Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans

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The first appearance and evolution of the crown group Cetacea – Mysticei (baleen whales) and Odontoceti (toothed whales and dolphins) – from archaeocete ancestors corresponds with major climatic and oceanographic changes shortly before the Eocene–Oligocene boundary (ca. 34.0 Ma). These environmental changes impacted marine productivity and may have sparked the evolution of the distinct bulk-feeding strategy used by mysticete whales today. The movements and feeding habits of living cetaceans can be tracked using the isotopic composition of the structural carbonate within bioapatite of their bones and teeth, which records latitudinal gradients in marine δ 13C and δ 18O values. Here, we exploit this relationship to determine the past movements and feeding habits of late-surviving archaeocetes (kekenodontids) and early odontocetes and mysticetes sampled from Oligocene fossil sites in the USA (latitude: ~30°N) and New Zealand (latitude: ~50°S). Bioapatite δ 13C and δ 18O values for fossilized tooth enamel and bullae from fossil cetaceans were surprisingly similar to those for living cetaceans, which indicates that the feeding habits of these species and the isotopic composition of Oligocene seawater (ca. 28 Ma) were very close to present-day conditions. Values for toothed mysticetes and odontocetes match expectations based on cetacean species feeding at these latitudes today, suggesting these individuals were residents that foraged in close proximity to where their fossils were discovered. In contrast, the extremely low δ 13C and δ 18O values for some edentulous mysticetes from New Zealand are more similar to values observed in extant mysticetes that seasonally migrate to high latitudes, where they bulk-feed on lipid-rich zooplankton. Enamel δ 13C values for kekenodontids showed the greatest range and overlapped with both edentulous mysticetes and resident species; these differences correlate most strongly with tooth type and may reflect an ontogenetic shift in diet associated with the transition from nursing to marine prey. When combined with evidence of increasing morphological disparity, fossil bioapatite δ 13C and δ 18O values support interpretations that the Oligocene was an interval of heightened taxonomic and ecological diversification within Cetacea.

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1. Introduction

The emergence of modern cetaceans (whales, dolphins and porpoises) at the close of the Eocene (ca. 34.0 Ma) marks a major advance in the feeding strategies used by marine cetaceans (Fordyce, 2003). Prior to the appearance of crown Cetacea (Neoceti), early cetaceans of the paraphyletic group Archaeoceti were primarily piscivorous (Swift and Barnes, 1996; O’Leary and Uhen, 1999; Thewissen et al., 2007) and captured prey by raptorial snap-feeding, which is an effective method for securing slippery prey. Many modern cetaceans still use this feeding style, but most have developed additional or alternative feeding strategies that are associated with the divergence of modern cetaceans into the Odontoceti (toothed whales, dolphins, porpoises) and Mysticeti (baleen whales) (Fig. 1). Odontocetes maintained the dietary focus of their archaeocete ancestors by favoring individual prey items hunted with the use of echolocation, while mysticetes followed a different path and evolved baleen for efficient bulk filter-feeding on shoals of small, but abundant prey (zooplankton, schooling fish and squid). This feeding style, which involves engulfing large quantities of small prey that are strained from seawater within the oral cavity, is, within Cetacea, unique to the Mysticeti (Croll et al., 2009). Though a few species of pinnipeds and sea birds are known to consume zooplankton as part of their diet (Croll et al., 2009), none are as committed to this diet as the mysticetes, which are suspected to have evolved this method of feeding only once in the past (Deméré et al., 2008).

Along with changes in feeding morphologies, the postcrania of late Eocene and Oligocene cetaceans exhibit increasing modification towards a streamlined fusiform body plan, which aided in more
efficient swimming. Of particular note was the neomorphic evolution of tail flukes and vertically-oscillating caudal propulsion by the Pelageti (Basilosauridae + Neoceti) (Uhen, 2008a). These modifications allowed cetaceans to become fully aquatic, and to colonize pelagic waters worldwide. Support for this model of functional shift/geographic spread comes from the spatial distribution of cetacean fossils: from an early Eocene origin in the Indo-Pakistan region, cetaceans spread outward, achieving a southern temperate distribution (Köhler and Fordyce, 1997) and expanding into the tropical eastern Pacific (Uhen et al., 2011) by the late middle Eocene (Bartonian, Uhen, 2010). Fluke-propelled pelagic cetaceans could exploit widely spaced, highly productive areas of upwelling — oceanic features that were, in turn, enhanced as ocean circulation patterns and global climate changed in response to the opening of the Southern Ocean and establishment of permanent ice on Antarctica (Berger, 2007; Pagani et al., 2011). Today, productivity at upwelling zones is often seasonally variable, especially at high latitudes (Bost et al., 2009); accordingly, mysticete whales generally move to temperate waters when productivity declines in the winter (MacKintosh, 1965). Enhanced polar-to-tropical temperature gradients and regions of upwelling were established by the Oligocene (Coxall and Pearson, 2008; Katz et al., 2008) and the morphological adaptations of pelagicetes would have allowed them to take full advantage of the seasonally abundant resources that these conditions produced.

The fossil record and phylogenetic patterns among Cetacea (Fitzgerald, 2006; Uhen, 2010; Marx, 2011) indicate a rapid diversification of Neoceti from the latest Eocene onwards, linked to large-scale changes in productivity (Fordyce, 2003; Lindberg and Pyenson, 2007; Marx and Uhen, 2010) that attest to the importance of physical drivers in Neoceti history. Previously, Neoceti were thought to have exploited the progressively-modernizing Oligocene oceans, with Archaeoceti displaced rapidly by mysticetes and odontocetes (Fordyce and Barnes, 1994). It is now clear, however, that Archaeoceti-like cetaceans typified by the genus *Kekenodon* Hector, 1881 coexisted with late Oligocene Odontoceti and Mysticeti in New Zealand and probably beyond: thus, archaeocetes were not simply displaced by Neoceti (Fig. 1) early in the Oligocene. Opinions have varied as to the affinities of *Kekenodon* because of the fragmentary nature of the type material for *Kekenodon onomata*. The species has sometimes been considered a basal mysticete (Fordyce and Barnes, 1994; Barnes and Sanders, 1996; Fordyce and de Muizon, 2001), but recently-recognized skulls of *Kekenodon*-like taxa are of archaeocete design, without the apomorphies of Mysticeti or Odontoceti (Fig. 2). Fordyce (2002) placed *Kekenodon*-like cetaceans as a sister clade to Neoceti. Thus, *Kekenodon* and relatives are taken to represent late-surviving archaeocetes (Fordyce, 2002; Uhen, 2008b), and our working hypothesis is that they constitute the taxon *Kekenodontidae* (on taxonomic rank, see Fordyce and Barnes, 1994).

