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Changes in otolith structure of seagrass siganid Siganus canaliculatus during settlement

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Abstract. Coral reef fishes upon settlement undergo morphological changes. Their otoliths or ear bones that provide auditory and balance functions reflect integral changes associated with the transition from pelagic larval to demersal juvenile stages. In the seagrass siganid *Siganus canaliculatus*, otolith sulcus area grew at a slower rate with sagittal area and body size in both stages. Sulcus area apparently contracted or remained constant during this transition. The one-day difference between sampling of preand post-settled fish did not produce significant difference in sulcus area. Sulcus area-to-sagittal area ratio was higher at pre- than at post-settled fish. Sagittal area increased and it grew at faster rate with body size which indicates a shift to improved food availability and less harsher environment for the young fish. Sagittal growth was higher at post- than at pre-settlement. Body size and otolith area were several magnitude larger than sulcus area, thus, they dimensionally outgrew the sulcus. The faster growth of sulcus before settlement suggests the fish depends more on it during this phase than after settlement.

Key Words: Siganus canaliculatus, otolith area, settlement, sulcus, growth.

Introduction. Settlement is the transition of organism from pelagic to benthic environment which coincides with metamorphosis (Wellington & Victor 1992). During metamorphosis there are various changes occurring in the external and internal characteristics as well as the behavior of the fish (Fukahara 1988). Sagittal otoliths of newly metamorphosed and settled flatfishes display distinct secondary growth centres (accessory primordia) at the circumference of the larval otolith (Karakiri et al 1989; Sogard 1991). Alhossaini et al (1989) and Karakiri et al (1989) showed that settlement of North Sea plaice (*Pleuronectes platessa*) is synchronous during the formation of accessory primordia, a secondary growth center in the otolith structure associated during metamorphosis.

The otolith of *Siganus fuscescens* and *Siganus guttatus* during settlement is associated with rapid reduction of otolith increment width and increase in Strontium and Calcium ratio 4–5 days before the event (Yamada & Shibuno 2007; Yamada & Baba 2009). Otolith microstructural changes shown in the transition zone in the daily increment pattern are believed to occur during settlement (Sponaugle & Cowen 1994). This transition zone is characterized by rapid reduction of otolith increment width and lessening of increment opacity in *S. guttatus* (Soliman et al 2009).

Otolith growth, morphometrics and shape vary even at intra-specific level due to difference in growth of the fish (Campana & Casselman 1993) and life history (Ballagh et al 2012). Variability in growth during the larval stage is typically high and has been attributed to three causes: water temperature during the larval life stages (McCormick & Molony 1995), food availability (McCormick & Molony 1993) and delays in settlement once a stage of physiological competence has been reached (Cowen 1991). Differences in otolith structure depend not only on differential growth rates but also on the consistency of the environmental conditions encountered during the life history (Pothin et al 2006) and otolith can be completely reshaped by environmental conditions during ontogeny (Vignon 2012). The difference in metabolic rates linked to environmental factors may

influence the shape and growth rate of the otoliths (Wilson 1985). Siganids are highly lunar periodic spawners which occurs on or a day about new moon, and restricted settlement period of one to three days with a short planktonic larval duration (Soliman et al 2010). In growth evaluation of *S. fuscescens* before, during and after settlement, it showed that during settlement there is sudden increase in the growth rate with influence of spatial difference (Mellin et al 2009).

