lagoon and peripheral marsh environment. Sr/Ca shell ratios have been converted to Sr/Ca water ratios using D_{Sr} of 0.12 for *Praeeoxgyra* (circles) and 0.30 for *Praemytilus* (triangles). During dry summer, main lagoon is cut–off from peripheral (algal) marsh. During this time, calcite precipitation in algal marsh drives Sr/Ca upward. In following wet season, increased precipitation causes algal marsh to flood, forcing marsh runoff with low $\delta^{18}O$ values and high Sr/Ca ratios into lagoon. In this way, the lagoon's Sr/Ca ratio increases with time. Although this process occurs in numerous seasonal steps, it can be modeled as a single (time-integrated) step involving mixing between a wet-season algal marsh water source with low $\delta^{18}O$ values and high Sr/Ca ratios and a dry-season lagoonal water source with higher $\delta^{18}O$ values and lower Sr/Ca. Initial Sr content of each oyster lagoon is fixed by paleosalinities determined from Sr material balance calculations. Reasonably good fit between calculated curves and Sr/Ca and $\delta^{18}O$ data show that model parameters used in Sr material balance calculations are consistent with paleohydrological model of a restricted lagoon. Symbols are same as in Figure 8A.

in arid environments may include larger contributions from groundwaters, which are generally higher in solute concentration and Sr/Ca ratio than surface waters (Odum, 1957a). The occurrence of pseudomorphs after gypsum in the stromatolite that caps the Kildon-nan Member is strong evidence that evaporation affected the Kildonnan Member lagoons (Fig. 3; Hudson, 1970).

One explanation for the negative covariant relationship between Sr/Ca and $\delta^{18}O$ is that the lagoons became hydrologically restricted as a
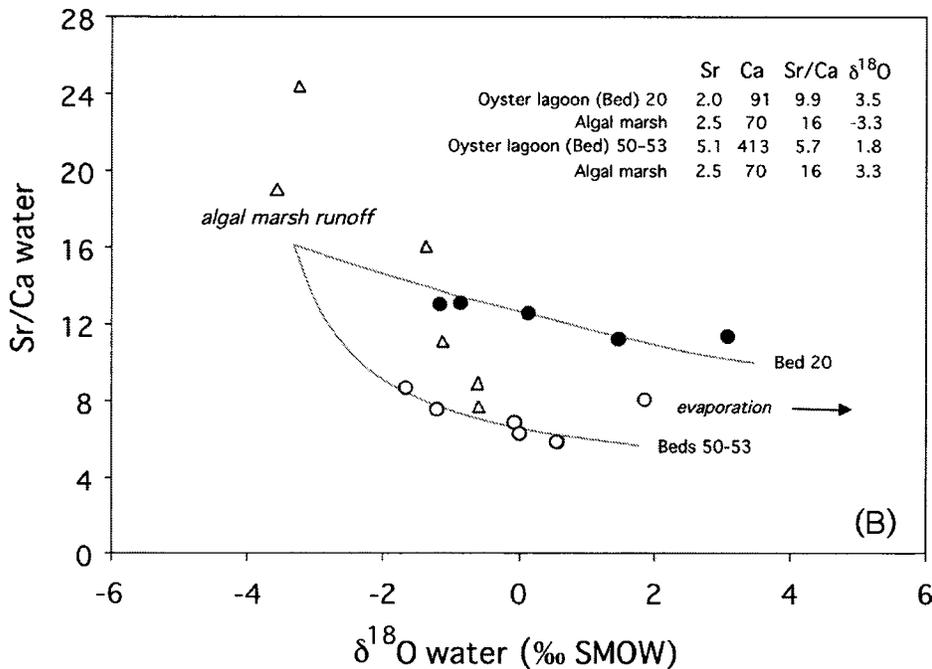
	Sr	Ca	Sr/Ca	$\delta^{18}O$
Oyster lagoon (Bed) 20	2.0	91	9.9	3.5
Algal marsh	2.5	70	16	-3.3
Oyster lagoon (Bed) 50-53	5.1	413	5.7	1.8
Algal marsh	2.5	70	16	3.3

Figure 8. (*Continued.*)

result of evaporative water loss and carbonate precipitation drove lagoonal Sr/Ca ratios to higher values without changing the $^{87}Sr/^{86}Sr$ ratio. This is unlikely, because closed-basin evolution of the lagoons would yield a positive covariance between Sr/Ca and $\delta^{18}O$, not the negative covariance recorded in the molluscs. The oyster *Praeexogyra* from the Duntulm Formation also exhibits a negative covariant trend between $\delta^{18}O$ and Sr/Ca (Fig. 8, A and B). These additional data will be presented before the potential significance of this relationship is discussed further.

