Oldest isotopically characterized fish otoliths provide insight to Jurassic continental climate of Europe

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ABSTRACT

Large, shallow, epeiric seas and adjacent lagoons such as those described herein likely played a significant role in moderating Jurassic coastal and continental climate. Jurassic (Bathonian) ocean surface temperatures in Scotland have been calculated from $\delta^{18}O_{(CaCO_3)}$ values of a suite of the oldest well-preserved fish otoliths analyzed to date. Otolith $\delta^{18}O$ values range from –4.7‰ to –1.9‰ (Vienna Peedee belemnite, VPDB), while $\delta^{13}C_{(CaCO_3)}$ values vary from –5.4‰ to +1.5‰ (VPDB), representing the oldest stable isotopic record of paleodiet, paleoecology, and fish migration to date. Using a global ocean $\delta^{18}O_{(H_2O)}$ value of –1.0‰ (Vienna standard mean ocean water, VSMOW) for an ice-free Jurassic, fish species that migrated from estuarine to open marine water record time-averaged temperatures of 23 °C. Estuarine fish, assuming a similar temperature, record variation in $\delta^{18}O_{(H_2O)}$ values from –3.7‰ to –2.0‰ (VSMOW). That significant mixing of fresh water and seawater occurred in the Jurassic in Scotland is in general agreement with data presented by others (molluscan fauna, lithostratigraphy, paleogeography, and paleocirculation models). The $\delta^{18}O$ values and temperatures derived in this study correspond to the meteorologic and hydrologic parameters of a mid-latitude maritime climate with low seasonality, a mean temperature of 23 °C, and abundant precipitation and humidity. The $\delta^{18}O_{(H_2O)}$ values calculated from estuarine fish indicate that rainfall must have a $\delta^{18}O_{(H_2O)}$ value lower than –3.7‰ (VSMOW). Values of $\delta^{18}O$ and $\delta^{13}C$ suggest an environment hydrologically similar to that observed in the Everglades of south Florida or the estuaries of south Texas, both notable fish nurseries today. However, sea-surface temperatures were lower than those of modern Florida or Texas as evidenced by reduced evaporative enrichment of $\delta^{18}O_{(H_2O)}$ values.

INTRODUCTION AND STUDY AREA

The Great Estuarine Group of the Inner Hebrides of Scotland (Fig. 1) has long yielded exceptionally well preserved aragonitic remains of vertebrate and invertebrate fauna (e.g., Hudson et al., 1995, and references therein). The group includes sediment that accumulated in water ranging from fresh (Salinity, S‰ = 0) to marginal marine, on the basis of macroinvertebrate and microinvertebrate fossil assemblages and isotope data (e.g. Hudson, 1963, Tan and Hudson, 1974). The unit examined here (the Kildonnan Member) was studied in detail by Hudson et al. (1995), and Wakefield (1995). Estimates of paleosalinity based on faunal analysis and stable isotope values of mollusks provide the background for stable isotope data from fish otoliths presented in this paper.

Otoliths and Stable Isotope Values

Otolith aragonite $\delta^{18}O$ and $\delta^{13}C$ values from fresh water and marine fish can provide a wealth of information on thermal history and metabolism (e.g., Patterson, 1998, and references therein). The $\delta^{18}O_{(CaCO_3)}$ values of otoliths show minimal vital effects in several empirical studies, suggesting that otolith aragonite faithfully records paleoenvironmental conditions such as temperature and $\delta^{18}O_{(H_2O)}$ values (e.g., Patterson et al., 1993; Thorrold et al., 1997). Two temperature-fractionation relationships have been published for fishes (one each for freshwater and marine species). Patterson et al. (1993) derived equation 1 by empirical study of a suite of fresh-water fish species raised in aquaria or captured from well-characterized environments, and Thorrold et al. (1997) focused their efforts on a single marine species raised over a range of temperatures (equation 2). The two equations have the same slope but slightly different y-intercepts. The difference in the two equations may represent minor fractionation associated with different osmoregulatory strategies in fresh water vs. marine fish.