The Siganus canaliculatus commonly known as seagrass siganids characterized by a "V" shaped sulcus (Figure 1). The sulcus is a depression on the medial surface of the sagittal otolith (Secor et al 1991) that forms where the maculus or sensory tissue comes into contact with the otolith (Aguirre & Lombarte 1999). The sulcus and the growth of the macula may reflect their function as organs of equilibrium and hearing (Gauldie 1988; Lombarte 1992; Lombarte & Popper 1994; Arellano et al 1995). Gauldie (1988) modeled otolith function in which the sagittal otolith acts as a mechanism of levers through which sound waves are transformed into shearing forces in the plane of the hair cell in the macula. The change in the macula parallels growth of the sulcus, which has something to do with the fish auditory responses. Moreover, the shape of the sensory macula also varies through ontogenetic development of teleost fishes (Platt & Popper 1981) due to difference in auditory feedback on fish hearing (Aguirre & Lombarte 1999; Lombarte 1992; Arellano et al 1995). Changes in sulcus acusticus shape could occur in relation to fish growth and greater complexity in the crystalline structure of the sulcus acusticus (Montanini 2015). Importance in the relationship of sagitta area and sulcus is related on their function as a mechanical receptor that processes acoustic and postural information has well been established (Schuijf 1981; Fay 1984; Gauldie 1988). Similarly, the variation in the sensory macula and the shape of the sagittal otolith could be a form of adaptation in variable environments.



Figure 1. Characteristic of *S. canaliculatus* otolith (Sagitta) with prominent horn shaped rostrum and anti-rostrum and its "V" shaped sulcus indicated by gray dotted line.

The sagittal size is associated with environmental characteristics as depth and low-light of the environment (Paxton 2000); Ekau (1991) also reported a relationship between the shape of the fish, its ecotype and otolith size. The relation of environmental condition and otolith morphology could provide a way for explaining characteristic of biological significance. The objectives of the study were to compare the relationships of otolith area, sulcus area and fish body size associated during the settlement of *Siganus canaliculatus*. Variation in otolith shape and growth in reef fishes within and among

species were affected by changes in the environmental condition along the fish life history (Pothin et al 2006; Wilson 1985).

Material and Method

Field sampling. Samples were collected on the month of May 2010 during the siganid "fry run" or recruitment that usually occur in the east coast of San Miguel Island in the region; pre-settled juveniles were caught by bagnet that operated offshore and post-settled juveniles were caught by encircling net that operated in the seagrass areas. The island is in Lagonoy Gulf (Bicol Region), northeastern Philippines (Figure 2). The gulf is endowed with a wide array of habitats with varying productivity. Garces & Valmonte-Santos (1995) characterized the gulf into three habitat namely coral reef/seagrass and seaweeds area, estuary and deeper area as to productivity. Productivity estimate using zooplankton biomass, chlorophyll a, and using the light and dark bottle consistently reveal that estuary is the most productive followed by coral reef/seagrass and seaweeds area, and the less productive is the deeper area of the gulf. The period of sampling of post-settled juveniles was done a day after the pre-settled individuals collection. The 30 individuals were collected for each stage (pre-settlement and post-settlement) sorted from other species of siganids, then preserved in 95% ethanol.



Figure 2. Location where *S. canaliculatus* samples were obtained (shaded red) from the east coast of San Miguel Island in Lagonoy Gulf, Philippines (original drawing).

Laboratory procedures. Fish body lengths were measured to the nearest mm at 0.01 mm accuracy using vernier caliper. Total length (TL) was measured from the tip of the upper jaw to the tip of the tail and standard length (L_s) was measured from the tip of the upper jaw to the caudal peduncle, body depth (BD) vertical distance between the dorsal and ventral margins of the body measured at the base of the pectoral fin where it joins the body. Right sagittal otolith was used in the analysis. Sagittae were used in the study because of its high degree of variability in shape compared to lapilli and asteriscii. The otolith non-linear morphometrics were obtained using the image analysis software Digimizer (Version 3.7.0.0).

The assumption of pre-settled and post-settled juvenile was verified and resolved through microstructure analysis of the sagittae. The presence or absence of settlement mark was the basis for classifying between post-settled and pre-settled fish. The

transition from pelagic larval (pre-settled) to demersal stage (post-settled) corresponds to a marked reduction in opacity of otolith increment and abrupt width reduction relative to preceding increments where the reduced increment is the settlement mark (Soliman et al 2010).