Duntulm Formation

We have established from the $^{87}Sr/^{86}Sr$ data that the oyster *Praeexogyra* inhabited lagoonal waters with a significant fraction of seawater-derived strontium, consistent with paleoecology, but without evidence for dynamic seawater-freshwater mixing. Strontium in *Unio* from the freshwater intercalation is substantially more radiogenic, consistent with a freshwater habitat. Values of $\delta^{18}O$ and $\delta^{13}C$ indicate evaporation, as for the Kildonnan Member.

In common with *Praemytilus*, the oyster Sr/Ca ratios exhibit a negative covariant trend between $\delta^{18}O$ and Sr/Ca with little variation in $^{87}Sr/^{86}Sr$ ratio (Fig. 8, A and B). The observed covariance is stronger than in *Praemytilus*, but the Sr/Ca ratios span a narrower range of values. The negative covariant trend is observed

in different species from different stratigraphic levels in the Great Estuarine Group, and sampling of the shell fragments was performed without consideration of the shell growth stage; thus, we view the negative covariant trend between $\delta^{18}O$ and Sr/Ca as a time-integrated record of potential environmental or hydrodynamic change in the lagoons recorded amongst several generations of shells.

Earlier, we ruled out temperature as the main environmental factor influencing shell $\delta^{18}O$ values on the basis that $\delta^{18}O$ variance in *Praemytilus* was too large and too well correlated with $\delta^{13}C$. But temperature is known to produce negative covariant seasonal trends between Sr/Ca and $\delta^{18}O$ in some modern molluscan species. For example, inversely correlated sinusoidal variations between Sr/Ca and $\delta^{18}O$ are found in single specimens of the modern bivalve *Mercenaria mercenaria* (Stecher III et al., 1996) and the gastropod *Clavilithes macrospira* (Purton et al., 1999). Calcification in summer imparts a low $\delta^{18}O$ signature to molluscan shell, reflecting higher lagoonal water temperatures and higher Sr/Ca, which suggests either a fundamental temperature dependence on the value for D_{Sr}, or a temperature influenced change in kinetic factors like growth rate or metabolic efficiency (Klein et al., 1996). Two data points from the *Mercenaria mercenaria* time–series that represent the magnitude of summer and winter extrema in Sr/Ca and $\delta^{18}O$ are plotted in Figure 8A. The slope of the resulting trend is sim-

ilar to that observed in *Praeexogyra* from the Duntulm Formation, but is too shallow to explain the Sr/Ca variance in *Praemytilus* from the Kildonnan Member.

Although temperature and related metabolic effects should always be borne in mind, it seems unlikely that environmental temperature would be the main controlling influence on Sr/Ca and $\delta^{18}O$ variations in shallow, salinity stressed lagoons. Hendry et al. (2001) addressed this issue in their $\delta^{18}O$ and $\delta^{13}C$ and trace element (Sr, Mg, Ba) time-series study of the aragonitic bivalve *Isognomon* from the Brora Coal Formation (Middle Jurassic, northeast Scotland). Depositional and hydrological features of the lagoonal facies, including evidence for salinity variation, hydrological restriction, and high evaporation rates are similar to the Great Estuarine Group. The high Sr/Ca ratios inferred for the waters of Brora lagoon (7–17 for $D_{Sr} = 0.3$) and the lack of a strong temperature signal in the $\delta^{18}O$ time-series are significant to the present study. Hendry et al. (2001) argued that the Mg/Ca ratio in *Isognomon* records the changing water temperature of the lagoon, and it is significant that Sr/Ca does not track Mg/Ca or $\delta^{18}O$. Accordingly, we consider it unlikely that the wide range in Sr/Ca ratios displayed by the Great Estuarine Group molluscs is a temperature effect.

A hydrodynamic explanation for the negative covariant trend between Sr/Ca and $\delta^{18}O$ must be considered carefully because lagoonal $^{87}Sr/^{86}Sr$ ratios are uniform. If the observed lowering of molluscan $\delta^{18}O$ values represents dilution of the lagoon from increased freshwater inputs, the source of freshwater must have originated in large part from direct input of precipitation with low $\delta^{18}O$ (approx -7‰: cf. Marshall and Ashton, 1980; Hudson and Andrews, 1987). Precipitation contains negligible strontium and could account for changes in the $\delta^{18}O$ of the lagoons without affecting $^{87}Sr/^{86}Sr$. Local runoff from peripheral marsh environments is also a plausible mechanism if the marshes contained mostly recycled strontium from the lagoons. Therefore, we propose that the negative covariant trend between Sr/Ca and $\delta^{18}O$ and the positive covariant trend between $\delta^{18}O$ and $\delta^{13}C$ recorded in *Praemytilus* and *Praeexogyra* results from a seasonal flooding cycle between the main lagoon and a supratidal, peripheral, algal marsh environment.