Regarding morphological characteristics related to feeding ecology, kekenodontids lack the skull modifications sometimes linked with bulk-feeding in early toothed mysticetes (Fig. 2); for example, the posterior of the attenuated rostrum is steep-sided, without a laterally-produced flange of maxilla, the cheek-teeth are vertically inserted and in a row, the palate has embrasure pits, the palate lacks extensive vascular foramina, the rostral bones are firmly sutured, rather than loose, and the mandibular symphysis is elongate. As in late Eocene dorudontine archaeocetes (e.g., *Dorudon*), the...
smaller species of *Kekenodon* have upper and lower premolar and molar teeth with prominent small and keeled denticles but, in contrast to dorudontines, there are significant diastemata between the cheekteeth. In occlusion, the upper and lower cheekteeth alternate, potentially forming a sieve-like feeding apparatus that might have been used to strain small prey from the water — a behavior reported in the living crabeater seal *Lobodon carcinophaga* (Croll et al., 2009). This combination of features suggests kekenodontids could possibly filter-feed, in turn raising questions about the evolution of this feeding strategy among Cetacea.

Knowledge of the movements and feeding habits of extant cetaceans has significantly benefited from the application of stable isotope analysis (Newsome et al., 2010), a tool that has also been applied to address questions of the ecology of early fossil whales (Thewissen et al., 1996; Roe et al., 1998; Clementz et al., 2006; Thewissen et al., 2011). Differences in the stable isotopic composition of cetacean prey items, or waters directly or incidentally ingested when feeding, are subsequently incorporated into cetacean tissues and biological apatites or “bioapatites” (e.g., bone, dentin, enamel; typically, apatite with carbonate and hydroxyl components), leaving an isotopic label that can be traced back to the original food or water source (Yoshida and Miyazaki, 1991; Clementz and Koch, 2001). Within extant species, intra- and inter-individual variations in the stable isotopic composition of cetacean tissues have provided information on the migratory movements of cetacean species (Schell et al., 1989a,b; Hobson and Schell, 1998). Where the preservation quality of skeletal materials permits (Thomas et al., 2011), stable isotopic studies of fossil cetaceans should reveal the foraging habits and movement patterns of cetaceans through deep time.

Here we examine the feeding habits of co-occurring kekenodontids, odontocetes and mysticetes from Oligocene sediments in New Zealand and South Carolina by examining the stable isotopic composition of structural carbonates from the bioapatite of tooth enamel and osteosclerotic bone (i.e., bone of increased density), which, here, refers mostly to the preservation quality of skeletal materials permits (Thomas et al., 2011), stable isotopic studies of fossil cetaceans should reveal the foraging habits and movement patterns of cetaceans through deep time.

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2. Marine isoscapes — latitudinal gradients in δ¹³C and δ¹⁸O values

The stable isotopic compositions of consumer tissues, including bioapatite, reflect that of an animal’s diet or drinking water, thereby providing an environmental label that can be used to track the movements and foraging habits of marine consumers (Koch, 2007; Newsome et al., 2010). Bioapatites contain a significant quantity of structural carbonates (CO₃²⁻) in place of phosphate in the mineral lattice (−2–4% by weight), which are suitable for δ¹³C and δ¹⁸O analyses (LeGeros and LeGeros, 1984; Kohn and Cerling, 2002; Pasteris et al., 2008). Stable isotopic compositions of consumer tissues are typically enriched in the heavier isotope (¹³C, ¹⁸O) relative to diet or surface waters; this isotope enrichment (ε*) is calculated following the approach recommended by Cerling and Harris (1999) in which the apparent fractionation factor (α*) between bioapatite and surface waters:

$$\alpha_{\text{bioapatite-water}} = \left(1000 + \delta^{18}O_{\text{bioapatite}}\right)/\left(1000 + \delta^{18}O_{\text{sw}}\right)$$

or between bioapatite and diet:

$$\alpha_{\text{bioapatite-diet}} = \left(1000 + \delta^{13}C_{\text{bioapatite}}\right)/\left(1000 + \delta^{13}C_{\text{diet}}\right)$$

is converted to ε* using the following equation and reported in units of per mille (‰):

$$\varepsilon^* = (\alpha - 1) \times 10^3.$$  

The apparent fractionation factor accounts for all processes that fractionate isotopes following ingestion through assimilation, being irreversible once bioapatite is precipitated. The internal and external factors that most strongly influence the carbon and oxygen isotopic compositions of structural carbonates in mammalian bioapatite are discussed in more detail below.

Bioapatite is precipitated in isotopic equilibrium with an animal’s body water, a process that is strongly affected by temperature. Living mammal body core temperatures are relatively constant, and such a homeothermic condition is assumed to be true for fossil species as well. Thus, δ¹⁸O values of structural carbonate in bioapatite will reflect the oxygen isotopic composition of body water, which is controlled by the isotopic compositions of external oxygen sources (e.g., drinking water, food, atmospheric O₂) and by physiological functions that affect the flow and fractionation of oxygen within an animal (Bryant and Froelich, 1995; Kohn, 1996). Empirical δ¹⁸O data for marine cetaceans show a strong correlation with surface water δ¹⁸O (€₁₆/C₁₆/C₁₇) (Yoshida and Miyazaki, 1991) as the major oxygen flux for marine cetaceans is seawater, either through transcutaneous exchange (Hui, 1981; Andersen and Nielsen, 1983; Kohn, 1996) or through direct ingestion or incidental ingestion when feeding (Costa, 2002). Low environmental variation in seawater δ¹⁸O values leads to low within-population variance (1 standard deviation (σ) ≤ 0.5‰) for most marine species (Clementz and Koch, 2001), though variation may be greater for those species with home ranges that span wide ranges in latitude or move between waters of different oxygen isotopic compositions (Roe et al., 1998; Clementz and Koch, 2001).