The otolith images were obtained using Olympus CX41 microscope with a digital image system (CMOS Camera) attached. Digital images of the otolith were analyzed using Digimizer to determine the parameters otolith area (Oa) and sulcus area (Sa) for the two settlement stages (Figure 3).



Figure 3. Schematic representation of sagittal otolith (Secor et al 1999), the shaded part represent the sulcus area (Sa) and the non-shaded part is the otolith area (Oa).

Data analysis. Test for normality of size distribution was performed using Shappiro Wilks. Statistical differences in the fish morphometrics between the two stages were done using T-test. Functional relationships of the fish standard length, Oa and Sa were examined though least squares linear regression. Growths of the sagittal area and sulcus area relative to fish length were determined by the slope of the regression equation. The slope coefficients (b) for the growth relationship between the area of the Oa and L_{s} , the area of the Sa and L_s and the area of the Sa and Oa, were determined by fitting a power equation $y = ax^{b}$ to the data and tested for significant deviations from isometry. In the equation the value of the dependent variable (y), what is being predicted or explained, Alpha (a) constant; equals the value of Y when the value of X = 0 sometimes referred to as the intercept. X is the value of the Independent variable and Beta (b) the coefficient of X; the slope of the regression line. Negative allometric growth was exhibited by sulcus area with respect to fish L_s and Oa except for the Oa relative to fish L_s which showed positive allometry for the two settlement stages of S. canaliculatus. Gould (1966) as cited by Arellano et al (1995) showed that slope (b) of sagittal area and sulcus area regression equal to a value of 2 indicates isometry. A slope differing from 2 shows either positive allometry (> 2) or negative allometry (< 2) with respect to length. Growth of sulcus relative to otolith area is isometric if the slope equal to 1, otherwise growth is allometric. Comparisons in the slope were tested to determine significant difference during the transition stage. The test statistic is Student's t, computed as the difference between the two slopes divided by the standard error of the difference between the slopes (Cohen et al 2003).

Results

Population structure. Sixty *S. canaliculatus* specimens (larvae and juveniles) were obtained from samples caught by bagnet and seine net (Table 1). The pre-settled fish from bagnet ranged from 22.68 to 27.84 mm L_s while the post-settled fish from seine net ranged from 25.28 to 28.88 mm L_s. Otolith area of pre-settled fish was 1.82 x 10⁶ – 2.78 x 10⁶ μ m² and for post-settled fish it was 2.04 x 10⁶ to 2.92 x 10⁶ μ m². Area of sulcus in pre-settled group was 5.21 x 10⁵ – 7.58 x 10⁵ μ m². Post-settled group had a range of 5.96 x 10⁵ - 7.61 x 10⁵ μ m² in sulcus area. The ratio of sulcus area to otolith area in pre-settled group was 3.61–4.01 and it was 3.26-3.83 in post-settled group. Pairwise comparison using Student t-test showed that body size (L_s, TL and BD), and Oa as well as sulcus to otolith/sulcus area ratio were significantly different between the two settlement stages. Sulcus areas between the stages were not significantly different.

Table 1

Fish and otolith morphometric measurements of *S. canaliculatus* specimens

Morphometric variable	Pre-settled (Mean ± S.D.)	Post-settled (Mean ± S.D.)
Standard length (mm)*	25.58 ± 1.270	26.95 ± 0.884
Total length (mm)*	29.62 ± 1.589	31.772 ± 0.939
Body depth (mm)*	7.86 ± 0.498	8.254 ± 0.438
Otolith area (sqµm)*	222556.08 ± 25273.459	234088.53 ± 21064.296
Sulcus acusticus area (sqµm) ^{ns}	65416.61 ± 5808.67	63308.61 ± 3158.65
Otolith area/Sulcus area (Oa:Sa)*	3.798 ± 0.106	3.470 ± 0.116

*Significantly different at a = 5%; ns – not significant.

