

## NOTE

Influence of swimming form on otolith  $\delta^{13}\text{C}$  in marine fish

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**ABSTRACT:** While temperature records are available from otolith  $\delta^{18}\text{O}$  profiles in fish, interpreting changes in otolith  $\delta^{13}\text{C}$  remains ambiguous. We compiled a global database of published otolith  $\delta^{13}\text{C}$  values for 60 species representing 30 families of marine fishes. Species' mean otolith  $\delta^{13}\text{C}$  ranged from +0.5 to -8.6 ‰. Among-family variance in otolith  $\delta^{13}\text{C}$  was uniquely explained by a morphometric index for aerobic swimming activity (caudal aspect ratio,  $r^2 = 0.61$ ). The models that consistently explained the maximum among-species variance in otolith  $\delta^{13}\text{C}$  included caudal aspect ratio and maximum depth of occurrence. Our analysis supports the use of otolith carbon-isotope ratios to indicate metabolism (primarily active) in marine fish. This information may be applied to studies of fish feeding and related food-web structure, both past and present.

**KEY WORDS:** Otolith · Stable isotopes ·  $\delta^{13}\text{C}$  · Marine fish · Metabolism · Swimming activity · Caudal aspect ratio · Morphometrics

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Stable isotope analysis is one of the most powerful tools available in the study of natural systems. Examples include the use of stable isotope ratios of nitrogen ( $^{15}\text{N}$ : $^{14}\text{N}$ ) and carbon ( $^{13}\text{C}$ : $^{12}\text{C}$ ) to explore complex food-web relationships (Vander Zanden et al. 1999), nitrogen to reconstruct historical trends in fish abundance (Finney et al. 2000), and oxygen ( $^{18}\text{O}$ : $^{16}\text{O}$ ) to infer pre-historic sea surface temperatures (Andrus et al. 2002). In all cases, the successful application of stable isotope techniques relies on a good understanding of the biological and environmental factors that influence isotopic ratios (isotopic fractionation) for the material under examination.

Fish otoliths (earstones) are aragonite ( $\text{CaCO}_3$ ) structures best known to biologists as recorders of fish age (Campana & Thorrold 2001), but they also have a long history in oxygen and carbon isotope analysis (Devereux 1967, Degens et al. 1969). Oxygen precipitates at or near isotopic equilibrium with ambient water in

otoliths, and otolith  $\delta^{18}\text{O}$  is thus useful for estimating temperature of precipitation (Thorrold et al. 1997). Otolith carbon, on the other hand, is a complex mixture of dissolved inorganic carbon (DIC) from ambient water and respired (metabolic) carbon (Thorrold et al. 1997), which makes interpreting changes in carbon isotope ratios difficult: ambient (seawater) DIC has a distinct  $\delta^{13}\text{C}$  signature (~1‰; Schwarcz et al. 1998) compared to metabolic carbon  $\delta^{13}\text{C}$  (~-18‰ for metabolizable tissue of many marine fish; Davenport & Bax 2002). Indeed, variations in otolith  $\delta^{13}\text{C}$  have been argued to reflect several factors, including metabolism (e.g. Kalish 1991a; no attempt has been made to differentiate between active and resting metabolism), diet  $\delta^{13}\text{C}$  (e.g. Begg & Wiedman 2001), trophic position (e.g. Gauldie 1996), DIC  $\delta^{13}\text{C}$  (e.g. Schwarcz et al. 1998), depth (e.g. Mulcahy et al. 1979), and temperature (e.g. Kalish 1991a). Kinetic isotope effects have been considered and, for the most part, discounted in the formation of fish otoliths; see Kalish (1991a) for a complete discussion of kinetic effects. Otolith  $\delta^{13}\text{C}$  could be influenced by all of the above factors. However, few have actually been tested, and the relative importance of each remains uncertain. In the present study, we make use of a wealth of isotope data contained in the literature and spanning over 30 yr to empirically assess the relative influence of metabolism (both active and resting), diet, trophic position, depth and temperature on otolith carbon-isotope ratios.

**Methods.** Our analysis is based on taxonomic-level variations in swimming form, body size, diet, trophic position, and maximum depth of occurrence ( $Z_{\text{max}}$ ), as well as published otolith  $\delta^{18}\text{O}$  values (a proxy for temperature) for 60 species from 30 families of marine fishes from around the globe (Table 1).