A calcifying algal marsh facies with algal growth during wet spells and pseudomorphs after gypsum recording desiccation has been described by Andrews and Walton (1990) as surrounding the lagoonal facies in the Dun-

tulm Formation. During the dry season, the peripheral algal marshes became increasingly hydrologically restricted, and under these conditions carbonate precipitation (aided by desiccation of the marsh) caused the Sr/Ca ratio of residual marsh waters to increase to values higher than those of the main lagoon. Flooding during the wet season reestablished the hydrologic connection between the lagoon and marsh, pumping marsh waters with high Sr/Ca, low $\delta^{18}O$, and low $\delta^{13}C$ into the main lagoon. Strontium is recycled between the lagoon and peripheral marsh system, the $^{87}Sr/^{86}Sr$ ratio remains relatively uniform between them, and the spread in $\delta^{18}O$, and, thus, Sr/Ca ratio recorded between individual mollusks, represents a time-integrated record of seasonal changes in the hydrochemistry of the lagoon. The model further implies that the lagoons were nearly hydrologically closed to surface water inputs from both rivers and the marine realm over the lifetime of the lagoons, as recorded by shell beds of *Praeexogyra* and *Praemytilus*. The existence of repeatedly flooded peripheral marshes in the environmental setting of the Great Estuarine Group is consistent with sedimentological evidence for shallow lagoons with gently shelving and fluctuating shorelines and with the evidence of strong seasonality. The scenario for the Duntulm Formation is illustrated by Hudson and Trewin (2003, their Figs. 11–19).

Neomiodon and the Sr/Ca Ratio of Middle Jurassic Seawater

Unlike the other molluscs we studied, the small euryhaline bivalve *Neomiodon* appears to have inhabited the seawater-freshwater mixing zone. *Neomiodon* shells from the Duntulm and Staffin Bay formations were separated from three hand samples from three shell beds: one from the freshwater intercalation in the Duntulm Formation (Bed 9) and two in the Upper Ostrea Member, Staffin Bay Formation (Beds UO 5b, 5c) directly underlying the Belemnite Sands Member. Each shell bed defines a different correlated trend in $^{87}Sr/^{86}Sr$ and Ca/Sr ratio (Fig. 9A). All three trends converge at a low $^{87}Sr/^{86}Sr$ of ~0.7068, which is close to the composition of late Bathonian (~0.70698) to early Callovian (0.70690) seawater (Fig. 6; note that Ca/Sr is plotted rather than Sr/Ca because when the former is plotted against $^{87}Sr/^{86}Sr$, mixing lines are represented by straight lines). The correlative trends supply graphical evidence that *Neomiodon* inhabited the seawater-freshwater mixing zone. Convergence of the shell mixing lines at the seawater composition reflects the nearly con-
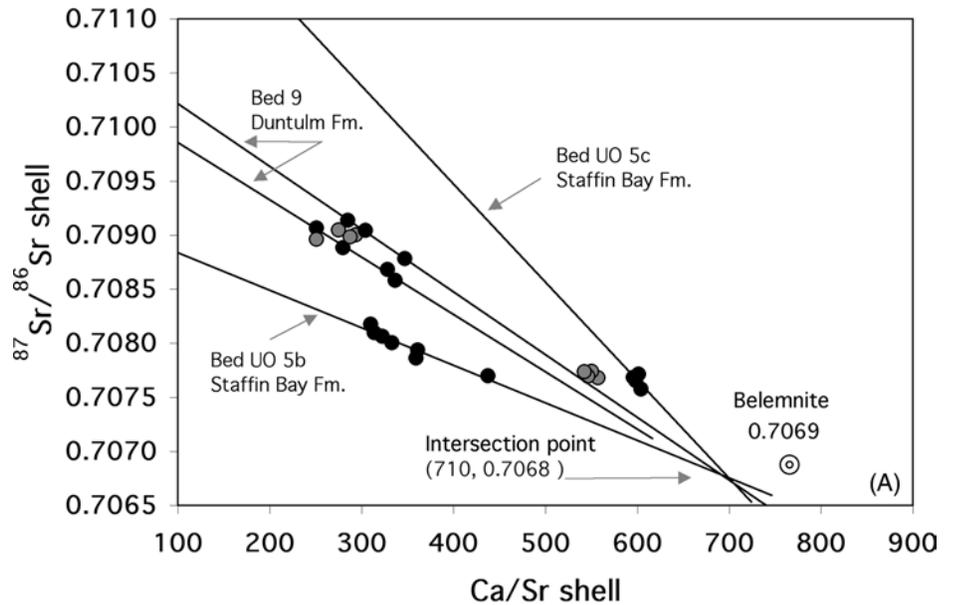