Diet is the source of carbon for structural carbonates in mammal bioapatite (Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Cerling and Harris, 1999). The carbon isotopic composition of cetacean bioapatite is offset from that of diet by a large and consistent factor (εbioapatite-diet = 9.0–10.0‰), which is similar in magnitude to most terrestrial carnivores (Lee-Thorp et al., 1989; Topperoff, 2002). The δ¹³C value of diet is ultimately derived from that of primary producers within a food web. In marine environments, primary producers use the same photosynthetic pathway as that of C₃ terrestrial plants (Farquhar et al., 1989), but their δ¹³C values are also strongly controlled by the physical conditions associated with growth in an aquatic environment. Variation in the carbon isotopic composition, concentration, and source of dissolved inorganic carbon (DIC) as well as a significant reduction in the rate of diffusion of CO₂ in water versus air can cause the δ¹³C values for marine phytoplankton and macrophytes to deviate from those of terrestrial plants (Osmond et al., 1981; Rau et al., 1989; Wainright and Fry, 1994; Raven et al., 2002). Furthermore, these factors can generate strong spatial gradients in marine producer δ¹³C values; nearshore, benthic producers typically have higher δ¹³C values than those for phytoplankton sampled from surface waters offshore (France, 1995; Clementz and Koch, 2001; Hobson et al., 2002). These spatial differences in producer δ¹³C values are then passed on to consumers along with slight δ¹³C enrichment in consumer tissues with each trophic step (εTL* = 0.8‰) (Vander Zanden and Rasmussen, 2001).
Though small, this offset, when compounded over multiple trophic levels within a marine food chain, can produce differences in \( \delta^{13}C \) values large enough to differentiate consumers foraging at the top of a food web from those foraging at its base. Stable isotopic tracers in marine ecosystems are also suitable for identifying consumers foraging over larger distances. Environmental differences in temperature, salinity and productivity lead to significant gradients in the carbon and oxygen isotopic compositions of marine phytoplankton and seawater with latitude in today’s oceans (Rau et al., 1989; Bigg and Rohling, 2000; LeGrande and Schmidt, 2006). Both isotope systems show a negative correlation with latitude (Fig. 4A,B), a trend likely to have existed since at least the late Paleogene (Clementz and Sewall, 2011). The general trend between isotope values and latitude is observed globally, but the magnitude of this relationship can vary greatly between the northern and southern hemispheres (Fig. 4A,B). Between 30°N and 30°S, seawater \( \delta^{18}O \) values and marine phytoplankton \( \delta^{13}C \) values are relatively stable and consistent across hemispheres as a result of similar temperature, nutrient, and oceanic conditions. Warm temperatures are associated with enhanced evaporation in the tropics and lower \( \delta^{18}O \) solubility in seawater, producing seawater \( \delta^{18}O \) values that are typically \( 18^\circ \text{O} \)-enriched relative to standard mean ocean water (VSMOW: 0.0‰; Fig. 4A) and high phytoplankton \( \delta^{13}C \) values that fall between −22.0‰ and −18.0‰ (Fig. 4B). At higher latitudes (>40°), cooler temperatures reduce net evaporation while increasing \( \delta^{18}O \) solubility, which leads to a drop in both \( \delta^{18}O \) and \( \delta^{13}C \) values. The magnitude of this drop, however, differs for each isotope system in each hemisphere. The drop in seawater \( \delta^{18}O \) values is stronger in the northern hemisphere where seawater \( \delta^{18}O \) values can be as much as 2.0‰ lower than SOW, whereas in the southern hemisphere the drop is closer to 0.5‰. This pattern contrasts with that observed for phytoplankton \( \delta^{13}C \) values in which phytoplankton from the southern hemisphere (−30.0‰ to −26.0‰) are significantly more depleted in \( 13^\text{C} \) than those from high latitude sites to the north (−24.0‰ to −22.0‰). This pattern is observed in both the Atlantic and Pacific basins, though the offset in seawater \( \delta^{18}O \) values between low and high latitude \( \delta^{18}O \) values in the North Atlantic is more pronounced than that in the North Pacific. As shown in Fig. 4C, a combination of these values produces distinct isotopic patterns for low latitudes versus high latitudes in the northern and southern hemispheres, which can be used to label the tissues of marine consumers foraging in these waters. These spatial differences in the stable isotopic composition of marine surface waters can be used to create a map, or isoscapes, within which the movements of living marine consumers can be determined through analysis of the stable isotopic composition of their tissues and skeletal material (Bowen, 2010; Graham et al., 2010). If similar isoscapes can be created for earlier time periods, the same approach can be applied to questions of the movement patterns of fossil cetaceans as well.

3. Materials and methods

3.1. Modern cetacean material

Skulls and teeth from 134 specimens of extant cetacean species (Table 1; Appendix 1) were selected for stable isotopic analysis (Mysticeti: 11 species; Odontoceti: 10 species). Most of the specimens were sampled from collections at the Smithsonian Institution’s National Museum of Natural History (USNM) with a few additions from collections at the Los Angeles County Museum of Natural History (LACM) and Otago Museum (OM); isotopic data from LACM specimens were originally published in Clementz and Koch (2001). Locations where these specimens were recovered are shown on the map in Fig. 3A. For small- and medium-sized odontocetes with small home ranges, these locations are a good representation of the latitudes inhabited by these individuals (e.g., *Phocoena phocoena*, *Tursiops truncatus*). However, most mysticetes and large odontocetes move over much larger distances each year, which makes the locations where specimens of these cetaceans were recovered less representative of their true latitudinal range. In these instances, the maximum latitude at which an individual for a given species was recovered was used for that species and is listed in Table 1. As many of these species primarily forage at higher latitudes, stable isotope values for prey and seawater at these latitudes are assumed to represent most closely the stable isotope composition of carbon and oxygen sources recorded in cetacean bioapatite. For most species sampled in this study, these locations do not represent the maximum extent traveled by these individuals, and should thus be viewed as a minimum estimate of their foraging range.

For teeth, enamel was primarily sampled, though for some species with little or no enamel (e.g., *Physeter macrocephalus*) or with teeth that were too small to yield sufficient enamel for analysis (e.g., *Phocoena phocoena*), dentin from the base of the tooth was sampled instead. Bone powder was collected from the skulls by drilling a small hole (<5 mm diameter) at the base of the skull in one of the occipital condyles; this site was selected to ensure consistent and comparable sampling among species, regardless of body size, and to ensure collection of bone that had precipitated at core body temperatures (~37°C).

