Journal of Fish Biology (2003) **63,** 1341–1346
doi:10.1046/j.1095-8649.2003.00238.x, available online at http://www.blackwell-synergy.com

Allometric growth of the sulcus in *Cynoscion* spp. (Sciaenidae)

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(Received 24 April 2003, Accepted 18 August 2003)

The sulcus of *Cynoscion* spp. exhibited strong positive allometric growth relative to the medial surface of the otolith, and the ratio between the area of the sulcus and the otolith (S:O) increased dramatically with size. The S:O ratios of larger specimens are the highest that have so far been reported.

Key words: allometry; *Cynoscion*; otoliths; Sciaenidae; S:O ratio; sulcus.

Recently, the relationship between the area of the sagitta (saccular otolith or otolith) and the area of the sulcus has received attention because of its potential influence on fish hearing (Gauldie, 1988; Lombarte, 1992; Arellano *et al.*, 1995; Aguirre & Lombarte, 1999). The sulcus is a depression on the medial surface of the otolith that forms where the maculus or sensory tissue comes into contact with the otolith. The relative size of the sulcus is typically described as a ratio of the area of the sulcus (S) to the area of the medial surface of the otolith (O), the S:O ratio (Gauldie, 1988). Gauldie (1988) presented a model according to which fishes with a relatively large sulcus (as a proxy for the maculus) are more sensitive to sound. The extent to which the sulcus changes shape and relative size as the otolith grows, however, is poorly known. Allometric changes in the relative size of the sulcus have only rarely been reported in the literature and generally are not thought to be important. Gauldie (1988) reported maculus (M) to otolith (M:O) and S:O ratios have constant values over large size ranges. This was based, however, primarily on observations made on three species: *Hoplostethus atlanticus* Collett, *Hoplostethus mediterraneus* Cuvier and *Trachurus declivis* (Jenyns). Significant increases in S:O ratios with body length have since been documented in merluccids (Lombarte, 1992), gobiids (Arellano *et al.*, 1995) and mullids (Aguirre & Lombarte, 1999).

The Sciaenidae, commonly known as drums or croakers, are highly sonic perciform fishes with characteristically large otoliths that have a large, 'tadpole-shaped' sulcus (Fig. 1). Both the otolith and sulcus have been important in the

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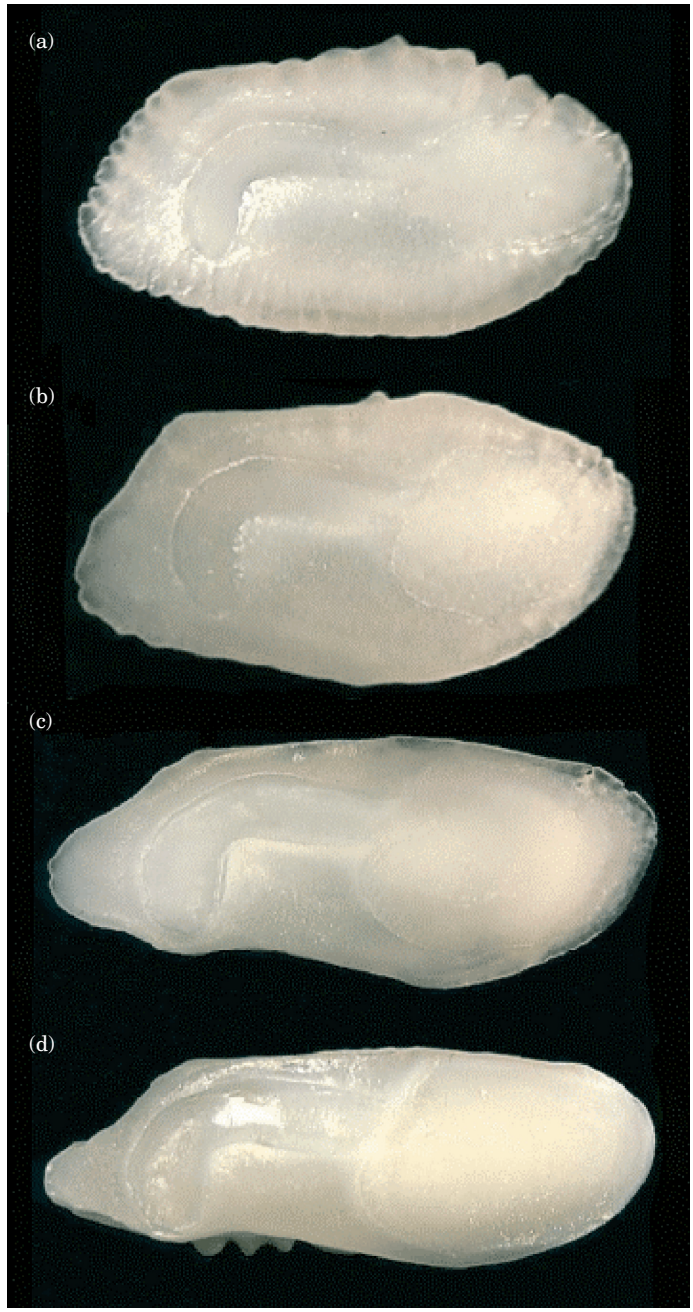