$$1000\ln\alpha_{(H_2O\text{-}CaCO_3)} = 18.56(10^3K^{-1}) - 33.49 \quad (1)$$

$$1000\ln\alpha_{(H_2O\text{-}CaCO_3)} = 18.56(10^3K^{-1}) - 32.54 \quad (2)$$

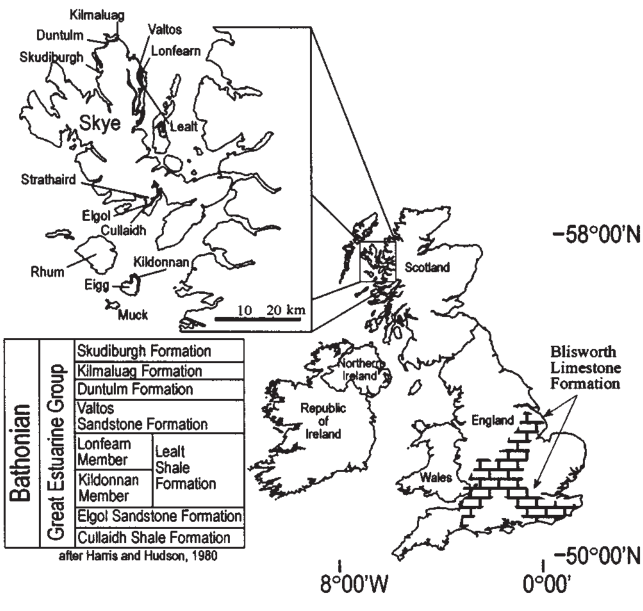

Figure 1. Study area outcrops and stratigraphy. Great Estuarine Group (169–175 Ma) outcrops are in scattered locations on Inner Hebridean isles of Skye, Eigg, and Raasay (from Harris and Hudson, 1980). Pattern area in England represents extent of Blisworth Limestone Formation. This study focused on bed 3g of Kildonnan Member type section found on isle of Eigg, 2.5 km north of village of Kildonnan (U. K. National Grid Reference NM 495 870).

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The $\delta^{13}C_{(CaCO_3)}$ values are more difficult to interpret in terms of environmental conditions. Values of $\delta^{13}C_{(CaCO_3)}$ probably represent a metabolic signal superimposed upon $\delta^{13}C_{(DIC)}$ (dissolved inorganic carbon). High-resolution micromilling of otolith carbonate has yielded $\delta^{18}O$ and $\delta^{13}C$ values that generally covary, suggesting a temperature effect on metabolic rate (Patterson, 1998). This is substantiated by comparison to $\delta^{13}C$ values of dissolved inorganic carbon (DIC) in studies of lake water carbon cycling (e.g. Drummond et al., 1995). Lake $\delta^{13}C_{(DIC)}$ values generally display seasonal variation with productivity (creation of biomass) causing increases in $\delta^{13}C_{(DIC)}$ values in the summer, while contemporaneously otolith $\delta^{13}C_{(CaCO_3)}$ values generally decrease. However, because $\delta^{13}C$ values of food are ultimately a function of $\delta^{13}C_{(DIC)}$ values, general trends and values can be defined as characteristic of distinct environments.

Methods and Source of Material

Fish otoliths were collected from bed 3g of the Kildonnan Member (Hudson, 1997) of the Lealt Shale Formation on the Isle of Eigg. Otoliths were photographed under standard optical microscopes and a Hitachi S-570 scanning electron microscope for identification by comparison to published morphological descriptions (e.g., Martin and Weiler, 1957, 1965; Stinton and Torrens, 1968). Preservation was evaluated by scanning electron microscope (SEM) and X-ray diffraction (XRD) examination. XRD analysis using a Gandolfi camera and SEM images demonstrated that otoliths were well-preserved, pristine aragonite, retaining original crystal morphology.