3.2. Fossil cetacean material

Enamel and bone from 28 fossil specimens were sampled for this study (Table 2). Tooth enamel was sampled from two specimens of toothed stem mysticetes (undescribed specimens ChM PV4757 and ChM PV5720) and one specimen of odontocete (undescribed specimen ChM PV2764), all from the Charleston Museum (ChM), Charleston, SC, USA (Geisler and Sanders, 2003, including information on systematic relationships). The ChM specimens are from two late Oligocene (Chattian Stage: 28.4–23.0 Ma) formations, the Ashley Formation and overlying Chandler Bridge Formation, which were deposited in nearshore marine environments and grade into estuarine and fluvial deposits towards the top of the Chandler Bridge Formation (~33°N) (Sanders et al., 1982). Of these three specimens, ChM PV4745 from the Ashley Formation is the oldest; ChM PV5720 and CHM PV2764 are younger and from the Chandler Bridge Formation. Geisler and Sanders (2003) give more details of the ChM specimens. We acknowledge that taxonomic diversity of cetacean fossils from these formations is much greater than what we have included here; sampling restrictions based on the quality and abundance of material limited the number of ChM specimens available to us for destructive analysis.

The remaining fossil specimens were from sedimentary formations of comparable age (Chattian, late Oligocene) from South Island, New Zealand (~45°S): the Kokoamu Greensand and conformably overlying Otekaike Limestone. These units span the local upper Whaiangaroa to Duntroonian Stages (Kokoamu Greensand), and Duntroonian to lower or middle Waitakian Stages (Otekaike Limestone), Chattian (Cooper, 2004; Nelson et al., 2004). Compared to the Charleston assemblages, a greater diversity of fossil cetaceans was available for sampling from the collections of the Geology Museum, University of Otago (OU), Dunedin, New Zealand: early odontocetes (archaic platanistoids, squalodontids, and archaic delphinoids), toothed stem mysticetes (mammalodontids), edentulous crown and possibly stem mysticetes (eomysticeti, archaic balaenopteroids), and kekenodontid archaeocetes. The kekenodontids are not known above the transitional Kokoamu Greensand–Otekaike Limestone, about 26 Ma. For specimens with tooth material, enamel from anterior teeth (mostly canines) was preferentially sampled, though cheek-teeth from three specimens of kekenodontid were sampled instead. Bullar bone, which was often more readily available than teeth for most specimens, was sampled from all edentulous mysticetes and from any specimens of toothed cetaceans that lacked teeth or possessed teeth too small for sampling.

Alteration of the stable isotopic composition of bioapatites by diagenesis can occur following an organism’s death, and the extent of alteration must be assessed before any viable ecological interpretations can be drawn from analysis of fossil materials. Enamel is the
bioapatite most routinely sampled by paleontologists and geochemists because its high density, large crystal size and low organic content make it less susceptible to alteration than other mineralized tissues (e.g., bone, dentine) (Lee-Thorp and van der Merwe, 1987; Wang and Cerling, 1994; Koch et al., 1997; Zazzo et al., 2004). However, the edentulous state of living and most fossil mysticetes means enamel is make it less susceptible to alteration than other mineralized tissues (e.g., bone, dentine) (Lee-Thorp and van der Merwe, 1987; Wang and Cerling, 1994; Koch et al., 1997; Zazzo et al., 2004). However, the edentulous state of living and most fossil mysticetes means enamel is make it less susceptible to alteration than other mineralized tissues (e.g., bone, dentine) (Lee-Thorp and van der Merwe, 1987; Wang and Cerling, 1994; Koch et al., 1997; Zazzo et al., 2004). However, the edentulous state of living and most fossil mysticetes means enamel is

Table 1 Bioapatite δ13C and δ18O values for modern cetacean species.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Common name</th>
<th>Max. lat.</th>
<th>Ocean</th>
<th>Trophic level*</th>
<th>Element</th>
<th>N</th>
<th>δ13C (ppm)</th>
<th>δ18O (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mysticeti: Balaenopteridae</strong></td>
<td>Megaptera novaeangliae</td>
<td>Humpback</td>
<td>54.3</td>
<td>Atlantic</td>
<td>3.6</td>
<td>Bone</td>
<td>5</td>
<td>−12.1</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Balaenoptera acutorostrata</td>
<td>Minke</td>
<td>57.3</td>
<td>Pacific</td>
<td>3.4</td>
<td>Bone</td>
<td>7</td>
<td>−11.7</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>Balaenoptera musculus</td>
<td>Blue whale</td>
<td>52.0</td>
<td>Atlantic</td>
<td>3.2</td>
<td>Bone</td>
<td>1</td>
<td>−11.5</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Balaenoptera physalus</td>
<td>Fin whale</td>
<td>52.0</td>
<td>Atlantic</td>
<td>3.4</td>
<td>Bone</td>
<td>6</td>
<td>−11.8</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Balaenoptera edeni</td>
<td>Bryde’s whale</td>
<td>34.0</td>
<td>Atlantic</td>
<td>3.7</td>
<td>Bone</td>
<td>1</td>
<td>−10.7</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Balaenoptera borealis</td>
<td>Sei whale</td>
<td>65.0</td>
<td>Atlantic</td>
<td>3.4</td>
<td>Bone</td>
<td>5</td>
<td>−13.9</td>
<td>1.1</td>
</tr>
<tr>
<td><strong>Mysticeti: Balaenidae</strong></td>
<td>Eubalaena glacialis</td>
<td>N. right whale</td>
<td>56.0</td>
<td>N. Pacific</td>
<td>3.2</td>
<td>Bone</td>
<td>3</td>
<td>−14.9</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Eubalaena australis</td>
<td>S. right whale</td>
<td>62.6</td>
<td>S. Atlantic</td>
<td>3.2</td>
<td>Bone</td>
<td>2</td>
<td>−15.6</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>Balaena mysticetus</td>
<td>Bowhead whale</td>
<td>71.3</td>
<td>Arctic</td>
<td>3.2</td>
<td>Bone</td>
<td>2</td>
<td>−14.2</td>
<td>2.1</td>
</tr>
<tr>
<td><strong>Mysticeti: Eschrichtiidae</strong></td>
<td>Eschrichtius robustus</td>
<td>Gray whale</td>
<td>60.0</td>
<td>Pacific</td>
<td>3.3</td>
<td>Bone</td>
<td>13</td>
<td>−10.2</td>
<td>0.6</td>
</tr>
<tr>
<td><strong>Mysticeti: Neobalaenidae</strong></td>
<td>Caperea marginata</td>
<td>Pygmy right whale</td>
<td>41.0</td>
<td>S. Pacific</td>
<td>3.2</td>
<td>Bone</td>
<td>1</td>
<td>−10.4</td>
<td></td>
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<tr>
<td><strong>Odontoceti: Delphinidae</strong></td>
<td>Tursiops truncatus</td>
<td>Bottlenose dolphin</td>
<td>33.4</td>
<td>N. Pacific</td>
<td>4.2</td>
<td>Teeth</td>
<td>12</td>
<td>−9.9</td>
<td>0.8</td>
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<td></td>
<td>Delphinus capensis</td>
<td>Long-beaked common dolphin</td>
<td>32.5</td>
<td>Pacific</td>
<td>4.2</td>
<td>Teeth</td>
<td>9</td>
<td>−10.2</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Cephalorhynchus hectori</td>
<td>Hector’s dolphin</td>
<td>45.0</td>
<td>Pacific</td>
<td>4.2</td>
<td>Teeth</td>
<td>2</td>
<td>−8.4</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>Phocoena phocoena</td>
<td>Harbor porpoise</td>
<td>36.6</td>
<td>N. Pacific</td>
<td>4.1</td>
<td>Teeth</td>
<td>5</td>
<td>−9.7</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Pseudorca crassidens</td>
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<td>Bone/teeth</td>
<td>15</td>
<td>−10.4</td>
<td>0.6</td>
</tr>
</tbody>
</table>

* Estimate of trophic level from Pauly et al. (1998).