Swimming form can be indexed by caudal aspect ratio ( $K_{\text{caud}}$ ; Webb 1984), which is given as:  $K_{\text{caud}} = h^2/s$ , where  $h$  is the height of the caudal fin, and  $s$  is the sur-

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Table 1. Otolith carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope ratios, caudal aspect ratio ( $K_{\text{caud}}$ ), asymptotic length ( $L_{\text{inf}}$ ), trophic position (TP), diet, and maximum depth of occurrence ( $Z_{\text{max}}$ ) for 60 species from 30 families of marine fishes. Isotope data are given as mean value for each species/study. Isotope data sources: (1) Dufour et al. (1998); (2) Degens et al. (1969); (3) Kalish (1991a); (4) Gauldie et al. (1994); (5) Iacumin et al. (1992); (6) Gao et al. (2001a); (7) Edmonds & Fletcher (1997); (8) Gaughan et al. (2001); (9) Gao et al. (2001b); (10) Schwarcz et al. (1998); (11) Wiedman & Millner (2000); (12) Begg & Weidman (2001); (13) Stephenson et al. (2001); (14) Radtke (1987); (15) Edmonds et al. (1999); (16) Gao & Beamish (1999); (17) Radtke et al. (1987); and (18) Gauldie (1996)  $K_{\text{caud}}$ ,  $L_{\text{inf}}$ , TP, diet,  $Z_{\text{max}}$  data are from Froese & Pauly (2003). nd: no data