Whole otoliths (generally about 1 mm in longest dimension) were roasted in a vacuum at 200 °C to remove water and volatile organic contaminants and were reacted at 73 °C with four drops of anhydrous phosphoric acid in a Finnigan Kiel-I carbonate preparation device directly coupled to the inlet of a Finnigan MAT 251 ratio mass spectrometer at the University of Michigan, or in a Kiel-III device coupled to a Finnigan MAT 252 at Syracuse University. Isotopic values were corrected for acid fractionation and ^{17}O contribution and reported in per mil notation relative to the Vienna Peedee belemnite (VPDB) standard. Precision and calibration of data were monitored through daily analysis of NBS-18 and NBS-19 powdered carbonate standards. The $\delta^{18}O$ values of the samples were bracketed by those of the standards. Precision is better than ±0.1‰ for both carbon and oxygen isotopic values.

RESULTS AND DISCUSSION

The $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values representing environmental conditions and physiology of Jurassic fish were obtained for 50 specimens (Fig. 2). The $\delta^{18}O_{(CaCO_3)}$ values range from –4.7‰ to –1.9‰ (VPDB) while $\delta^{13}C_{(CaCO_3)}$ values range from –5.4‰ to +1.5‰ (VPDB). Calculation of paleotemperature from $\delta^{18}O$ values of biogenic carbonate is restricted by difficulties in estimating $\delta^{18}O_{(H_2O)}$ values of environmental water and the influence of vital effects on $\delta^{18}O_{(CaCO_3)}$ values. Because otoliths are precipitated in isotopic equilibrium with environmental water, only the $\delta^{18}O_{(H_2O)}$ value must be estimated. Temperatures calculated from otolith $\delta^{18}O_{(CaCO_3)}$ values using a single $\delta^{18}O_{(H_2O)}$ value are more variable than expected for the Jurassic (apparent range of nearly 14 °C). Using an ice-free Jurassic seawater $\delta^{18}O_{(H_2O)}$ value of –1.0‰ (VSMOW, from Zachos et al., 1994), temperatures range from 19 °C to 33 °C (equation 1). Whole otoliths were analyzed, resulting in time-averaging of thermal information, indicating that the observed range is a minimum estimate of actual temperature variability.

Because the range of temperatures is well outside that estimated by other proxy data (e.g. bivalves, Hudson et al., 1995), it is assumed that $\delta^{18}O_{(H_2O)}$ values must have varied significantly. The $\delta^{18}O_{(H_2O)}$ values may change as a function of variable $\delta^{18}O_{(H_2O)}$ (rainfall) values and evaporation, or the fish may migrate to waters of different $\delta^{18}O_{(H_2O)}$ value. By assuming that the highest values represent carbonate precipitated by migratory individuals in marine water, the temperature range is significantly narrowed to less than 8 °C.

Using a seawater $\delta^{18}O_{(H_2O)}$ value of –1.0‰ (VSMOW), these shallow-water marine fishes permit calculation of sea-surface temperature. If the calculated sea-surface temperature is assumed to represent regional maritime climate conditions (maritime lowland), $\delta^{18}O_{(H_2O)}$ values can be calculated from estuarine fish assuming that estuarine waters will have temperatures similar to the adjacent marine water. To address the variation in $\delta^{18}O_{(H_2O)}$ values, several studies using molluscan material are compared to otolith $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values.