** SD = standard deviation, except when n = 3, in which case range in values is reported instead.

The effects of these environmental changes will be taken into account when comparing fossil cetacean stable isotopic values to expected ecological patterns derived from analysis of extant species.

### 3.3. Bioapatite preparation

Bioapatite preparation for enamel and bone samples, both modern and fossil, followed Koch et al. (1997) and began by collecting a minimum of 10 mg of powder from specimens using a dental drill. Organic matter (e.g., collagen, lipids) was oxidized and removed from powders by soaking in 30% H2O2 (1 mL of H2O2: 25 mg of powder) for 48 h and rinsing with distilled waters (5 times). Non-lattice bound carbonates, either original or produced during the preceding oxidation step, were dissolved and removed from powders by soaking for 24 h in 1 M calcium acetate/acetate acid buffer solution (1 mL of buffered acetic acid:25 mg of powder) at 4 °C and rinsing with distilled water (5 times). Powders were then frozen for 1 h and lyophilized overnight using a Labconco 4.5 L freeze-drier.

### 3.4. Isotopic analyses

Each stable isotopic analysis used ~1.5 mg of bone powder prepared for measurement of the lattice-bound carbonate portion of bioapatite. Analyses were conducted on a Thermo Finnegan GasBench linked to a
Thermo Finnegan DeltaPLUS XP continuous flow IRMS in the University of Wyoming Stable Isotope Facility. Samples were weighed into individual reaction vials, capped, evacuated under helium, and then dissolved in 100% phosphoric acid overnight at room temperature. For small samples (<1.0 mg), cryogenic freezing trapped and concentrated resulting CO2 before admittance to the mass spectrometer for analysis. The inter-lab isotope standard was NBS-19 and values are reported in standard delta (δ) notation, where \[ \delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \] and \( R \) is \(^{13}\text{C}/^{12}\text{C}\) for carbon and \(^{18}\text{O}/^{16}\text{O}\) for oxygen. Units are per mil (‰) and values are reported as the per mil deviation from the internationally accepted standard for carbon (Vienna PeeDee Belemnite, V-PDB) and oxygen (Vienna Standard Mean Ocean Water, V-SMOW). Precision of isotopic analysis was assessed via multiple analyses of an in-house elephant enamel standard (δ\(^{13}\text{C}: 1 \sigma = 0.1\%\); δ\(^{18}\text{O}: 1 \sigma = 0.2\%\); n = 24 for both).

3.5. Statistical analyses

For species or genus-level differences in mean value within and among sites, a Student’s t-test (two tailed, assumption of unequal variance) was used for comparisons between two species and a single-factor ANOVA (Analysis of Variance) was used for comparisons of more than 2 species with subsequent pair-wise comparisons of taxa evaluated by a post-hoc Bonferroni test. Significant differences in variance between species and groups were evaluated using a standard F-test. For multiple comparisons that did not meet the criteria necessary to perform parametric statistics, a non-parametric Kruskal–Wallis one way ANOVA (OW-ANOVA) on Ranks was used and followed by evaluation of pair-wise comparisons of taxa using Dunn’s Method. Correlations between stable isotope data and latitude and between specimen δ\(^{13}\text{C}\)

Fig. 3. Map of locations where (A) extant cetaceans (circles) and (B) Oligocene-aged cetacean fossils were recovered (circles). The location of sample localities included in this study (1. South Carolina; 2. New Zealand) is represented by white stars. Modern map was generated using the software PanMap and Oligocene map was generated from the Paleobiology Database (www.pbdb.org) on December 15, 2011.
and δ\(^18\)O values were evaluated using Reduced Major Axis (RMA) regression. This regression was selected over standard ordinary least squares (OLS) regression because all stable isotope measurements were made with equivalent degrees of error, and, as noted above, all estimates of latitude included significant uncertainty; under these conditions, RMA is more appropriate than OLS (Sokal and Rohlf, 2012). For all comparisons, the level of statistical significance was set at \(p < 0.05\). All statistical measurements were performed using SigmaStat v.3.1 or KaleidaGraph v.3.6 software.

4. Results and discussion

4.1. Latitudinal variation in modern cetacean isotopes

Mean bioapatite stable isotope values for extant species of mysticetes and odontocetes are listed in Table 1. Values for individual specimens are provided in Appendix 1. Specimens covered a large range in δ\(^13\)C values (9.3‰), extending from −16.0‰ for one specimen of southern right whale (Eubalaena australis) to a high value of −6.7‰ for a Hector’s dolphin (Cephalorhynchus hectori). The range in bioapatite δ\(^18\)O values was smaller, but still significant (6.7‰), and extended from a low of 23.4‰ for a bowhead whale (Balaena mysticetus) to a high value of 30.1‰ for a sperm whale (Physeter macrocephalus).

These results showed that living marine cetaceans foraging in waters at different latitudes record environmental differences in isotopic values (Fig. 4A–C) surprisingly well and exhibit tight values for most species (Fig. 5). Bioapatite δ\(^18\)O values were more strongly correlated with latitude (Fig. 5A; \(r^2 = 0.829\)) than bioapatite δ\(^13\)C values (Fig. 5B; \(r^2 = 0.591\)), but both relationships were statistically significant (\(p < 0.001\)). The correlation between δ\(^13\)C and δ\(^18\)O values of bioapatites was high (Reduced Major Axis regression: \(y = 1.077 \pm 0.135 \times X – 39.60 \pm 12.85; r^2 = 0.654, p < 0.001;\) Fig. 5C) and similar to that observed between environmental δ\(^13\)C and δ\(^18\)O values (Fig. 4C).