FIG. 1. Characteristic size series of *Cynoscion nebulosus* otoliths. Medial view of left otoliths with the anterior end towards the right. The sulcus is the large 'tadpole-shaped' depression. Otoliths are not scaled to actual size. Standard length and otolith length of specimens (mm): (a) 57·9 and 3·87; (b) 107·5 and 6·49; (c) 298 and 16·53; (d) 544 and 26·15.

systematics of the group (Moshin, 1973; Trewavas, 1977; Chao, 1978; Sasaki, 1989; Schwarzhans, 1993), as well as for species identification (Félix, 1994; Laerm *et al*., 1997). Reports of allometric growth of sciaenid otoliths, however, are sparse and usually non-quantitative (Volpedo & Echeverría, 1999). In this study the S:O ratios were quantified for the first time for the family Sciaenidae in eight species of weakfish of the genus *Cynoscion* and the relationship between the S:O ratio and standard length (L_S) was assessed. The relationship between the growth of the area of the sulcus and the area of the medial face of the otolith, as well as between the area of the otolith and sulcus and L_S were also evaluated, and allometric coefficients for these relationships are presented and tested for significant deviations from isometry.

Four species from the eastern Pacific and four from the western Atlantic were included in this study (Table I), with species chosen based on their availability. Standard length was measured from the tip of the snout to the distal end of the last caudal vertebra. Specimens included ranged from *c*. 45 to 550 mm L_s, but size ranges varied among species (Table I). Otoliths were extracted from 25 fresh specimens per species, cleaned gently with water and air-dried. All otoliths were incorporated into the Gulf Coast Research Laboratory (GCRL) otolith collection in Ocean Springs, Mississippi, U.S.A. Digital images of the otoliths were captured using a Panasonic model GP-KR222 Industrial Color CCD camera and measured with Sigma Scan Pro Image Analysis System version 5.0. The area of the sulcus and medial surface of the left otolith were measured, and the S:O ratio was calculated by dividing the area of the sulcus by the total area of the medial surface of the otolith. Standard length and the area of the sulcus and otolith were $\log_{10}$ transformed for statistical analyses. The allometric coefficients (b) for the relationship between the area of the sulcus and otolith, the area of the otolith and L_s, and the area of the sulcus and L_s were calculated for

TABLE I. Standard length (ranges and means), allometric coefficient (b ± S.E.) of relationship between $\log_{10}$ area of the sulcus (S) and $\log_{10}$ area of the medial surface of the otolith (O), S:O (ranges and means), and coefficients of determination (r^2) for the relationship between S:O ratio and $\log_{10}$ standard length for eight species of *Cynoscion* ($n = 25$ per species). Superscript numbers indicate where specimens were collected: 1, eastern Pacific, Gulf of Guayaquil, Ecuador; 2, western Atlantic, northern Gulf of Mexico, U.S.A.; 3, western Atlantic, Atlantic coast of the U.S.A.

Species	L_s range	Mean	b (S *v*. O)	S:O range	S:O mean	r^2
C. albus (Günther)[1]	126–435	271	1·189 ± 0·010	0·376–0·555	0·486	0·938
C. analis (Jenyns)[1]	170–330	220	1·203 ± 0·044	0·389–0·513	0·439	0·492
C. arenarius Ginsburg[2]	44–260	171	1·235 ± 0·016	0·255–0·547	0·438	0·865
C. nebulosus (Cuvier)[2]	50–543	284	1·230 ± 0·009	0·278–0·623	0·501	0·958
C. nothus (Holbrook)[2, 3]	50–216	144	1·218 ± 0·010	0·316–0·529	0·456	0·949
C. phoxocephalus Jordan & Gilbert[1]	122–368	257	1·205 ± 0·021	0·398–0·592	0·507	0·770
C. regalis (Bloch & Schneider)[3]	150–287	207	1·259 ± 0·027	0·424–0·581	0·479	0·808
C. squamipinnis (Günther)[1]	117–383	216	1·120 ± 0·012	0·440–0·591	0·511	0·784