Calculation of Estuarine $\delta^{18}O_{(H_2O)}$ Values

Several workers have addressed the difficulties in calculating salinity and $\delta^{18}O_{(H_2O)}$ values of Jurassic estuarine water, using molluscan carbonate. Hudson et al. (1995), reevaluated molluscan $\delta^{18}O$ and $\delta^{13}C$ data (from bed 5e of the Kildonnan Member at the same location studied here), originally presented in Tan and Hudson (1974) applying corrections to calculations, which formerly utilized a temperature fractionation relationship for calcite. Wakefield (1995) presented salinity profiles which were based on estimated salinity tolerance of ostracods. In these studies, trends in salinity were distinguished from those of temperature through comparison of faunal assemblages with $\delta^{18}O$ and $\delta^{13}C$ values. Hendry and Kalin (1997) presented molluscan $\delta^{18}O$ and $\delta^{13}C$ data from a slightly younger Bathonian restricted marine platform located nearby to the south and east in England. These studies suggest that Kildonnan Member sediment was deposited in restricted but relatively fresh water, whereas Middle Jurassic sediment of England was deposited in restricted water that was modified to a great degree by evaporation. Using $\delta^{18}O_{(CaCO_3)}$ values of Great Estuarine Group otoliths, and assuming water temperatures of the estuary are similar to adjacent shallow seawater, a range of $\delta^{18}O_{(H_2O)}$ values can be calculated.

Florida Bay and the Everglades have been proposed as a modern analog for water chemistry during deposition of the Great Estuarine Group (e.g., Hudson et al., 1995). The $\delta^{18}O_{(H_2O)}$ values of Florida Bay determined by Swart et al. (1999) indicate substantial evaporative modification, with values several per mil higher than seawater, and higher than fresh water from the Everglades. The $\delta^{18}O_{(H_2O)}$ values of precipitation in the Florida Bay vicinity average –3.0‰ (VSMOW, Swart et al., 1989), a value heavier than the freshest end member calculated for the Great Estuarine Group. Meyers et al. (1993) determined that south Florida fresh-water $\delta^{18}O_{(H_2O)}$ values were modified to the maximum possible value given prevailing meteorological conditions. On the basis of $\delta^{18}O_{(H_2O)}$ estimates and calculated temperatures, evaporation and temperatures were probably lower in Jurassic Scotland than modern-day south Florida. Using equation 1 and a marine $\delta^{18}O_{(H_2O)}$ value of –1.0‰ (VSMOW), the mean sea-surface temperature is calculated to be 21 °C to nearly 25 °C. At 23 °C (average temperature calculated for the six presumed migratory fish), estuarine $\delta^{18}O_{(H_2O)}$ values are calculated to range from –3.5 to –1.9‰ (V-MOW) (Fig. 3), a range similar to those found in modern low-latitude fresh water dominated es-

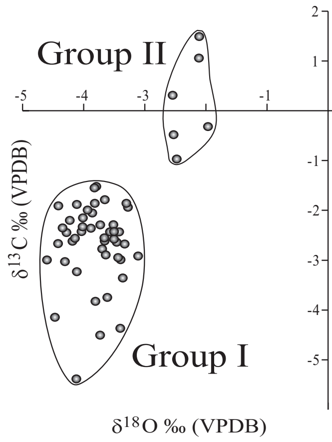

Figure 2. $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values of Jurassic fish otoliths from Kildonnan Member of the Great Estuarine Group. Otolith $\delta^{18}O$ values range from –4.7 to –1.9‰ (Vienna Peedee belemnite, VPDB), while $\delta^{13}C_{(CaCO_3)}$ values vary from –5.4 to +1.5‰ (VPDB). Values can be readily separated into two distinct groups. Those with relatively low $\delta^{18}O$ and $\delta^{13}C$ values represent fish that occupied fresh to oligohaline water throughout their lives (Group I), while higher $\delta^{18}O$ and $\delta^{13}C$ values represent fish that migrated to fully marine water (Group II).