Figure 9. (A) Specimens of *Neomiodon* from two shell beds in Staffin Bay Formation (UO 5b, 5c) and one shell bed from Duntulm Formation (Bed 9) are sole molluscan fossils identified thus far in Great Estuarine Group that record dynamic (estuarine-type) seawater–freshwater mixing. This is indicated by correlation between $^{87}Sr/^{86}Sr$ and Ca/Sr in shells from each of three beds and convergence of resultant trend lines at $^{87}Sr/^{86}Sr$ ratio of ~0.7068, which is consistent with known early Callovian seawater composition of ~0.70690 (Fig. 6) and consistent with 0.70688 ratio of belemnite measured from Belemnite Sands Member (Table 1). To achieve maximum possible convergence of trend lines, samples shown in grey were not included in linear regressions. Negative slopes of mixing lines reveal freshwater end-member to have higher Sr/Ca ratio than seawater end-member. (B) Shell mixing lines are converted to water mixing lines using D_{Sr} values shown. To determine Sr/Ca ratio of Middle Jurassic seawater, a D_{Sr} for *Neomiodon* of 0.28 ± 0.3 is applied to best correlated mixing line (UO 5b), yielding a Sr/Ca of 5.4 ± 0.6 for early Callovian seawater.
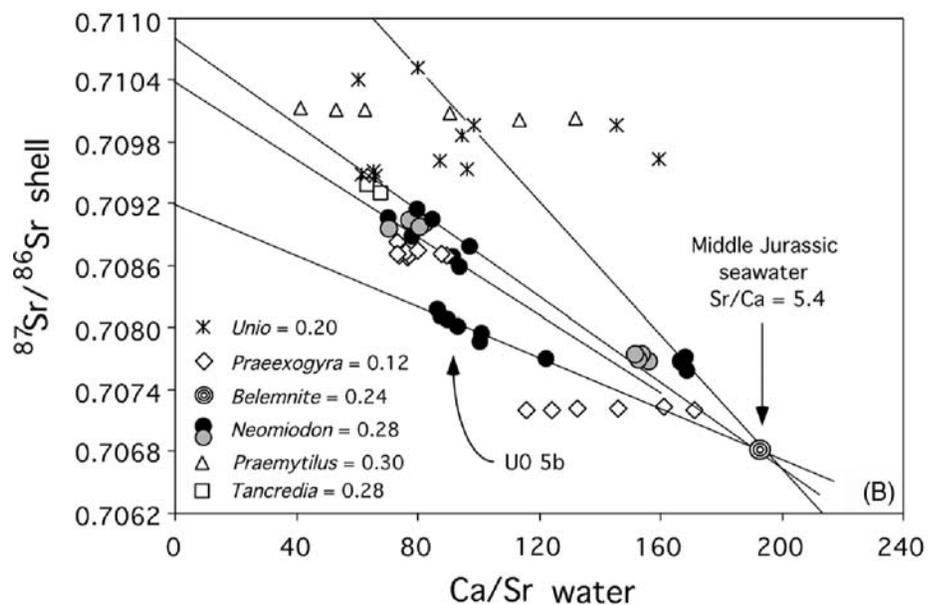

Figure 9. (*Continued.*)

stant $^{87}Sr/^{86}Sr$ of seawater over the depositional interval, and the different slopes of the shell mixing lines are caused by differences in freshwater $^{87}Sr/^{86}Sr$ or Sr/Ca input into each lagoon. The negative slopes of the mixing lines indicate that continental freshwaters discharging into the Great Estuarine Group lagoons had higher Sr/Ca ratios than Middle Jurassic seawater, which is indicative of at least a seasonally dry climate.

To achieve the best possible convergence of the *Neomiodon* mixing lines, some specimens were omitted from inclusion in the linear regressions. Specimens not included are shown using open symbols. For example, Ca/Sr ratios in specimens from Bed 9 of the Duntulm Formation can be divided into two subpopulations such that regression lines projected through the separated data will converge at the same composition. The existence of different subpopulations could reflect changing hydrodynamic conditions in the lagoons that took place while the shells were accumulating—specifically, a shift in the Sr/Ca ratio of the freshwater end-member or changing kinetic factors might have affected the magnitude of D_{Sr} in populations of *Neomiodon*.

The convergence of the *Neomiodon* mixing lines may be used to estimate the Sr/Ca ratio of Middle Jurassic seawater. This task is complicated by the fact that *Neomiodon* is extinct, and its correct D_{Sr} is unknown. To estimate D_{Sr} values in *Neomiodon* and the other molluscan taxa, we employed the $^{87}Sr/^{86}Sr$–Ca/Sr diagram and the following criteria: (1) D_{Sr} values must fall within the range of modern values for molluscs of calcite or aragonite mineralogy; (2) D_{Sr} values should be chosen that keep the Sr/Ca ratios for habitat waters less than ~16, in line with modern data from dry climate rivers; and (3) D_{Sr} values should be chosen to maximize the overlap of Sr/Ca ratios within the graphical field defined by the *Neomiodon* mixing lines on the $^{87}Sr/^{86}Sr$–Ca/Sr diagram. The results are shown in Figure 9B. *Praemytilus* is assigned the highest D_{Sr} value of 0.30, reflecting the fact that it has the highest Sr/Ca ratios, whereas *Unio* is assigned a D_{Sr} of 0.20 to overlap the field of the *Neomiodon* mixing lines. *Neomiodon* also exhibits high shell Sr/Ca ratios and should be assigned a relatively high D_{Sr} value. Consideration of the oyster data and criterion (3) yields additional constraints on the magnitude of this value. Oysters from Beds 50–53 have uniform $^{87}Sr/^{86}Sr$ ratios that are close to the seawater end-member but display a wide range in their Sr/Ca ratios. If the oysters are assigned a D_{Sr} of 0.12, which is the low end of the range for calcite-secreting molluscs ($0.12 < D_{Sr} < 0.20$),