The Shappiro-Wilks test for normality showed that the size distribution of *S. canaliculatus* during the settlement stages (pre-settled p = 0.4871, post-settled p = 0.8412) came from normally distributed population as shown in Figure 4. Fish body length in the two settlement stages had both unimodal distribution.



Figure 4. Length-frequency distribution of *S. canaliculatus* during the two settlement stages.

Growth of the otolith area (Oa) and the sulcus area (Sa). The linear regressions between Oa, Sa and L_S are presented in Figures 5a-c and Table 2. Significant relationship was exhibited between Oa and L_S both in pre-settled ($r^2 = 0.91$, n = 30) and post settled ($r^2 = 0.89$, n = 30) stages. The Sa versus L_S also showed high relationship in pre-settled ($r^2 = 0.95$, n = 30) and post-settled ($r^2 = 0.77$, n = 30) fish. Similarly, growth of Sa relative to Oa showed functional relationship in both pre-settled ($r^2 = 0.95$, n = 30) and post-settled ($r^2 = 0.80$, n = 30) stages.



Figure 2. Regression relationships of standard length (L_s), otolith area, and sulcus area during the transition from pre-settled to post-settled stage of *S. canaliculatus*.

Table 2

Regression equations and parameters of standard length, otolith and sulcus area

					Degrees of freedom
Stages	Model (Equation)	r^2	а	b	(df)
Pre-settled	$L_S v. Oa (Oa = a x L_S^b)$	0.91	5.26	2.32	29
	L _S v. Sa (Sa = a x L _S ^b)	0.95	5.02	1.86	29
	Oa v. Sa (Sa = a + b x Oa)	0.95	11161.2	0.33	29
Post-settled	L _S v. Oa (Oa = a x L _S ^b)	0.89	4.16	2.49	29
	L _S v. Sa (Sa = a x L _S ^b)	0.77	6.67	1.35	29
	Oa v. Sa (Sa = a + b x Oa)	0.80	33219.7	0.15	29

The pairwise comparison of the slope (b) using t-test was made to test the difference between the growth in settlement stages of S. canaliculatus (Table 3). Relative to $L_{S_{ij}}$ significant difference was observed in Oa (t = -8.10, p < 0.05) and Sa (t = -2.11, p < 0.05). Sulcus was significantly different (t = -8.30, p < 0.05) with respect to otolith area. Growth of sulcus with respect to fish length and otolith area is relatively higher in presettled higher than in post-settled. Otolith areas are significantly different between the stages.

Regression	Slope	of line	t stat	df	n
	Pre-settled	Post-settled	1-3141.	u	
L _s vs otolith area*	2.176	2.491	-8.100	56	60
L _s vs sulcus area*	1.862	1.350	-2.116	56	60
Otolith area vs sulcus area*	0.335	0.146	-8.304	56	60

Pairwise comparison of slope of otolith and sulcus area using Student *t*-test

Table 3

Significantly different at a = 5%.

Discussion. The significant difference of change in body size of the settling S. canaliculatus juveniles indicated a physiologic activity involving growth (Leis & McCormick 2002). Change in body size was associated with change in growth (slope) of sulcus and otolith area during metamorphosis. Early life ecology of several siganids species such as S. canaliculatus includes pelagic larvae (Woodland 2001). This transition from pre-settled to post-settled stage implies abundance of food towards the settlement area (McCormick & Molony 1992; Soliman et al 2010), and it could be that the conditions obtaining stimulated in direct and subtle ways a differential increase in growth (positive allometry) of otolith area relative to fish length. An increase of one variable (fish body size) was concomitant with the increase of the other (otolith area) at a relatively faster rate of growth. Improved situation of settling area enhanced the growth of fish that contributed to the otolith size difference. The general shape of the sagittal change in relation to fish size (Gonzalez Naya et al 2012), fast growing fish tend to form long and thin otolith in contrast with slow growing fish that posses compact and short ones (Campana & Thorrold 2001).