Family	Species (n)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	Source	$K_{\text{caud}}$	$L_{\text{inf}}$ (cm)	TP	Diet (% pelagic)	$Z_{\text{max}}$ (m)
Acanthuridae	<i>Acanthurus triostegus</i> (8)	-3.7	-0.6	1	2.2	27	2.8	0	90
Ariommatidae	<i>Ariomma regulus</i> (1)	-5.5	0.8	2	4.6	25	3.4	33	500
Arripidae	<i>Arripis esper</i> (2)	-4.0	0.6	3	3.2	96	4.3	92	80
	<i>Arripis trutta</i> (25)	-5.6	0.3	3	4.0	89	3.9	50	30
Berycidae	<i>Beryx splendens</i> (11)	-2.5	0.5	4	2.6	70	4.0	34	1300
Bramidae	<i>Brama brama</i> (2)	-6.5	0.4	3	3.3	100	4.1	100	1000
Carangidae	<i>Trachurus declivus</i> (2)	-5.4	1.1	3	2.8	64	3.6	100	460
	<i>Trachurus trachurus</i> (5)	-1.3	0.6	5	3.2	70	3.6	65	600
Centracanthidae	<i>Maena maena</i> (16)	-4.1	1.7	5	3.5	25	3.7	100	130
Centrolophidae	<i>Centrolophus niger</i> (1)	-3.2	1.3	2	2.5	150	4.0	100	600
	<i>Hyperoglyphe bythites</i> (1)	-1.2	-0.2	2	nd	60	nd	nd	nd
	<i>Psenopsis obscura</i> (1)	-0.9	1.1	2	1.5	20	nd	nd	800
	<i>Schedophilus pemarko</i> (1)	-3.6	-0.1	2	0.7	50	nd	nd	500
	<i>Seriola violacea</i> (1)	-0.6	1.0	2	2.5	65	nd	100	nd
Chaetodontidae	<i>Chaetodon ulietensis</i> (8)	-4.8	-0.3	1	2.1	15	3.3	0	30
Cheilodactylidae	<i>Cheilodactylus macropterus</i> (4)	-6.1	0.4	3	3.9	70	3.4	0	450
Clupeidae	<i>Clupea pallasii</i> (92)	-2.8	-1.8	6	2.6	46	3.4	100	150
	<i>Sardina pilchardus</i> (19)	-6.1	0.6	5	3.0	25	3.4	100	100
	<i>Sardinops sagax</i> (403)	-6.9	0.9	7	3.9	40	2.5	97	200
	<i>Sardinops sagax</i> (185)	-7.0	0.7	8	3.9	40	2.5	97	200
Engraulidae	<i>Engraulis encrasicolus</i> (27)	-4.3	-0.2	5	2.2	20	2.9	100	400
Gadidae	<i>Gadus merlangus</i> (8)	-1.7	2.2	5	1.2	70	3.9	23	200
	<i>Gadus minutus</i> (2)	-2.4	2.4	5	1.5	40	3.8	32	400
	<i>Gadus morhua</i> (1)	0.3	1.9	2	1.8	200	4.1	25	600
	<i>Gadus morhua</i> (10)	-1.2	2.1	9	1.8	200	4.1	25	600
	<i>Gadus morhua</i> (61)	-0.4	nd	10	1.8	200	4.1	25	600
	<i>Gadus morhua</i> (11)	-1.0	2.8	11	1.8	200	4.1	25	600
	<i>Melanogrammus aeglefinus</i> (100)	-0.9	1.3	12	1.8	100	3.3	0	450
	<i>Melanogrammus aeglefinus</i> (1)	0.5	1.5	2	1.8	100	3.3	0	450
Gempylidae	<i>Thyrustes atun</i> (4)	-5.3	0.8	3	2.9	200	3.9	100	550
Lutjanidae	<i>Lutjanus sebae</i> (396)	-4.2	-0.6	13	2.2	116	4.1	38	180
	<i>Pristipomoides filamentosus</i> (1)	-4.2	-0.9	14	2.1	100	3.6	44	400
Merlucciidae	<i>Merluccius bilinearis</i> (1)	-0.8	1.4	2	0.8	76	4.4	83	914
	<i>Merluccius merluccius</i> (10)	-2.9	2.0	5	0.9	140	4.2	72	1000
Moridae	<i>Pseudophycis barbatus</i> (4)	-1.4	1.1	3	0.7	63	3.5	0	300
Moronidae	<i>Dicentrarchus labrax</i> (1)	-5.5	0.5	5	1.7	103	3.8	50	10
	<i>Roccus lineatus</i> (1)	-4.4	nd	2	2.0	200	4.6	70	30
Myctophidae	<i>Ceratoscopelus maderensis</i> (1)	-4.1	2.0	2	1.4	8	3.1	100	700
Nototheniidae	<i>Notothenia squamifrons</i> (2)	-3.8	2.7	3	1.2	55	3.3	42	680
Osmeridae	<i>Osmerus mordax</i> (1)	-2.5	-1.5	2	2.1	36	3.2	34	150
Pomatomidae	<i>Pomatomus saltatrix</i> (226)	-4.2	0.7	15	2.2	130	4.3	71	200
Salmonidae	<i>Oncorhynchus nerka</i> (34)	-4.5	0.8	16	2.6	84	3.4	100	250
Sciaenidae	<i>Corvina nigra</i> (9)	-1.5	0.6	5	0.9	47	4.1	50	100
Scombridae	<i>Thunnus maccoyii</i> (2)	-7.9	-1.6	3	5.4	245	3.9	60	50
	<i>Thunnus thynnus</i> (3)	-8.6	-1.5	17	6.0	458	4.4	80	100
Serranidae	<i>Epinephelus multinotatus</i> (327)	-4.6	-0.8	13	2.2	100	3.9	33	100
	<i>Serranus scriba</i> (1)	-4.7	-0.2	5	1.3	36	3.9	50	150
Sparidae	<i>Boops boops</i> (11)	-6.4	0.4	5	3.3	36	3.2	50	350
	<i>Boops salpa</i> (8)	-6.9	0.3	5	4.2	51	2.0	0	70
	<i>Dentex dentex</i> (6)	-3.5	0.5	5	3.9	100	4.5	100	200
	<i>Diplodus annularis</i> (1)	-7.3	-0.1	5	2.6	24	3.4	20	90
	<i>Diplodus sargus sargus</i> (2)	-6.0	0.7	5	4.2	45	3.0	0	50
	<i>Diplodus vulgaris</i> (2)	-2.6	1.4	5	3.8	45	3.2	25	160
	<i>Lithognathus mormyrus</i> (6)	-5.7	-0.7	5	3.0	55	3.4	0	150

Table 1 (continued)