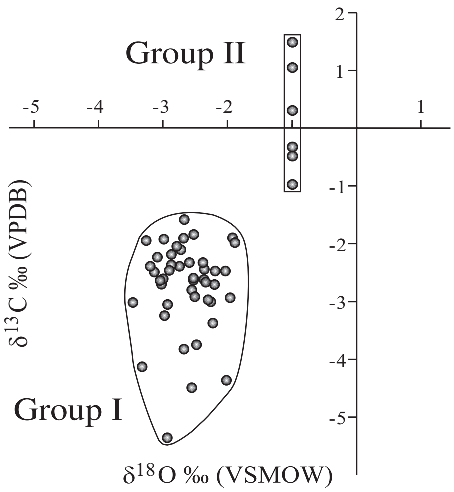

Figure 3. Calculated $\delta^{18}O_{(H_2O)}$ values of Jurassic water and $\delta^{13}C_{(CaCO_3)}$ values of fish otoliths. Otoliths with highest $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values are used to establish marine water temperatures (Group II) which are applied to the adjacent shallow-water estuarine environment in order to determine $\delta^{18}O_{(H_2O)}$ value. $\delta^{18}O_{(H_2O)}$ values vary from –3.5 to –1.9‰ (Vienna standard mean ocean water, VSMOW) (Group I), a reasonable range for estuary in humid maritime climate with mean temperature of 23 °C.

tuaries. Andrews (1986) suggested that freshwater micrites and cement fringes from the Duntulm Formation could have been precipitated from meteoric water with $\delta^{18}O$ value of ~–4‰ (VSMOW) assuming temperatures of 20 to 25 °C.

Estuarine $\delta^{13}C_{(DIC)}$ Values

The $\delta^{13}C_{(CaCO_3)}$ values of otoliths and molluscan shell material are a function of $\delta^{13}C_{(DIC)}$ overprinted by a contribution of metabolically derived CO_2 (e.g., Kalish, 1991; Iacumin, et al., 1992; Klein et al., 1996), making precise inference of $\delta^{13}C_{(DIC)}$ values difficult. Laboratory and field studies indicate a direct relationship between dietary $\delta^{13}C$ and $\delta^{13}C_{(tissue)}$, a relationship observed in many organisms (e.g., DeNiro and Epstein, 1978; Fry and Parker, 1979). Lloyd (1964) interpreted Florida Bay gastropod $\delta^{13}C_{(CaCO_3)}$ values to be an indication of $\delta^{13}C_{(DIC)}$ values, which are in turn a function of restriction in circulation (i.e., residence time). Patterson and Walter (1994) and Swart et al., (1999) conducted detailed geochemical surveys including analysis of bank water for salinity and $\delta^{13}C_{(DIC)}$. These studies concluded that bank water $\delta^{13}C_{(DIC)}$ values are a function of restriction and associated recycling of organic matter both within the water column and the sediment. Patterson and Walter (1994) found that $\delta^{13}C_{(DIC)}$ values decreased from open marine values of ~+2‰ (VPDB) to values as low as –5‰ (VPDB) in hypersaline Florida Bay water, and as low as –8‰ (VPDB) in Everglades water. Although there is no simple relationship between salinity and $\delta^{13}C_{(DIC)}$ due to organic matter recycling, Bahama Bank water $\delta^{13}C_{(DIC)}$ values (like those of Florida Bay and the Everglades), are only positive in near normal marine salinity (Patterson and Walter, 1994).

