



Calcium isotopes reveal the trophic position of extant and fossil elasmobranchs

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ABSTRACT

Recent calcium isotope studies recovered a trophic level effect in marine ecosystems. However, elasmobranchs are virtually absent from such studies despite their important ecological role, their diversity and their extensive fossil record. Enameloid of extant elasmobranchs representing differing known ecologies were measured for $\delta^{44/42}\text{Ca}$. The results reveal that their calcium isotope values have a distribution (from -0.27 to -0.78%) that follows a stepwise decrease ($\Delta^{44/42}\text{Ca}$) of about -0.14% across recognized trophic levels: zooplanktivores, primary, secondary, and tertiary consumers. Although the recovered calcium isotope distributions partly match the ecological divisions of extant elasmobranchs, data for marine mammals are more variable and cannot be explained by trophic segregation alone. Nevertheless, our results reopen perspectives for the study of ancient marine assemblages using calcium isotopes. As a case study, the calcium isotope values of a Pliocene fish assemblage parallel the results obtained from extant elasmobranchs and allow inferring that the giant shark *Megaselachus megalodon* fed at a slightly higher trophic level than the contemporaneous Great White shark.

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1. Introduction

The isotope reconstruction of dietary ecology and foraging preferences in living marine animals is mostly restricted to carbon and nitrogen isotopes in soft tissues (Minagawa and Wada, 1984). The elemental strontium/calcium (Sr/Ca) and barium/calcium (Ba/Ca) ratios offer an alternative for the fossilizable mineral phase of bone and teeth (Peek and Clementz, 2012). However, diagenesis (Balter et al., 2011) and seawater temperature (Balter and Lécuyer, 2010) are two independent parameters that can overprint the primary dietary Sr/Ca and Ba/Ca signatures. To date, there is little work on alternate isotope markers such as calcium, which is particularly bioavailable in the ocean (average concentration of ~ 420 ppm e.g. Elderfield and Schultz, 1996) and incorporates the shell and bioapatite skeleton of both invertebrate and vertebrate organisms. Moreover, the isotope composition of seawater is identical at the global scale due to the relatively long residence time of calcium in the ocean (~ 1 Ma e.g. Zhu and Macdougall, 1998) and seawater calcium composition has not significantly changed in the last 5 Ma (De La Rocha and De Paolo, 2000; Fantle and De Paolo, 2005; Griffith et al., 2008) relative to the biological variation measured in previous work (Clementz et al., 2003). Early work on calcium isotopes showed a significant decrease in calcium isotope ratios with increasing

trophic level in both terrestrial and marine ecosystems (Skulan et al., 1997; Skulan and DePaolo, 1999). Subsequently, Clementz et al. (2003) analyzed a number of extant and fossil marine mammals and showed that their calcium isotope values also matched the first noted trend in decreasing values with increasing trophic level.

Because of their high diversity and abundance worldwide, elasmobranchs play an important role in marine ecosystems and previous studies have shown that large sharks have the potential to shape marine communities (Ferretti et al., 2010). But elasmobranch calcium isotope data are virtually absent from the literature. Due to their breadth of feeding ecology (from zooplanktivores to tertiary consumers), the various species of elasmobranchs provide a testable mean to assess the utility of calcium isotopes in dietary reconstruction. If there is a trophic effect on calcium isotopes for marine invertebrates and mammals, then this should also be reflected in extant elasmobranchs, which have high modern diversity, and are also abundant in the fossil record.

Here, we examine the calcium isotope composition of tooth apatite from 18 extant species of elasmobranchs of known ecologies (Table 1) using Multi-Collection Inductively Coupled Plasma Mass Spectrometry (MC-ICP-MS). We show that significant differences exist between elasmobranch groups with different feeding ecologies. We discuss the calcium isotope variability of elasmobranchs in the context of marine food webs and finally assess the utility of this geochemical tool in paleoecology with a case study from two Pliocene (ca. 5 Ma) fish assemblages.

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Table 1
 Ca stable isotope values of elasmobranch teeth, fish teeth and marine mammal bone and teeth analyzed in this study together with taxonomic and ecological information. ¹: consumer level inference from this study; for body lengths: *: estimate; **: extrapolation from Adnet et al. (2010); ***extrapolation from Gottfried et al. (1996). Abbreviations: n, replicates; TL: total length for sharks; DW: disk width for rays.