Family	Species (n)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	Source	$K_{\text{caud}}$	$L_{\text{inf}}$ (cm)	TP	Diet (% pelagic)	$Z_{\text{max}}$ (m)
Acanthuridae	<i>Acanthurus triostegus</i> (8)	-3.7	-0.6	1	2.2	27	2.8	0	90
	<i>Oblada melanura</i> (10)	-5.7	0.3	5	3.7	34	3.3	0	30
	<i>Pagellus erythrinus</i> (3)	-3.5	1.3	5	2.0	60	3.2	25	300
	<i>Pagrus auratus</i> (64)	-2.0	1.7	15	3.2	130	3.4	40	200
	<i>Puntazzo puntazzo</i> (1)	-4.6	1.1	5	3.7	60	2.9	0	150
	<i>Sparus auratus</i> (3)	-4.0	0.5	5	2.0	70	3.6	40	150
	<i>Spondyliosoma cantharus</i> (3)	-3.3	1.3	5	3.0	60	3.1	0	300
Stromateidae	<i>Pampus argenteus</i> (1)	-4.0	0.2	2	2.9	60	3.3	52	110
	<i>Peprilus triacanthus</i> (1)	-4.6	-1.1	2	3.1	30	3.9	50	15
	<i>Stromateus stellatus</i> (1)	-0.8	0.9	2	2.7	25	nd	nd	nd
Trachichthyidae	<i>Hoplostethus atlanticus</i> (1)	-2.3	nd	18	1.4	75	4.1	80	1810
	<i>Hoplostethus atlanticus</i> (10)	-1.0	2.4	3	1.4	75	4.1	80	1810
Triglidae	<i>Prionotus evolans</i> (1)	-0.2	-0.2	2	1.0	45	4.1	50	180

face area of the caudal fin extending to the narrowest part of the caudal peduncle;  $h$  and  $s$  were estimated from digital images available online<sup>1</sup>.  $K_{\text{caud}}$  should relate to the active component of a fish's metabolism; high values are typical of more streamlined, continuously active fish (e.g. tuna), while low values are associated with comparatively less active, benthic feeders (e.g. cod) (Webb 1984). Resting (standard) metabolism is typically a decreasing function of body mass and an increasing function of temperature (e.g. Gillooly et al. 2001). As opposed to considering body mass (as a proxy for standard metabolism), we used asymptotic length ( $L_{\text{inf}}$ ) for the practical reason that body length data was available for a broader range of species. Given the wide range of body sizes represented in our data set (Table 1), these 2 variables become virtually interchangeable, despite the fact that different species can have different length/weight relationships. Unless otherwise stated, we assumed that otolith isotope data was for adult fish, which should be approaching asymptotic sizes. Again, this assumption should be valid considering the range of adult body sizes represented by the 60 species included in our analysis (Table 1). Diet was calculated as occurrence of prey of pelagic origin (zooplankton and nekton) in the diet of adults as a percentage of the total number of diet observations; variation in  $\delta^{13}\text{C}$  of marine organisms is strongly related to habitat (i.e. pelagic vs benthic; Davenport & Bax 2002). Detailed diet data as well as trophic position estimates and length and depth data are available online (Froese & Pauly 2003). We assumed that any uncertainties in these parameters (for individual species) will be outweighed by the larger among-species variation contained in our data set.

<sup>1</sup>Froese R, Pauly D (2003) FishBase. World Wide Web electronic publication (www.fishbase.org)

Stable isotope ratios (see individual source studies for detailed analytical techniques) are expressed in  $\delta$  notation in ‰-deviation from a standard material (Peedee belemnite limestone, or equivalent). For stable carbon,  $\delta^{13}\text{C} = \{[(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}}] - 1\} \times 1000$ . We explored the effect of all variables ( $K_{\text{caud}}$ ,  $L_{\text{inf}}$ , diet, trophic position,  $Z_{\text{max}}$  and otolith  $\delta^{18}\text{O}$ ) on otolith  $\delta^{13}\text{C}$  at both species and family levels (employing linear and multiple regression).