then a relatively high D_{Sr} of 0.28 assigned to *Neomiodon* will position low Sr/Ca oysters from Beds 50–53 and 20 in the field defined by the *Neomiodon* mixing lines. We have chosen to focus on oysters with low Sr/Ca ratios because of the tendency for lagoonal Sr/Ca ratios to increase with time due to precipitation of molluscan shell material. Only in the event of massive dissolution of calcite or aragonite in the lagoon, or increased seawater input, will the lagoon Sr/Ca ratio decrease with time. The former event is unlikely, and the latter event will change the $^{87}Sr/^{86}Sr$ ratio of the oyster lagoons, which is not observed.

If the best-correlated mixing line from Bed UO 5b is used (samples TR638) along with the estimate of D_{Sr} given above, a Sr/Ca ratio of 5.4 is determined for early Callovian seawater. This dictates a D_{Sr} of 0.24 for belemnites because they are marine and must also fall on the seawater–freshwater mixing line. It is difficult to assess the magnitude of the uncertainty that should be attached to the deduced Sr/Ca ratio for Middle Jurassic seawater. The molluscan Sr/Ca ratios are very precise, but the D_{Sr} uncertainty limits the accuracy to which the Sr/Ca ratio of Middle Jurassic seawater can be known. For example, increasing the D_{Sr} for *Neomiodon* from 0.28 to 0.31 requires about the same D_{Sr} of 0.12 to keep the oysters with low Sr/Ca ratios in alignment with the *Neomiodon* mixing lines but increases the belemnite D_{Sr} to 0.26 and lowers the inferred Sr/Ca ratio of Jurassic seawater to 4.9. Alternatively, if the D_{Sr} for *Neomiodon* is lowered to 0.25, the required oyster D_{Sr} drops to 0.10, the belemnite D_{Sr} drops to 0.22, and the inferred Sr/Ca ratio of Jurassic seawater rises to 6.0. Any further decrease in the D_{Sr} of *Neomiodon* will drop the oyster D_{Sr} below 0.10, a value not commonly observed among modern calcite-secreting molluscs. Therefore, if the D_{Sr} of *Neomiodon* is considered to have an uncertainty of 0.28 ± 0.3, this yields a Sr/Ca ratio for middle Jurassic seawater of 5.4 ± 0.6, which is 40% lower than the present-day Sr/Ca ratio of seawater.

A lower Sr/Ca ratio for past seawater is consistent with Sr/Ca ratios measured in planktonic forams formed over the past 110 Ma, which show a decreasing trend reaching a value of 0.64 ± 0.13 in the early Cretaceous (Delaney and Boyle, 1986; Renard, 1986). Using a foraminiferal calcite D_{Sr} of 0.16 ± 0.2 (Graham et al., 1982), the Sr/Ca ratio of early Cretaceous seawater may have been as low as 2.8 or as high as 5.5. A problematic feature of the Sr/Ca secular curve is the potential for diagenetic loss of strontium in older forams to give a false indication of decreasing seawater

Sr/Ca with time. However, the low Sr/Ca of seawater in the Middle Jurassic deduced from our mixing zone strategy confirms that the seawater Sr/Ca ratio has changed through time, in accordance with the foraminiferal data, and that it was likely lower than today over much of the past 180 Ma. Variance in seawater Sr/Ca ratio has been linked to changing hydrothermal water fluxes through mid-ocean ridges, which are linked, in turn, to seafloor spreading rates, ocean ridge volume, and sea level (Graham et al., 1982; Renard, 1986; Delaney and Boyle, 1986). Hydrothermal circulation of seawater through mid-ocean ridges exchanges seawater Mg for basaltic Ca, which would lower the Sr/Ca of seawater during periods of high seafloor spreading. The impact of spreading rates on the hydrothermal Sr flux is less clear. The cycling of Sr in seawater is also influenced by the ratio of aragonite to calcite precipitation in the oceans and storage in sediments, which further complicates interpretations of a Sr/Ca secular curve.