Taxon	Vernacular name	Diet	Provenance	Coll number	Habitat	Consumer level	Total Length or Disc Width (cm)	δ44/42Ca (‰ ICP Ca Lyon)	2SD	replicate analysis	δ44/42Ca (‰ IAPSO SW)	2SD
<i>Extant</i>												
<i>Cetorhinus maximus</i>	basking shark	plankton	North Sea	REC0946M	pelagic	zooplanktivore	383 TL	−0.48	0.08	5	−0.89	0.10
<i>Manta birostris</i>	manta ray (male)	plankton	Baja California	NS83-003	pelagic	zooplanktivore	500* DW	−0.27	0.07	3	−0.68	0.09
<i>Scyliorhinus stellaris</i>	spotted dogfish/nursehound	opportunistic	Mediterranean Sea	REC0185M	benthic	primary	90 TL	−0.51	0.03	3	−0.92	0.07
<i>Mustelus punctulatus</i>	houndshark	crustaceans	Mediterranean Sea	REC0321M	demersal	primary	121 TL	−0.38	0.10	6	−0.79	0.12
<i>Myliobatis aquila</i>	common eagle ray	mainly malacophagous	Mediterranean Sea	REC1119M	benthic	primary	max. 100* DW	−0.50	0.05	4	−0.90	0.08
<i>Oxynotus centrina</i>	angular roughshark	invertebrates	Mediterranean Sea	REC0251M	demersal	primary	72 TL	−0.45	0.05	3	−0.86	0.08
<i>Dasyatis centroura</i>	rougthead stingray	invertebrates	Mediterranean Sea	REC0627M	benthic	primary	85 TL	−0.47	0.06	3	−0.88	0.09
<i>Odontaspis ferox</i>	small-toothed sandtiger shark	fish, crustaceans	Pacific	-	demersal	secondary	max 300* TL	−0.57	0.03	2	−0.98	0.07
<i>Galeorhinus galeus</i>	school shark	piscivorous/opportunistic	Mediterranean Sea	REC0347M	demersal	secondary	146 TL	−0.57	0.07	3	−0.98	0.09
<i>Carcharhinus brevipinna</i>	spinner shark	piscivorous	Mediterranean Sea	REC0270M	pelagic	secondary	95 TL	−0.54	0.06	3	−0.95	0.09
<i>Prionace glauca</i>	blue shark	piscivorous/opportunistic	Mediterranean Sea	-	pelagic	secondary	max 300* TL	−0.59	0.09	4	−1.00	0.11
<i>Lamna nasus</i>	porbeagle shark	piscivorous	Mediterranean Sea	REC0136M	pelagic	secondary	140 TL	−0.58	0.19	4	−0.99	0.20
<i>Squalus acanthias</i>	spiny dogfish	piscivorous/opportunistic	Mediterranean Sea	REC0223M	pelagic	secondary	72 TL	−0.58	0.12	3	−0.99	0.13
<i>Alopias vulpinus</i>	common thresher shark	piscivorous	Mediterranean Sea	REC0159M	pelagic	secondary	404 TL	−0.63	0.15	3	−1.04	0.16
<i>Dalatias licha</i>	kitefin shark	opportunistic (mainly fish)	Mediterranean Sea	REC0254M	demersal	secondary	87 TL	−0.46	0.08	5	−0.87	0.10
<i>Carcharodon carcharias</i>	white shark	fish, turtles, birds, mammals	unknown	-	pelagic	tertiary	300* TL	−0.74	0.07	3	−1.15	0.09
<i>Hexanchus griseus</i>	sixgill shark	opportunistic (inc. dead mammals)	Mediterranean Sea	REC0201M	demersal	tertiary	58 TL	−0.66	0.06	3	−1.07	0.08
<i>Hexanchus griseus</i>	sixgill shark	opportunistic (inc. dead mammals)	Mediterranean Sea	REC0204M	demersal	tertiary	200 TL	−0.68	0.13	3	−1.09	0.14
<i>Carcharodon carcharias</i>	white shark	fish, turtles, birds, mammals	Mediterranean Sea	REC0610M	pelagic	tertiary	max 400* TL	−0.78	0.12	4	−1.19	0.13
<i>Mysticete indet.</i>	whale (vertebra)	plankton	unknown	ISEM-no num	pelagic	zooplanktivore	-	−0.12	0.10	5	−0.53	0.12
<i>Dugong dugon</i>	dugong (tooth)	seagrass	unknown	N170	coastal	herbivore	-	−0.67	0.10	3	−1.08	0.12
<i>Dugong dugon</i>	dugong (bone)	seagrass	unknown	N170	coastal	herbivore	-	−0.83	0.05	4	−1.24	0.08
<i>Odobenus rosmarus</i>	walrus (enamel)	invertebrates, fish	unknown	N374	coastal	omnivore	-	−0.86	0.09	4	−1.27	0.11
<i>Odobenus rosmarus</i>	walrus (bone)	invertebrates, fish	unknown	N374	coastal	omnivore	-	−1.07	0.16	4	−1.48	0.17
<i>Tursiops truncatus</i>	dolphin (tooth)	mainly fish	unknown	ISEM-no num	pelagic	piscivore	-	−1.33	0.07	5	−1.74	0.09
<i>Tursiops truncatus</i>	dolphin (bone)	mainly fish	unknown	ISEM-no num	pelagic	piscivore	-	−1.64	0.11	4	−2.05	0.13
<i>Fossil</i>												
<i>Sphyracidae indet</i>	barracuda	-	Early Pliocene, Libya	ALA 041	-	primary ¹	max. 100* TL	−0.61	0.13	5	−1.02	0.14
<i>Sparidae indet.</i>	seabream	-	Early Pliocene, Libya	ALA 042	-	primary ¹	max. 200* TL	−0.44	0.08	3	−0.85	0.10
<i>Myliobatis sp.</i>	shell-crushing ray	-	Early Pliocene, Libya	ALA 040	-	primary ¹	max. 70* DW	−0.45	0.05	2	−0.85	0.08
<i>Carcharodon carcharias</i>	white shark	-	Early Pliocene, Libya	ALA 005	-	tertiary ¹	450** TL	−0.72	0.09	5	−1.13	0.11
<i>Megaselachus megalodon</i>	megalodon	-	Early Pliocene, Libya	ALA 001	-	tertiary ¹	700*** TL	−0.87	0.13	5	−1.28	0.14
<i>Megaselachus megalodon</i>	megalodon	-	Pliocene, New Caledonia	-	-	tertiary ¹	900*** TL	−0.87	0.08	3	−1.28	0.10

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