**Results and discussion.** Caudal aspect ratio explained 61% of the among-family (Fig. 1) and 44% of the among-species (Table 2) variance in otolith  $\delta^{13}\text{C}$ . No other variable was significant in a multiple regression at the family level. At the species level, the model that explained the maximum variance included caudal aspect ratio, log-maximum-depth of occurrence, diet and trophic position ( $r^2 = 0.61$ ; see Table 2 for equations). Log  $Z_{\text{max}}$  and otolith  $\delta^{18}\text{O}$  were significantly, positively correlated ( $r^2 = 0.26$ ,  $p < 0.0001$ ). Asymptotic

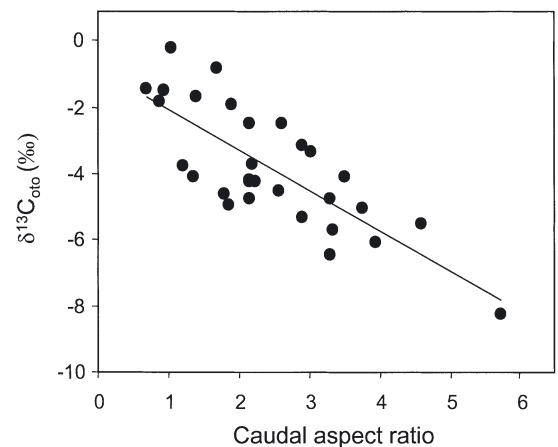


Fig. 1. Otolith  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_{\text{oto}}$ ) plotted against caudal aspect ratio for 30 families of marine fishes ( $r^2 = 0.61$ ,  $p < 0.0001$ )

Table 2. Results of multiple linear regressions correlating otolith  $\delta^{13}\text{C}$  with various predictor variables for full data set (Table 1) and reduced data set (Table 1, where  $n \geq 4$ ).  $K_{\text{caud}}$ : caudal aspect ratio; TP: trophic position;  $Z_{\text{max}}$ : maximum depth of occurrence. Note: equation(s) of form  $\delta^{13}\text{C}_{\text{otolith}} = a + b_1 \times (k_{\text{caud}}) + b_2 \times (\log Z_{\text{max}}) + b_3 \times (\text{diet}) + b_4 \times (\text{TP})$  (see text for details).  $\text{SE}_{\text{est}}$ : standard error of estimate; na: not applicable

Predictor variables	<i>a</i>	<i>b</i> <sub>1</sub>	<i>b</i> <sub>2</sub>	<i>b</i> <sub>3</sub>	<i>b</i> <sub>4</sub>	<i>r</i> <sup>2</sup>	<i>p</i>	<i>n</i>	<i>SE</i> <sub>est</sub>
Full data set									
<i>k</i> <sub>caud</sub>	-0.5	-1.2	na	na	na	0.44	<0.0001	64	1.6
<i>k</i> <sub>caud</sub> , <i>Z</i> <sub>max</sub>	-3.6	-1.1	1.1	na	na	0.53	<0.0001	62	1.5
<i>k</i> <sub>caud</sub> , <i>Z</i> <sub>max</sub> , diet	-3.5	-1.1	1.3	-0.01	na	0.57	<0.0001	60	1.4
<i>k</i> <sub>caud</sub> , <i>Z</i> <sub>max</sub> , diet, TP	-6.7	-1.0	1.3	-0.02	0.8	0.61	<0.0001	60	1.4
Reduced data set									
<i>k</i> <sub>caud</sub>	0.1	-1.5	na	na	na	0.52	<0.0001	31	1.5
<i>k</i> <sub>caud</sub> , <i>Z</i> <sub>max</sub>	-3.5	-1.3	1.3	na	na	0.58	<0.0001	31	1.4

length (log transformed) was not significantly related to otolith carbon-isotope ratios among species or families. We considered the possibility that our results may be biased by small sample sizes used to calculate species-mean otolith isotope values in some studies (Table 1). We thus re-analysed the data set including only species-mean isotope values where  $n \geq 4$  (arbitrary). In this case, the model that explained the maximum variance in otolith  $\delta^{13}\text{C}$  included only caudal aspect ratio and depth ( $r^2 = 0.58$ , Table 2). Overall, caudal aspect ratio and depth had the largest and most consistent effects on otolith carbon-isotope ratios.