$^{87}Sr/^{86}Sr$ PALEOSALINITY CALIBRATION

Despite the evidence that the Great Estuarine Group lagoons were subject to evaporative enrichment of dissolved salts, minimum paleosalinities based on the proportion of seawater entrained within the lagoons can be estimated by Sr material balance considerations. The accuracy of these calculations depends on correctly deducing the $^{87}Sr/^{86}Sr$ ratios and Sr concentrations of the marine and freshwater mixing end-members. This task is complicated by the fact that the seawater and freshwater compositions varied over the depositional interval. We use $^{87}Sr/^{86}Sr$ ratios in *Unio* from Bed 3h to set the freshwater input for the Kildonnan Member at 0.7105 and *Unio* from Bed 8 to set the freshwater input to the Duntulm Formation at between 0.7095 and 0.7099. For the three cases where we have observed a dynamic response to seawater–freshwater mixing in *Neomiodon*, the freshwater $^{87}Sr/^{86}Sr$ ratio is fixed by the equation for each mixing line using the model D_{Sr} of 0.28 and a Sr/Ca ratio for the freshwater end-member of 16. This approach yields freshwater compositions of 0.7084 and 0.7111 for lagoons represented by Beds UO 5b and 5c in the Staffin Bay Formation, and 0.7092 for the lagoon represented by Bed 9 in the Duntulm Formation. The latter result compares favorably with ratios 0.7095–0.7099 for *Unio* from the Duntulm Formation. Secular evolution of the seawater $^{87}Sr/^{86}Sr$ ratio was addressed earlier (Fig. 6), and specific ratios were assigned to the Kildonnan, Dun-

tulm, and Staffin Bay depositional intervals. The seawater Sr/Ca ratio is assumed to be constant at 5.4 over this period of time, and the low ratio indicates that either the Sr concentration of Jurassic seawater was lower than today or the Ca concentration was higher. For these calculations, we chose to split the difference, decreasing the Sr concentration from the modern seawater value of 7.8 ppm to a model Jurassic concentration of 6.37 ppm, and increasing the Ca concentration from the modern seawater value of 419 ppm to a model Jurassic concentration of 552 ppm. The model Sr concentration is taken to be 1.5 ppm for the freshwater end-member, which is near the high end of the modern range of concentrations for rivers draining the arid southwestern United States (Skougstad and Horr, 1963). A high Sr-concentration for the riverine end-member maximizes the calculated seawater proportions in the lagoons. The model parameters are summarized in Table DR1[1], and the appropriate isotope material balance equation is:

$$
\left(\frac{^{87}Sr}{^{86}Sr}\right)_{bw} = \frac{Sr_{sw}Sr_{fw}\left[\left(\frac{^{87}Sr}{^{86}Sr}\right)_{fw} - \left(\frac{^{87}Sr}{^{86}Sr}\right)_{sw}\right]}{Sr_{bw}(Sr_{sw} - Sr_{fw})}
$$
$$
+ \frac{Sr_{sw}\left(\frac{^{87}Sr}{^{86}Sr}\right)_{sw} - Sr_{fw}\left(\frac{^{87}Sr}{^{86}Sr}\right)_{fw}}{Sr_{sw} - Sr_{fw}}
$$

(2)

where sw, fw and bw represent seawater, freshwater, and brackish water compositions, respectively. An equation giving the proportion of seawater, x, in the brackish lagoon is:

$$
x = \left\{ Sr_{fw}\left[\left(\frac{^{87}Sr}{^{86}Sr}\right)_{bw} - \left(\frac{^{87}Sr}{^{86}Sr}\right)_{fw}\right]\right\}
$$
$$
\div \left\{ Sr_{sw}\left[\left(\frac{^{87}Sr}{^{86}Sr}\right)_{sw} - \left(\frac{^{87}Sr}{^{86}Sr}\right)_{bw}\right]\right.
$$
$$
\left. + Sr_{fw}\left[\left(\frac{^{87}Sr}{^{86}Sr}\right)_{bw} - \left(\frac{^{87}Sr}{^{86}Sr}\right)_{fw}\right]\right\}
$$
(3)

which may be converted to paleosalinity if it is assumed that Jurassic seawater had a salinity of 35‰. Paleosalinities are shown in Figures 4 and 5 relative to stratigraphic position

TABLE 2. CALCULATED MINIMUM PALEOSALINITY RANGES FOR GREAT ESTUARINE GROUP MOLLUSCS BASED ON PROPORTION OF SEAWATER DERIVED Sr IN GREAT ESTUARINE GROUP SHELLS

Salinity (‰)	Species				
	Unio	Praemytilus	Tancredia	Neomiodon	Oyster
28					
27					
26					D
25					
24					
23					
22					
21					
20				UO 5c	
19				UO 5c	
18				UO 5c	
17				UO 5c	
16					
15					
14					
13					
12					
11					
10					
9					
8					
7					
6				UO 5b, D	
5				UO 5b, D	D
4			K	UO 5b, D	D
3	K			UO 5b, D	D
2	D, K			UO 5b, K	D
1	D, K	K		UO 5b	
0	D , K				

Note: K—Kildonnan Member; D—Duntulm Fm.; UO 5b and 5c—Staffin Bay Fm.