Based on this relationship, Halley and Roulier (1999) determined $\delta^{13}C_{(CaCO_3)}$ and $\delta^{18}O_{(CaCO_3)}$ values of modern Florida Bay mollusks for comparison with mollusks recovered from cores to establish a long-term record of $\delta^{13}C_{(DIC)}$ values for Florida Bay water. Results were similar to those of Lloyd (1964), with values reflecting complex variation in $\delta^{18}O_{(H_2O)}$ and $\delta^{13}C_{(DIC)}$ values of Florida Bay (Fig. 4). Swart et al. (1996) found that Florida Bay corals recorded the decrease in estuarine and seawater mixing manifested as a function of decreased $\delta^{13}C_{(DIC)}$ values associated with the twentieth century construction of the railroad to Key West. In a study of the 454 Ma Mohawkian epeiric seaway, Holmden et al. (1998) found low distal $\delta^{13}C$ values trending to high $\delta^{13}C$ values proximal to the Iapetus ocean. Therefore, mollusks studied by Tan and Hudson (1974) and those studied by Hendry and Kalin (1997) record general trends in $\delta^{13}C_{(DIC)}$ associated with relative mixing of fresh (low $\delta^{13}C_{(DIC)}$ values) and marine water (comparatively ≈10‰ higher $\delta^{13}C_{(DIC)}$ values) with a metabolic overprint (Figs. 1 and 4). Because fish generally respire at a higher metabolic rate than do mollusks or corals, greater metabolic overprinting may be presumed for fish otolith $\delta^{13}C_{(CaCO_3)}$ values.

In Figure 2, the majority (group I) of Jurassic otolith $\delta^{13}C_{(CaCO_3)}$ values are within the range of –1.6 to –5.4‰ (VPDB), while $\delta^{18}O_{(CaCO_3)}$ values range from –4.7 to –3.1‰ (VPDB). The highest $\delta^{13}C_{(CaCO_3)}$ values (group II), ~+1.5‰ (VPDB) may represent fish that sought marine water clear of estuarine influence. Comparison with Hendry and Kalin (1997) demonstrates concordance with the evaporative trends intermediate between fresh meteoric water and the more restricted water of the Middle Jurassic of England. The spread in data suggests that the Kildonnan Member fauna inhabited waters much closer in chemistry to the Everglades than to Florida Bay.

Implications for Coastal and Continental Climate

This Jurassic environment has been compared to Florida Bay and the Everglades. Meteorological stations in South Florida from nearby Tavernier Key, Alligator Reef, and Key West indicate that Florida Bay and the Everglades have a higher mean annual temperature (25.2 °C, 26.0 °C, and 25.4 °C respectively) than did the Kildonnan Member waters. Modern south Florida receives both continental and maritime sourced moisture which averages –3.0‰ (VSMOW). In the ice-free Jurassic world, oceanic $\delta^{18}O_{(H_2O)}$ values of –1.0‰ (VSMOW) would generate atmospheric moisture with a value ~1.0‰ lower than the modern ocean at identical temperatures.

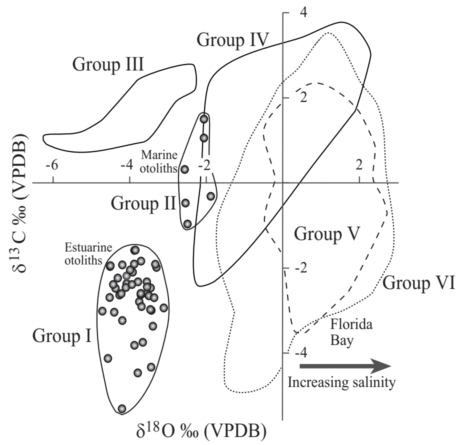

Figure 4. Comparison of fish otolith data with isotope values from mollusks of both Jurassic age and the modern Holocene analog, Florida Bay. Otolith values are intermediate to restricted estuarine values presented by Tan and Hudson (1974, Group III) and restricted marine platform values presented by Hendry and Kalin (1997, Group IV). $\delta^{18}O_{(H_2O)}$ and $\delta^{13}C_{(DIC)}$ values suggest that Great Estuarine Group water was significantly less evaporatively modified than modern Florida Bay water. Florida Bay mollusk data from Lloyd (1964, Group V, long dash line) and Halley and Roulier, (1999, Group VI, short dash line) are plotted for comparison. Evaporative increase of Florida Bay $\delta^{18}O_{(H_2O)}$ values is more similar to that of Bathonian restricted carbonate platform of Hendry and Kalin than estuary of Tan and Hudson (1974) and this study. Comparison indicates that Kildonnan Member was deposited in relatively fresh water with an average temperature of 23 °C. DIC—dissolved inorganic carbon; VPDB—Vienna Peedee belemnite.