Metabolism has long been argued to have a major influence on otolith carbon-isotope ratios (e.g. Kalish 1991a, Thorrold et al. 1997, Schwarcz et al. 1998). Our analysis fully supports this expectation, but in a manner not previously considered. Metabolism, and associated oxygen consumption of fish, are generally decreasing functions of body size and increasing functions of temperature (Gillooly et al. 2001). A size/age-dependent decline in specific oxidative respiration would mean decreasing metabolic influence on otolith carbon (via respired carbon) as fish grow, and hence, increasing otolith  $\delta^{13}\text{C}$  (i.e. towards the isotopic signature of DIC). This is indeed the line of reasoning that has been cited in support of a metabolism-otolith  $\delta^{13}\text{C}$  link (e.g. Schwarcz et al. 1998). However, otolith  $\delta^{13}\text{C}$  does not always increase (enrich) with age. In some cases, otolith  $\delta^{13}\text{C}$  tends to deplete (e.g. Radtke 1987), in others it does not change appreciably with size and age (e.g. Radtke et al. 1987, Gauldie et al. 1994, Edmonds et al. 1999), and in some it first enriches, and then either depletes or equilibrates (e.g. Gauldie et al. 1994, Gauldie 1996, Schwarcz et al. 1998). It would appear that size- and age-related changes in metabolism are inadequate to explain the diversity of patterns for otolith  $\delta^{13}\text{C}$  ontogeny that exists both among and within populations and species. Alternatively, ontogenetic patterns in otolith  $\delta^{13}\text{C}$  have been attributed to

changes in metabolism due to sexual maturation (e.g. Schwarcz et al. 1998). However, this should produce similar patterns across species. Furthermore, it is conceivable that patterns in otolith  $\delta^{13}\text{C}$  are related to differences in temperature preference over the life of a fish, although this has never been shown.

To understand putative links between metabolism and otolith carbon-isotope ratios, it is helpful to consider the bioenergetic budget of a fish in its entirety. For example, consider the following equation,  $G = C - A \times \text{SMR} - L$ , where  $G$  is growth rate (somatic and gonadal),  $C$  is consumption rate,  $A$  is an activity multiplier (unitless),  $\text{SMR}$  is standard metabolic rate (function of body size and temperature), and  $L$  is the sum of the cost of digestion and fecal and urinary losses (Rowan & Rasmussen 1996). Fish activity is typically poorly understood and undervalued in this budget. However,  $A$  can be highly variable among species (Rowan & Rasmussen 1996), populations (Boisclair & Leggett 1989), and stages of maturity (Rowan & Rasmussen 1996), as well as a function of diet and food-web diversity (Sherwood et al. 2002a,b), and environmental conditions (Boisclair & Rasmussen 1996). *In situ* estimates of  $A$  range from 1 (i.e. negligible) to 4–5 in some fish (Rowan & Rasmussen 1996), representing as much as half of a fish's energy budget. As such, total metabolism, including  $A$ , is less dependent on body size than on differences in activity, which can be independent of body size. In the present study, the lack of any relationship between log asymptotic length (corresponding to almost 4 orders of magnitude in body mass) and otolith  $\delta^{13}\text{C}$  ( $p = 0.50$ ) suggests that size-related changes in  $\text{SMR}$  (e.g. Gillooly et al. 2001) are relatively unimportant to otolith carbon-isotope ratios. On the other hand, a significant effect of maximum depth of occurrence (related to otolith  $\delta^{18}\text{O}$ ) on otolith  $\delta^{13}\text{C}$  at the species level (Table 2) could reflect depth or temperature-dependent changes in  $\text{SMR}$ , activity, or both. Depleted otolith  $\delta^{13}\text{C}$  values were

associated with shallower depths, which in turn are associated with depleted otolith  $\delta^{18}\text{O}$  values (indicative of warmer temperatures). Nevertheless, the strong relationship between caudal aspect ratio and otolith  $\delta^{13}\text{C}$  among both species and families supports the idea that taxonomic-level variations in aerobic swimming activity ( $A$ ) are very important in determining otolith  $\delta^{13}\text{C}$ .