for the Kildonnan Member and Duntulm Formation, and taxon specific paleosalinity ranges are given in Table 2. The Sr material balance calculations show that *Unio*, *Praemytilus*, *Neomiodon*, and *Tancredia* from the Kildonnan member of the Great Estuarine Group inhabited lagoonal waters with small to negligible amounts of seawater-derived strontium (0–10%) yielding relative paleosalinities of 0–4‰. The most surprising result is *Praemytilus* from Bed 5e, which yielded paleosalinities of up to 34‰ using an oxygen isotope calibration (Fig. 3) (Hudson et al., 1995) but only 1–2‰ salinity based on strontium isotopes. The highest seawater proportions of 75%, were found in oysters from the Duntulm Formation, yielding 26‰ for the relative paleosalinity in the lagoon represented by Beds 50–53. Much lower seawater proportions of 15% were determined in oysters for the lagoon represented by Bed 20, yielding a paleosalinity of ~2–5‰, depending on whether 0.7095 or 0.7099 is used as the freshwater end-member (Table DR1). *Neomiodon* from Bed 9 of the Duntulm Formation, which exhibits ⁸⁷Sr/⁸⁶Sr and Sr/Ca evidence for a dynamic response to seawater–freshwater mixing, yields lagoonal seawater proportions of between 8 and 17%, which gives paleosalinities of 3 to 6‰. *Neomiodon* from the Upper Ostrea Member, Bed UO 5b,

yielded lagoonal seawater proportions of 4 to 17%, with paleosalinities from 1 to 6‰, and *Neomiodon* from Bed UO 5c, immediately below the marine Belemnite Sands Member, yielded lagoonal seawater proportions of 48 to 55%, for a relative paleosalinity range of ~17 to 20‰. The paleosalinities for the lagoon represented by Bed UO 5c may be too high. The steepness of the slope of this mixing line, in conjunction with our assumption that the maximum Sr/Ca ratio in the freshwater end-member is 16, results in a relatively high freshwater ⁸⁷Sr/⁸⁶Sr of 0.7111. If the freshwater ⁸⁷Sr/⁸⁶Sr ratios obtained from the *Neomiodon* mixing relations are averaged, yielding 0.7097, the resulting paleosalinities would be slightly lower at 12–16‰.

Using the seawater proportions determined for the oyster lagoons of the Duntulm Formation, we revisit the proposed hydrodynamic origin of the negative covariant trend between Sr/Ca and δ¹⁸O in *Praeexogyra* to test whether the observed trend can be reproduced by mixing lagoonal waters with peripheral, algal marsh runoff. To do this we assume that molluscan Sr/Ca and δ¹⁸O data represent simple two-component mixing between a lagoon with low Sr/Ca and high δ¹⁸O (summer composition) and a peripheral algal marsh with high Sr/Ca and low δ¹⁸O (winter composition).

Thus, we approach quantification of the lagoonal system as if the observed trend developed over one seasonal cycle. Model parameters for the two oyster lagoons (Beds 20 and 50–53) are shown in Figure 8B. The evaporated lagoonal end-member is assumed to have an initial Sr concentration and Sr/Ca ratio given by the Sr material balance calculations performed for the estimations above; these are listed in Table DR1. For example, the lagoon represented by Beds 50–53 is composed of 75% seawater (with Sr/Ca of 5.4 and a model Sr concentration of 6.37 ppm) and 25% freshwater (with Sr/Ca of 16 and model Sr concentration of 1.5 ppm), which yields a lagoonal Sr/Ca ratio of 5.7, and Sr concentration of 5.1 ppm, which we set as the dry-season, lagoonal end-member. The wet-season, flooded algal marsh end-member is assumed to have a Sr/Ca of 16, similar to *Unio* from the Kildonnan Member. $\delta^{18}O$ values for the lagoon in the dry season, and the algal marsh in the wet-season, are set close to the maximum and minimum $\delta^{18}O$ values for each of the oyster data sets. Using these model parameters, and assuming a D_{Sr} of 0.12 for oysters, curves are fit to the oyster data (Fig. 8B). Despite the large number of assumptions, the results are reasonable and consistent with our knowledge of the paleohydrology and depositional setting. During the dry season, $\delta^{18}O$ values for the oyster lagoons range from 2.5‰ to 4.0‰ (SMOW), and in the wet season the flooded peripheral marsh water is about 3‰ (SMOW).

Interestingly, the model Sr concentration for the peripheral marsh waters is determined to be ~2.5 ppm, which is higher than the 1.5 ppm concentration used to determine the model paleosalinities. In making the paleosalinity calculations, however, we have assumed that the freshwater end-member was riverine, taking the 1.5 ppm concentration from modern dry climate rivers (Skougstad and Horr, 1963). The above result highlights the possibility that in many Great Estuarine Group lagoons, freshwater was not directly input from rivers, but was first processed in peripheral algal marsh environments or restricted freshwater lagoons analogous to the Florida Everglades. In such environments, the Sr/Ca ratio is increased by precipitation of calcite and aragonite. Increasing the Sr concentration of the freshwater end-member from 1.5 ppm to 2.5 ppm has a relatively small effect on the model salinities, however; for example, paleosalinities of 29‰ instead of 26‰ are found for oysters from Beds 50–53.