Species with the highest isotopic values were restricted to low and midlatitudes in the Atlantic and Pacific Oceans and include species of both odontocetes and mysticetes. Species that either exclusively (Balaena mysticetus, Delphinapterus leucas) or primarily (Balaenoptera borealis) foraged at higher latitudes (>45° latitude) had much lower isotopic values. This connection between isotopic values and latitude suggests that measurement of the isotopic composition of cetacean bone and tooth material could be used to track the movement patterns of these species. While field observations of living populations of cetaceans can provide this information as well, this process can be expensive and time consuming, often requiring multiple field seasons before meaningful information is obtained. Likewise, observational data are often unavailable for historical and older populations of the same species, which poses a problem when trying to understand how movement patterns for living species have changed over time. In these instances, stable isotope analysis of specimens from museums and research collections may be the only way to acquire this information.

Besides separation based on latitude, bioapatite δ\(^13\)C values for cetacean species were also separated based on trophic position (Fig. 6). The mean δ\(^13\)C value for all mysticete species (−12.0±1.8‰) was significantly lower than that of all odontocete species (−10.3±1.2‰) (Student’s t-test, \(t = 5.719, df = 74, p < 0.0001\)). This separation meets the expectations based on accrual of a small, but consistent isotopic enrichment with each step in trophic position between that of baleen whales, which feed on zooplankton and small fish, and that of odontocetes, which feed on larger squid, fish and warm-blooded vertebrates. Likewise, the difference between mean δ\(^18\)O values for all mysticetes (25.7±0.9‰) and odontocetes (27.7±1.2‰) was statistically significant (Student’s t-test, \(t = 9.875, df = 99, p < 0.0001\)).

Exceptions to the general trends observed between cetacean stable isotope values and latitude are found for five species of mysticetes, including onerorqual (Balaenoptera borealis), all species of balaenid sampled as part of this project (Balaena mysticetus, Eubalaena glacialis, Eubalaena australis), and the gray whale (Eschrichtius robustus). Bioapatite δ\(^18\)O values for two of these species (B. mysticetus, E. australis) match expected values based on the preferred foraging latitudes for these species (Fig. 5A), but values for the other species (B. borealis, E. glacialis, E. robustus) are significantly higher than expected. Likewise, δ\(^13\)C values for both right whales (E. australis, E. glacialis) are significantly lower than expected from the latitudes where they were recovered, whereas values for B. mysticetus and B. borealis closely match expectations and the value for E. robustus is considerably higher (Fig. 5B). The extremely high δ\(^18\)O value for E. robustus is most likely due to the benthic foraging of this species at high latitudes where benthic crustaceans exhibit elevated δ\(^18\)O values relative to prey items found in surface waters (Hobson et al., 2002).

For the other four species, their contrast from other cetaceans is most apparent when bioapatite δ\(^18\)O values are plotted against δ\(^13\)C values (Fig. 5C). Even though extremely low δ\(^13\)C values for phytoplankton in the southern hemisphere (Fig. 4B) could account for this observation in exclusively austral species (e.g., Eubalaena australis), the observation of extremely low δ\(^13\)C for species from high latitudes to the north (Balaena mysticetus, Eubalaena glacialis) suggests that location may not be the only factor contributing to these low values. One dietary character shared by these four species
Fig. 4. Bivariate plots of latitude vs. (A) seawater $\delta^{18}O$ values and (B) marine plankton $\delta^{13}C$ values for northern (white) and southern (gray) hemisphere seawater samples (Rau et al., 1989; Bigg and Rohling, 2000). Each symbol represents a mean value (error bars: ±1 SD) for seawater and plankton within a bin size of 5° latitude. (C) A combined plot of seawater $\delta^{18}O$ values and plankton $\delta^{13}C$ values for northern and southern hemisphere oceans. Values are the same as those shown in A and B.

Fig. 5. Bivariate plots of absolute latitude vs. (A) mean $\delta^{18}O$ and (B) $\delta^{13}C$ values (±1 SD) for modern cetaceans (odontocetes: gray; mysticetes: white). All mysticete species that primarily forage on zooplankton (balaenids and Balaenoptera borealis) are marked with an asterisk. (C) A combined plot of mean $\delta^{18}O$ vs. mean $\delta^{13}C$ values (±1 SD) for bioapatite sampled from modern cetaceans. Dashed lines in each graph represent the Reduced Major Axis regressions through the data.
is the consumption of significant quantities of copepods and euphausi-
siids during the year (Bannister, 2009). The high lipid content of these zooplankton may impart significantly lower δ13C values for cetaceans with surface-water copepods and euphausiids as a major component of diet at a given latitude (Schell et al., 1998). This isotopic offset from the observed latitudinal trend is significant and easily identified by the carbon isotopic composition of bone or tooth material, making it a potential proxy for zooplankton consumption and, therefore, filter-feeding by living and fossil cetaceans. Given the uniqueness of filter-feeding among living marine mammals and the poor preservation potential of baleen and other organic structures used for this style of feeding, a geochemical tracer could elucidate the origin of this feeding style in the fossil record.

4.2. Ancient marine isoscapes: Oligocene fossil deposits

Stable isotope analyses of tooth enamel from multiple species of early odontocetes and toothed mysticetes from fossil sites near Charleston, South Carolina, USA (~33°N) and Waitaki Valley region, New Zealand (~45°N) show trends in carbon and oxygen isotopic compositions similar to those observed for living cetacean species (Fig. 7; Table 2). Slightly elevated δ13C values (+1.9‰) among Oligocene cetaceans likely reflect both natural and post-industrial anthropogenic changes in the carbon isotopic composition of atmospheric CO2 since the Oligocene (Suess, 1955; Tipple et al., 2010); present-day atmospheric CO2 has a δ13C value of ~−8.0‰, whereas an estimate of values for most of the Cenozoic, including the Oligocene, is ~−6.1 ± 0.6‰ (Table 3).

In contrast, mean δ18O values for living and fossil cetaceans are surprisingly similar. The lack of a strong difference between values for these specimens suggests that the oxygen isotopic composition of seawater at this time (ca. 28 Ma) was very close to present-day values and that a significant quantity of 18O was sequestered in continental ice. These findings support recent estimations of ice-volume and seawater δ18O values (δ18Ow) based on other isotopic and elemental proxies (Lear et al., 2004; Lear and Rosenthal, 2006; Katz et al., 2008; Lear et al., 2008; Bohaty et al., 2012).

Lear et al. (2004) have generated the most detailed record of δ18Ow values over our time interval of interest (28.4 to 23.0 Ma; Fig. 8), and this record provided the basis for our marine isoscape for the Oligocene.