Our finding for a relationship between caudal aspect ratio and otolith  $\delta^{13}\text{C}$  (Fig. 1, Table 2) is similar to a relationship previously presented between oxygen consumption and otolith  $\delta^{13}\text{C}$  among species (Kalish 1991a). In fact, caudal aspect ratio, along with body weight ( $W$ ; g), temperature ( $T$ ;  $1000/^\circ\text{K}$ ), and a categorical variable for activity level (act: 0 for standard and routine metabolism, and 1 for active), significantly predicts relative  $\text{O}_2$  consumption ( $\text{VO}_2$ ,  $\text{mg kg}^{-1} \text{h}^{-1}$ ) among fish species (both freshwater and marine):  $\log \text{VO}_2 = 6.41 - 1.22 \times T - 0.26 \times \log W + 0.21 \times K_{\text{caud}} + 0.29 \times \text{act}$  ( $r^2 = 0.57$ ,  $p < 0.0001$  [all terms],  $n = 3480$   $\text{VO}_2$  observations from 119 species for which both  $\text{VO}_2$  and  $K_{\text{caud}}$  data are available online: see Froese & Pauly 2003; this excludes cases where some form of stress was applied). The range in  $K_{\text{caud}}$  within our data set (0.7 to 6.0) may thus involve a ca. 13-fold variation in relative  $\text{O}_2$  consumption among species. In comparison, the range in body sizes within our data set (0.2 to 680 kg) may be expected to produce a ca. 8-fold variation in relative  $\text{O}_2$  consumption. Within-species variations in oxygen consumption are likely to have a similar effect on otolith carbon-isotope ratios. It is important to note that the maximum reported ontogenetic range in otolith  $\delta^{13}\text{C}$  within a species (7.7‰; Edmonds et al. 1999) is almost as high as that among species (9.6‰; present study). The average ontogenetic range for all species is  $2.1 \pm 2.2\%$  (mean  $\pm 1$  SD,  $n = 64$ ; present study). This should include many cases for which the full range in otolith  $\delta^{13}\text{C}$  values was not measured.

Our total metabolism explanation for variations in otolith carbon-isotope ratios is much more flexible than explanations based on size- or age-related changes in standard metabolism and may be applied to understanding almost any ontogenetic, temporal and/or spatial pattern in otolith  $\delta^{13}\text{C}$ . We propose that patterns of enrichment in otolith  $\delta^{13}\text{C}$  with age and size, over time or among populations, can be indicative of shifts from active, pelagic feeding (e.g. zooplanktivory; this feeding mode may also be associated with active schooling behaviours) to relatively sedentary, benthic feeding. The reverse may be true for patterns of depletion. For example, cod *Gadus morhua* typically experience ontogenetic diet shifts from zooplankton to benthic invertebrates, and subsequently to pelagic forage fish (e.g. capelin *Mallotus villosus* when available;

Rose & O'Driscoll 2002). Based on this pattern of diet ontogeny, we would expect cod otolith  $\delta^{13}\text{C}$  to progress from depleted values to more enriched values, and return to more depleted values (when and if pelagic forage fish are available). Indeed, this pattern in cod otolith  $\delta^{13}\text{C}$  values has been observed (Schwarcz et al. 1998). Temporally or spatially, otolith  $\delta^{13}\text{C}$  may vary as a function of food availability. Low food availability may translate into higher activity (e.g. searching; Kerr 1971) and hence, more negative otolith  $\delta^{13}\text{C}$ . A significant decrease in maximum otolith  $\delta^{13}\text{C}$  values of Atlantic cod in Canadian waters from the late 1980s to the early 1990s (by  $\sim 1\%$ ; Schwarcz et al. 1998) coincides with a decline in size-at-age of cod over the same time period (Rose et al. 2000), a possible result of lower food resources and increased searching. Such a temporal shift in cod otolith  $\delta^{13}\text{C}$  has also been suggested to reflect movement to deeper waters, where ambient DIC  $\delta^{13}\text{C}$  is more negative (Schwarcz et al. 1998). Paradoxically, we find that depth is positively correlated with otolith  $\delta^{13}\text{C}$  (Table 2). This suggests that changes in metabolism with depth (over broad depth ranges) are more important than changes in DIC  $\delta^{13}\text{C}$ . This finding does not rule out the possibility that changes in vertical distribution over the upper few hundred meters of the water column (where most of the decline in DIC  $\delta^{13}\text{C}$  occurs; Schwarcz et al. 1998) may lead to changes in otolith  $\delta^{13}\text{C}$ . Future studies may address this question of depth more closely.