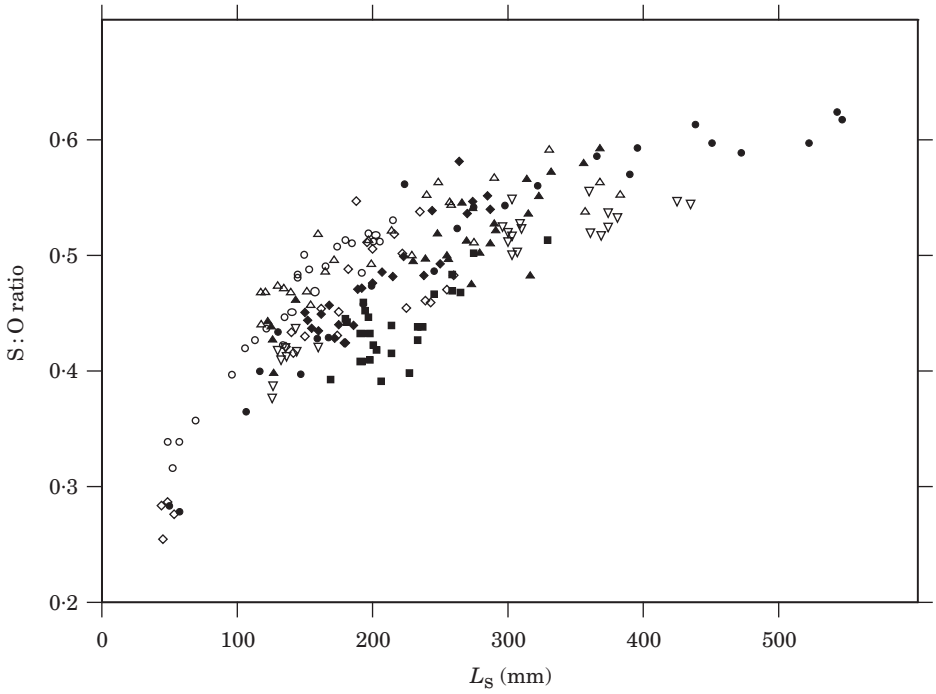

FIG. 2. The relationship between the S:O ratio and standard length of *Cynoscion albus* (▽), *C. analis* (■), *C. arenarius* (◇), *C. nebulosus* (●), *C. nothus* (○), *C. phoxocephalus* (▲), *C. regalis* (▲) and *C. squamipinis* (△).

each species using the log-linear version of the equation $y = ax^b$, and tested for significant deviations from isometry (b = 1 for area *v*. area comparisons, and b = 2 for area *v*. length comparisons).

The area of the medial surface of the otolith occupied by the sulcus increased significantly with L_s. The sulcus exhibited strong positive allometric growth relative to the otolith in all species (*t*-tests of $b = 1$, $P < 0{\cdot}05$). Allometric coefficients for this relationship ranged from 1·120 in *Cynoscion squamipinnis* (Günther) to 1·259 in *C. regalis* (Block & Schneider), and averaged 1·207 (Table I). The positive allometric growth of the sulcus relative to the otolith was also evidenced by the large increase of the S:O ratio with L_s. (Fig. 2). These two variables were strongly associated, with $\log_{10} L_s$ accounting for >75% of the variance in the S:O ratio pooled across species (least squares regression, d.f. = 1 and 198, $r^2 = 0{\cdot}762$, $P << 0{\cdot}0001$) indicating that size was the most important predictor of the S:O ratio. Although L_s had a large influence on S:O ratios, there were interspecific differences, with slopes for the relationship between S:O ratio and L_s differing significantly among species (ANCOVA, d.f. = 7 and 184, $P = 0{\cdot}0007$). Regressing S:O ratio on L_s individually for each species, L_s accounted for at least 49%, and on average 82%, of the within species variance of the S:O ratio. In *Cynoscion nebulosus* (Cuvier), the species with the largest size range, L_s accounted for 96% of the variance. In general, smaller specimens

had smaller S:O ratios, with the smallest S:O ratio measured (0·255) coming from a specimen of *C. arenarius* Ginsburg 45 mm L_s, and the largest (0·623) coming from a specimen of *C. nebulosus* 544 mm L_s. Consequently the S:O ratio of a species of *Cynoscion* will in large part be a function of the size of the specimens examined. Even S:O ratios of small specimens, however, were large relative to those of other taxa. Mean S:O ratios in this study ranged from 0·438 in *C. arenarius* to 0·511 in *C. squamipinnis* (Table I and Fig. 2) and are among the largest reported for any group of fishes, with the largest individual values surpassing all previously reported records (Arellano *et al.*, 1995; Aguirre & Lombarte, 1999).