Following a 1.5‰ increase across the Eocene–Oligocene boundary, δ18Ow values oscillated over short (~100 kyrs) and long (~2 Myrs) timescales in response to fluctuations in the extent of continental ice on Antarctica. Combined, these variations produce a 1.6‰ range in δ18Ow values, from a high of ~0.5‰ at 28–27 Ma to a low of ~−1.1‰ at ca. 24.0 Ma (Fig. 8). As this record was constructed from stable isotope analysis of benthic foraminifera, these values reflect the oxygen isotopic composition of Oligocene bottom waters, which are more or less uniform globally and representative of mean δ18Ow values (Zachos et al., 2001). As noted above, δ18Osw values deviate from δ18Ow values in response to latitudinal differences in net evaporation and precipitation. This relationship between δ18Osw values and latitude was true for the Oligocene (Clementz and Sewall, 2011), and was used to correct δ18Ow values to δ18Osw values for fossil localities in South Carolina, USA (paleolatitude = 33°N) and New Zealand (paleolatitude = 50.9°S) (Table 3). For the latter, we used the following equation from Zachos et al. (1994):

\[
\delta^{18}O_{sw} = 0.576 + 0.041 \left( \text{Lat.} \right) - 0.00178 \left( \text{Lat.} \right)^2 + 1.35 \times 10^{-5} \left( \text{Lat.} \right)^3.
\]

This equation is a third-order polynomial fit to a compilation of δ18Osw data from the southern hemisphere Atlantic and Pacific Oceans. Since a similar relationship has not been constructed for these oceans in the northern hemisphere, we used the offset between surface and bottom waters in the northern hemisphere Atlantic Ocean (see Fig. 1 in Clementz and Sewall, 2011) as a correction for Oligocene surface waters in South Carolina (Table 3).

Specimens from South Carolina include species of toothed stem (basal) mysticetes and a family of early odontocetes (an undescribed family) (Fig. 7; Table 2; on systematics, see Geisler and Sanders, 2003). Only three specimens were available for sampling, which limits evaluating the statistical significance of results. However, the position of the toothed mysticete specimens at the base of the mysticete clade means these results have bearing on ecological interpretations of the early stages of mysticete evolution. Enamel δ13C and δ18O values and seawater δ18O at ca. 24.0 Ma (Fig. 8) are ~6.1 ± 0.6‰ and ~−8.0‰, respectively.

![Fig. 6. Plot of trophic level for extant cetacean species against mean δ13C values (+1 SD) for bioapatite (odontocetes: gray; mysticetes: white). Estimated trophic level for each species was based on Pauly et al. (1998). Horizontal dashed lines separate low δ13C values for cetacean species that forage primarily at higher latitudes from those that forage at low latitudes. For most species, bioapatite δ13C values are lowest for species foraging at low trophic levels at high latitudes and are highest for species foraging at high trophic levels at low to midlatitudes. One exception is the gray whale (Eschrichtius robustus), which feeds mainly on benthic crustaceans at high latitudes and is marked by a dotted circle.

![Fig. 7. Bivariate plot of individual δ13C and δ18O values for Oligocene-aged fossil cetaceans from South Carolina, USA and New Zealand (data available in supporting Appendices 2 and 3). Symbols are the same as those used in Fig. 1 with families of Cetacea differentiated by color (Odontoceti: Squalodontidae = black, 7Dalpiazimidæ = dark gray, Squalodelphinidae = light gray, Delphinidae and undescribed taxa = white; Mysticeti: Eomysticeti = black, Balaenopteridae = dark gray, Mammalodontidae = light gray; Kekenoetiidae = white diamonds). Dashed line is the regression for modern cetacean isotope values shown in Fig. 5C after correction for changes in atmospheric CO2 δ13C values (late Oligocene: −6.1 ± 0.6‰; modern: −8.0‰) and seawater δ18O values (late Oligocene: −0.3‰; modern: 0.0‰) (Lear et al., 2000; Tipple et al., 2010).]
δ¹⁸O values did not differ substantially among all three specimens, though δ¹³C values for toothed mysticetes were slightly higher than those for odontocetes. Compared to the observed relationship for extant cetaceans, the stable isotope values are consistent with foraging at low latitudes (~30°N); enamel δ¹³O values are extremely high (mean δ¹³O = 28.9 ± 0.1‰), much higher than values for specimens from New Zealand (Fig. 9B), and consistent with expectations of elevated δ¹³Osw values at low latitudes in the Oligocene. Furthermore, these values are most consistent with estimates of maximum δ¹³Osw values for this time interval (Fig. 8), which implies the age of all three specimens would be ca. 28–27 Ma. In regard to feeding ecology, enamel δ¹³C values do not indicate that the toothed mysticetes filter-fed or fed low in the food chain. The stable isotope results would allow that filter-feeding arose later among mysticetes, closer to the crown-group Mysticeti, supporting recent interpretations based solely on morphological evidence that filter-feeding was not associated with the initial divergence of the Mysticeti and Odontoceti (Fitzgerald, 2006).

Compared to specimens from South Carolina, late Oligocene specimens from New Zealand exhibit much greater variation in enamel and bullae δ¹³C values (Figs. 7 and 9A; Table 2). The difference in δ¹³C values among four higher taxa of fossil cetaceans (odontocetes, edentulous mysticetes, toothed mysticetes, kekenodontids) was statistically significant (One-way ANOVA, F = 6.687, df = 36, p = 0.001), but post-hoc analysis (pairwise Bonferroni) showed that only the difference between odontocetes and edentulous mysticetes was significant (p = 0.001). Odontocete δ¹³C values were highest, values for edentulous mysticetes were lowest, and δ¹³C values for toothed mysticetes and kekenodontids fell in between the other two groups (Table 2; Fig. 8).

Oxygen isotope values, however, are statistically similar among higher taxonomic groups (One-way ANOVA, F = 1.310, df = 36, p = 0.2286) and consistent with all specimens having foraged at roughly the same latitude. Likewise, no statistically significant differences were detected among fossils of different ages (Kruskal–Wallis, 7.0227, p = 0.071), but given uncertainties in age assignments, as well as the coarse-level at which these assignments were made (>2.0 Myrs; Table 2 and Appendix 4), this result should be interpreted with caution.

---

### Table 3

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<th>Location</th>
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<th>Oligocene latitude</th>
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³ Eq. (1) from Zachos et al. (1994).