On a final note, both diet and trophic position have been hypothesized to influence otolith  $\delta^{13}\text{C}$  of various fishes (e.g. Kalish 1991b, Gauldie 1996, Schwarcz et al. 1998, Begg & Weidman 2001). Interestingly, we found only a minor effect of either variable on otolith  $\delta^{13}\text{C}$  among species of vastly different feeding habits and trophic position, which disappeared when we considered only the reduced data set (Table 2); neither variable was significant at the family level. There are 2 possible reasons for these poor relationships. First, the difference in pelagic versus benthic prey  $\delta^{13}\text{C}$  is not very large in marine systems. The absolute range in  $\delta^{13}\text{C}$  values for benthic versus pelagic endpoints from the Newfoundland shelf ecosystem is only 5‰; this value is even smaller ( $\sim 3\%$ ) for the ontogenetic range in cod muscle  $\delta^{13}\text{C}$  (G. D Sherwood unpubl. data). Thus, at  $M = 0.3$ , which represents a 30% contribution of metabolic carbon to the otolith carbon pool (e.g. Kalish 1991b), a high value for  $M$  (corresponding to a high metabolic rate), otolith  $\delta^{13}\text{C}$  could only vary by 1.5‰ (assuming a complete diet/habitat shift). A second reason not to expect diet and trophic position to have a large influence on otolith  $\delta^{13}\text{C}$  is that these variables may not be independent of swimming activity. Excluding tuna, which have very high caudal aspect ratios, trophic position was significantly negatively



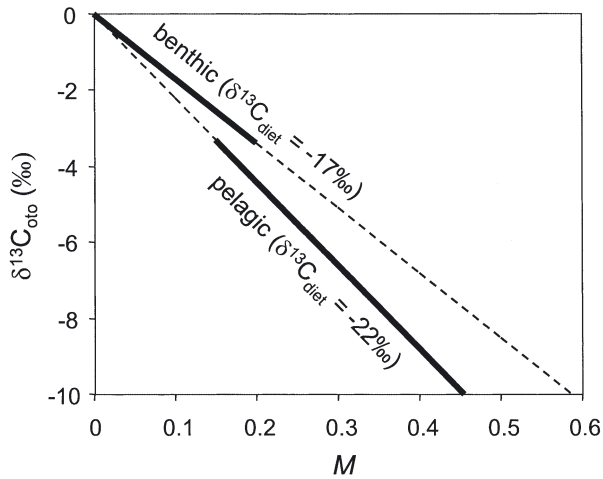


Fig. 2. Otolith  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_{\text{oto}}$ ) modelled as a function of relative contribution (fraction,  $M$ ) of metabolic (respired) carbon to otolith carbon pool and diet  $\delta^{13}\text{C}$  (dissolved inorganic carbon [DIC]  $\delta^{13}\text{C}$  assumed to be 0‰). Solid lines represent likely combination of  $M$  and diet  $\delta^{13}\text{C}$  for most fish species. The model assumes isotopic equilibrium between diet and metabolic carbon. Diet  $\delta^{13}\text{C}$  values from Newfoundland shelf ecosystem (G. D. Sherwood unpubl. data)

related to  $K_{\text{caud}}$  among species ( $r^2 = 0.18$ ,  $p < 0.001$ ). Thus, highly active species are likely to consume mainly pelagic prey of low to intermediate trophic position, while inactive, demersal species are likely to consume mostly benthic prey of relatively high trophic position. Fig. 2 is a conceptual representation of the expected combined effect of changes in  $M$  (argued here to be activity) and diet  $\delta^{13}\text{C}$  on otolith carbon-isotope ratios.

**Conclusions.** Overall, the strength of our findings lies in the simplicity of our approach. By making use of broad-scale variations in taxon-specific properties of fish, we have identified active metabolism (indexed by caudal aspect ratio) as the most important determinant of carbon isotope ratios in fish otoliths. Based on this analysis, we propose that carbon isotope ratios in fish otoliths have the potential to indicate changes in the aerobic activity and foraging patterns of wild fish. This knowledge should prove invaluable for making inferences about feeding relationships of fish and related food-web structure of marine systems, both contemporary and historical.

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