The $\delta^{18}O$ values and temperatures derived in this study correspond to the meteorologic and hydrologic parameters of a mid-latitude maritime climate with low seasonality, a mean temperature of 23 °C, and abundant precipitation and humidity. The $\delta^{18}O_{(H_2O)}$ values calculated from the putatively estuarine fish fossils indicate that rainfall must have a $\delta^{18}O_{(H_2O)}$ value lower than –3.5‰ (VSMOW) (the lowest value calculated), in agreement with a fresh water $\delta^{18}O$ value of –4 ‰ (VSMOW) suggested by Andrews (1986).

Generation of precipitation with $\delta^{18}O_{(H_2O)}$ values of –4‰ (VSMOW) or lower would require temperature similar to the mean annual temperature observed today in south Florida because the Jurassic seawater $\delta^{18}O$ value is 1.0‰ lower than modern seawater. Like Florida, which receives some precipitation that has undergone significant continental distillation, Kildonnan Member water was derived predominately from relatively unevolved maritime sources, but may have received significant input from distal highland runoff. This may explain the similarity in $\delta^{18}O_{(H_2O)}$ values as well as the disparity in temperatures and evaporation between the two environments. Lower temperature and reduced evaporation are both in agreement with the calculated Jurassic lowland air temperatures (derived from water temperature) and $\delta^{18}O_{(H_2O)}$ values, as well as *Praemytilus* $\delta^{18}O_{(CaCO_3)}$ values from higher in the section. Additional information on the seasonal position of the intertropical convergence zone may be required before seasonality in precipitation and evaporation can be adequately characterized. This is under investigation via modeling and analysis of otolith and mollusk seasonal growth structures as the next phase of research.

The low topographic relief landmasses of what is now northwestern Europe probably permitted extensive incursion of maritime airmasses deep onto the continent, thus moderating continental climate over a large geographic area. On the basis of the distribution of climate dependent sedimentology and mineralogy of Jurassic strata, Hallam (1984) proposed that incursion of a shallow sea increased humidity and precipitation in northwest Europe beginning in the Late Triassic. A significant moderation of continental climate as far inland as the most proximal significant topographic barrier would probably have been concomitant with the calculated increase in moisture

CONCLUSIONS

Fish otoliths from bed 3g of the Kildonnan Member of the Great Estuarine Group, representing the oldest otoliths analyzed for $\delta^{18}O$ and $\delta^{13}C$ values to date, characterize thermal and hydrologic conditions for the Middle Jurassic of Scotland. The suite of values indicates a complex ecology similar to that found in modern marginal marine environments such as Florida Bay and the Everglades. The Kildonnan Member had lower $\delta^{18}O_{(H_2O)}$ values compared to Florida Bay, suggesting that it was not as evaporatively modified and/or had lower temperatures. The $\delta^{13}C_{(CaCO_3)}$ values likewise suggest that water which deposited the Kildonnan Member was not as restricted as that of modern or even "pre-railroad" Florida Bay and/or had a less vegetated hinterland. It is significant that $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values of one group of specimens suggest migration to open marine water. Using a value of –1.0‰ (VSMOW) for open marine Jurassic seawater, a temperature of 23 °C is calculated. The low paleogeographic relief and comparatively low $\delta^{18}O_{(H_2O)}$ values for most specimens suggests that evaporation was limited (high humidity), and that lagoonal temperatures would have been similar to those of open marine water. The results of this study are in general agreement with previous studies of molluscan carbonate, but have further refined the comparison of freshwater to marine $\delta^{18}O_{(H_2O)}$ values. The $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values obtained in this study represent the most ancient quantitative fish life history stable isotope data including the earliest example of fish paleodiet, paleoecology, and migratory behavior published to date.

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