---

**Fig. 8.** Estimated δ¹⁸O values for late Eocene to early Miocene seawater (constructed from published data in Lear et al., 2004). Light gray area marks the time interval of interest for this study (28.4 to 23.0 Ma) and dark gray area highlights the New Zealand Duntroonian Stage (27.3 to 25.2 Ma). Time ranges for all New Zealand Stages and International Stages are reported in Appendix 4.

**Fig. 9.** (A) Boxplot of bioapatite δ¹³C values and (B) histogram of bioapatite δ¹⁸O values (bin size = 0.3‰) for late Oligocene fossil cetaceans from New Zealand and South Carolina. Statistically significant differences in δ¹³C values are noted by letters above each boxplot; values for odontocetes (A) are significantly higher than those for edentulous mysticetes (B), but neither are significantly distinct from those of toothed mysticetes (AB) nor anterior dentition sampled from kekenodontids (AB) (α = 0.05).
A histogram of all fossil $\delta^{18}O$ values (Fig. 9B) shows a bimodal distribution with one peak centered at 26.2±0.2‰ (n = 13), another at 27.3±0.3‰ (n = 15), and a single outlier at 24.5‰. Lack of an associated change in enamel $\delta^{13}C$ values (Fig. 7) suggests that this difference in $\delta^{18}O$ values was not caused by changes in home range or migratory movements of these specimens. Instead, this large difference in bioapatite $\delta^{18}O$ values is most likely age-related; the difference between these two peaks (1.1‰) is in good agreement with the estimated range in Oligocene $\delta^{18}O_{sw}$ values for this latitude (1.6‰; Table 3), and implies that these individuals inhabited the same area, but lived during two distinct time intervals (ca. 28–27 Ma and ca. 25–23 Ma; Fig. 8). As for the one outlier, its low enamel $\delta^{18}O$ value (24.5‰) is outside of the expected range of $\delta^{18}O_{sw}$ values for this time interval. Its enamel $\delta^{13}C$ value isn’t significantly lower than values for other odontocetes, which makes it difficult to explain the low $\delta^{18}O$ value as resulting from foraging at higher latitudes. Instead, we interpret the stable isotope values for this specimen as suggestive of foraging in estuarine environments. Aquatic mammals that favor these habitats today often have enamel $\delta^{13}C$ values similar to those of nearshore marine consumers, but much lower $\delta^{18}O$ values because of reduced salinities and greater freshwater inputs in estuaries (Clementz and Koch, 2001).

Though further analyses are needed to confirm this interpretation, this single result is interesting because it would represent the earliest evidence yet of the movement of Neoceti back into estuarine habitats.

As with fossil cetaceans from South Carolina, basal toothed mysticetes (Family Mammalodontidae) and odontocetes have similar $\delta^{13}C$ values and do not support filter-feeding on zooplankton by the mammalodontids, or feeding low in the food chain by either the mammalodontids or odontocetes. In contrast, bullae $\delta^{13}C$ values for edentulous mysticetes (Family Eonycticephalidae and stem-balaenopteroids) are extremely low with some specimens yielding values approaching −15.0‰. These low $\delta^{13}C$ values are significantly different from those of the toothed mysticetes or odontocetes from these sites and suggest that these mysticetes may have specialized on a diet of zooplankton similar to that of living balaenids and other mysticete whales (Figs. 7 and 9A). Given the lack of teeth and the present of osteological correlates for baleen in these specimens, filter-feeding is the assumed feeding style for these species — as is consistent with this isotope proxy.

What is unexpected, however, is the discovery of extremely low $\delta^{13}C$ values for tooth enamel from the kekenodontids, which represent a group of archaic whales (Archaeoceti) close to the Neoceti. The lowest $\delta^{13}C$ values for these specimens come from the analysis of the cheekteeth (−13.9±0.9‰, n = 3), which are about 3.0‰ lower than the anterior dentition (−11.0±0.3‰, n = 5) (Fig. 8). Based on examination of dental eruption in the basilosaurid Dorudon atrox (Uhen, 2000), molars are assumed to be the first adult teeth to erupt in advanced archaeocetes, followed by the more anterior dentition. If true for kekenodontids, the extremely low $\delta^{13}C$ values for the cheekteeth of these specimens could represent consumption of milk, which tends to have a lower $\delta^{13}C$ value than adult diet because of its high proportion of $^{13}C$-depleted lipids (Newsome et al., 2006). Evidence in support of this interpretation has come from analysis of multiple tooth types of a single specimen of Zygorhiza kochii, which shows a similar offset (−3.0‰) in $\delta^{13}C$ values between its cheekteeth and anterior dentition (Uhen and Clementz, 2010). Even after exclusion of cheekteeth from our analysis, enamel and bullae $\delta^{13}C$ values are still low and more similar to mean $\delta^{13}C$ values for toothed and edentulous mysticetes than odontocetes (Fig. 9A, Table 2). These low $\delta^{13}C$ values suggest that kekenodontids may have been feeding at a relatively low trophic position on small, schooling fish rather than the larger fish and squid, with higher $\delta^{13}C$ values, that would have been favored by coeval odontocetes. While these data do not irrefutably support filter-feeding by kekenodontids, they also do not rule out its possibility. Our results instead encourage further study of fossils from these enigmatic cetaceans to ultimately resolve this question.

5. Conclusions

Our data suggest that cetacean feeding ecology in the Oligocene was more diverse than hitherto reported. Multiple species of late-surviving archaeocetes, early odontocetes, and toothed and edentulous mysticetes were sympatric, and partitioned food resources in their shared habitat by feeding with or without echolocation or baleen, and low or high in the food chain. Major changes in the productivity of the world’s oceans in the Oligocene probably facilitated the development of filter-feeding, as upwelling of cold, nutrient-rich bottom waters intensified and plankton growth became increasingly restricted to large, seasonal blooms in cool temperate to polar regions. The evolution of bulk-feeding would have enabled large consumers to take advantage of these short, but regular bursts of an abundant food supply. This shift by some cetaceans to a lower trophic position would also have had a strong impact on the structure and composition of marine food webs, as suggested for the role of odontocete predation on the abundance and diversity of cephalopods (squid, octopus, nautilids) (Lindberg and Pyenson, 2007). Here we focused on climatic, tectonic and oceanic changes as major drivers of marine diversity and composition. The diversity of feeding strategies among Oligocene Cetacea suggests a need to consider the escalation of cetacean predation pressure on an ever-widening prey-base when reconstructing the history of marine ecosystems through the Cenozoic. The Oligocene was likely a time when this predation pressure intensified significantly.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2012.09.009.

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