Despite the large size of the otoliths of *Cynoscion* species, these exhibited strong negative allometric growth relative to L_s. Allometric coefficients for the relationship between otolith area and L_s ranged from 1·243 in *Cynoscion phoxocephalus* Jordon & Gilbert to 1·615 in *C. squamipinnis*, averaging 1.491, and all differed significantly from isometry (t-tests of $b=2$, $P<0{\cdot}05$). Although the sulcus exhibited strong positive allometric growth relative to the otolith, allometric coefficients for the relationship between the area of the sulcus and L_s ranged from 1·496 in *C. phoxocephalus* to 1·931 in *C. arenarius* (averaging 1·800), and were significantly <2 in five of the eight species (t-tests of $b=2$, $P<0{\cdot}05$), indicating negative allometric growth of the sulcus relative to L_s in these species. Allometric coefficients (±S.E.) were not significantly different from 2 in *Cynoscion analis* (Jenyns) ($b=1{\cdot}857\pm0{\cdot}088$, t-test, $0{\cdot}2>P>0{\cdot}1$), *C. arenarius* ($b=1{\cdot}931\pm0{\cdot}034$, t-test, $0{\cdot}1>P>0{\cdot}05$), and *C. regalis* ($b=1{\cdot}901\pm0{\cdot}058$, t-test, $0{\cdot}2>P>0{\cdot}1$). The increase in S:O ratios as specimens increase in L_s can thus be attributed to a decoupling of otolith and sulcus growth rates, with the otolith exhibiting strong negative allometry relative to L_s and the sulcus exhibiting much milder negative allometry or isometry.

The large relative size and distinctive shape of the sulcus is a characteristic feature of the Sciaenidae (Trewavas, 1977; Chao, 1978; Sasaki, 1989). In *Cynoscion*, and perhaps in sciaenids in general, however, the sulcus exhibits strong positive allometric growth relative to the medial surface of the otolith. The relative size of the sulcus of *Cynoscion* spp. will vary according to the size of the specimen examined, appearing greater in large specimens than in small specimens. Therefore, taking the allometric growth of the sulcus into consideration is important when otoliths are used to identify sciaenids. Furthermore, the allometric growth of the sulcus of *Cynoscion* is stronger than that previously reported for other taxa (Gauldie, 1988; Lombarte, 1992; Arellano *et al.*, 1995). Allometric coefficients for the area of the sulcus relative to the area of the otolith were larger in seven of the eight species of *Cynoscion* examined here (the exception was *C. squamipinnis*, $b=1{\cdot}120\pm0{\cdot}012$) than the largest previously published estimate, $b=1{\cdot}132\pm0{\cdot}0002$ for the merluciid *Merluccius paradoxus*-Franca (Lombarte, 1992). Although the characteristically large sulcus appears to be a feature that becomes more pronounced as specimens increase in length, the relatively large size of the otoliths of *Cynoscion*, which also characterizes sciaenids, decreased as specimens increased in length. A decrease in relative size of the otoliths with increasing body length has been reported for other taxa (Lombarte, 1992; Aguirre & Lombarte, 1999), and may be common in fishes.

This work was carried out while I was a graduate student at the Gulf Coast Research Laboratory, University of Southern Mississippi. S. Poss and B. Comyns provided valuable support, and N. Brown-Peterson, D. Waller, B. Pellegrin, D. Leffler, R. McMichael, J. Boylan, T. Targett, G. Fulling, C. Woodley, K. Larsen, M. Littmann, D. Chiluiza, D. Burke and V. Shervette assisted with the collection of specimens. The Instituto Nacional de Pesca and Dirección General de Pesca of Ecuador facilitated access to Ecuadorian species. M. Bell, W. al Gharaibeh and R. Geeta commented on an earlier version of the manuscript. Thoughtful suggestions from two anonymous reviewers are gratefully acknowledged.

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