CONCLUSIONS

It has been demonstrated that molluscan $^{87}Sr/^{86}Sr$ ratios coupled with Sr material balance calculations can be used to infer the proportion of seawater-derived Sr in Great Estuarine Group and Staffin Bay lagoons, which can then be converted to relative paleosalinities. The inferred paleosalinities are much lower than previously postulated, especially for *Praemytilus* and *Tancredia* from the Kildonnan Member. This requires that the Great Estuarine Group lagoons were more isolated from the sea than in previous interpretations and were subject to considerable, periodic evaporation of a predominantly freshwater inflow for the Kildonnan Member and a partly marine inflow for the oyster-bearing part of the Duntulm Formation. True paleosalinities must also take into account evaporative concentration of solutes, which may have been substantial in shallower lagoons inshore from the sea. Although evaporation effects can be inferred from $\delta^{18}O$ values in the molluscs, especially the oysters, it is difficult to quantify the magnitude of the effect because $\delta^{18}O$ in evaporating water tends to reach an isotopic steady state with respect to relative humidity and the isotopic composition of humidity independent of the paleosalinity of the residual evaporated water (cf. Hendry and Kalin, 1997).

An important feature of the Duntulm Formation oyster lagoons and the Kildonnan Member *Praemytilus* lagoons is the uniformity of $^{87}Sr/^{86}Sr$ within single shell beds. This is striking in light of the fact that marine and freshwater end-members have contrasting $^{87}Sr/^{86}Sr$ ratios and emphasizes the isolation of many of the lagoons from fresh or marine inflows over the time represented by the accumulation of a shell bed. Although lagoonal hydrodynamics are restrictive, we suggest that the $\delta^{18}O$ and Sr/Ca systematics of the fossils may be reconciled with seasonal or supraseasonal changes in local water balances in the lagoons that are driven by cycles of aridity and humidity.

Evidence for a dynamic response to seawater–freshwater mixing has been found only in specimens of the bivalve *Neomiodon* from the Staffin Bay Formation and Duntulm Formations. The differing habitats deduced for *Neomiodon* and *Praemytilus* may help to solve a long-standing puzzle as to why these two bivalves, both previously interpreted as low-salinity and euryhaline, are rarely found in the same bed. The data presented here suggest that only *Neomiodon* is truly euryhaline. The dynamic seawater–freshwater mixing trajec-tories recorded in the $^{87}Sr/^{86}Sr$–Ca/Sr systematics of *Neomiodon* indicate that the Great Estuarine Group lagoons had Sr/Ca ratios higher than those of contemporaneous late Bathonian to early Callovian seawater. Assuming that the D_{Sr} values deduced for *Neomiodon* and the other fossil taxa are correct, we have pegged the Sr/Ca ratio for late Bathonian to early Callovian seawater at 5.4 with a nominal uncertainty of ± 0.6. This is much lower than the present-day seawater ratio of 8.5, but it is consistent with the overall decreasing trend in the Sr/Ca ratio of seawater back to the Mesozoic inferred from Sr/Ca ratios in foraminifera from deep ocean sediments.

Our interpretation of the isotopic data and the high Sr/Ca ratios inferred for Great Estuarine Group lagoons is consistent with a dry coastal climate for the Bathonian of Britain, possibly of Mediterranean type. Tree-ring analysis of fossil woods supports this assertion: false tree rings indicative of environmental water stress during tree growth increase in frequency toward the British Middle Jurassic, culminating in the Bathonian, at the time of Great Estuarine Group deposition (Morgans, 1999). Gypsum moulds, typical of arid conditions, are also found at two horizons (Hudson, 1970). The high $\delta^{18}O$ values in some Great Estuarine Group molluscs are attributed to evaporative enrichment of $H_2^{18}O$ in Bathonian lagoons (Hendry and Kalin, 1997), and the high Sr/Ca ratios are indicative of carbonate precipitation in the lagoons and lagoonal watershed owing to the seasonally dry climate. Although we have emphasized aridity in explaining the $\delta^{18}O$ and Sr/Ca results, substantial precipitation in the hinterland is required to initiate and maintain the near-freshwater status of many of the Great Estuarine Group lagoons, notably in the Kildonnan Member, and to account for the voluminous sands episodically delivered to the basin during the Bathonian (Harris, 1989, 1992). These empirical data on Jurassic paleoenvironments can be compared to climate modeling results. Recent accounts by Sellwood et al. (2000) on the late Jurassic and Bjerrum et al. (2000) on the early Jurassic take somewhat different approaches and bracket the time period we studied. Both studies suggest strongly seasonal Jurassic climates, with temperatures ranging from the mid-20 °C in the summer to 10 °C in the winter; summers were dry and winters wet, with moisture excess leading to strong winter run-off, especially to the north of the study area in Scandinavia and Greenland.

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