Similarly, food variation, somatic growth and otolith growth are significantly correlated (Aquilera et al 2009). Habitat characteristic such as refuge availability (Adams & Ebersole 2004) and food availability (McCormick & Malony 1992) affect post-settlement juvenile abundance and number of recruits (McCormick & Malony 1993). Sulcus as part of otolith associated with the auditory function (Platt & Popper 1981) showed different pattern of growth (negative allometry) relative to fish length. Growth was most likely attributed to diminishing reliance to auditory sense during ontogeny. This is supported in Gauldie (1988) and Lombarte (1992) who reported that pelagic fishes are more sensitive to sound frequencies than demersal fishes. The higher average Sa Oa ratio of pre-settled fish is probably linked with pelagic nature of the juvenile. Pelagic migration would create intense physical contact between the sensory hairs of the macula and the sulcus due to environmental perturbation like strong current. This physical contact provides a fulcrum for the rotation of the otolith that generates the shearing forces to activate the kinocilia of the macula (Schuijf 1981).

The comparative study of otolith morphology and its relation to environmental parameters provides a method for elucidating characteristics of biological importance (Aquirre & Lombarte 1999). Significant difference in the growth (slope) of otolith area relative to fish length was manifested during the ontogenetic shift (from pre-settled to post-settled) of S. canaliculatus. Higher growth of otolith area with respect to body size in post-settled fish could be attributed to increased metabolic processes involved, thus, the incorporation of calcium carbonate could have been faster. It seems that during the transition or shift in the habitat, ecological factor greatly influenced and masked the expressions of the genetic factor in the formation of otolith by indirect influence on the growth rate (Campana & Casselman 1993). Primarily, change in growth during the transition from pre-settled to post-settled stages coincides with metamorphosis and associated morphological changes in some reef fishes (Leis & McCormick 2002), which could explain the pronounced difference in the otolith growth in the signaid juveniles.

Sulcus growth with respect to otolith area and body size in pre-settled fish was higher than in post-settled fish. Pelagic migration creates intense physical contact between the sensory hairs of the macula or its approximation the sulcus, because of environmental and biological perturbations such as strong current and predator avoidance and where visual impediment was experienced due to murky environment (Schuijf 1981). This may indicate that individuals with relatively larger sulcus area are more sensitive to sound frequency. Rogers & Cox (1988) also found that fishes are most sensitive to sound where the ambient noise is high such as in reef areas. Furthermore, Aguirre & Lombarte (1999) reported that in hakes, Mullus surmuletus which are associated with rocky reefs and *M. barbatus* which inhabit muddy bottoms, the slope of sulcus is increasing with body size. Both species of *Mullus* feed on benthic species mainly using sound perception, with little mobility and are either cryptic or hidden in the substratum whereby visual recognition is difficult. For the pre-settled S. canaliculatus, higher growth (slope) of sulcus could be expected as it performs its function as mechanoreceptors (auditory), in contrast to post-settled juveniles where environmental condition was relatively less turbulent and auditory function was very much compensated with visual senses in a clear environment of the seagrass beds where they settled. Changes in the growth of sulcus could have been associated with the reduction in auditory dependence and increase visual reliance in the seagrass area.

Conclusions. Pelagic to demersal transition of *S. canaliculatus* imposed a physiological change in the fish. These changes were evident in the otolith structure between presettled and post-settled stage. In the transition, only the growth of otolith area in post-settled fish relative to body length was relatively higher than in pre-settled. During ontogeny, the pattern of growth in otolith area and sulcus area was allometric. The rate of growth in otolith area was characterized by positive allometry which means there was increased rate of growth as the fish settled. The growth rate of sulcus exhibited negative allometry indicating a decrement in rate of growth during its transition from pre-settled to post-settled stage. This variation can be highly likely due to differences in food abundance and spatial niches habitat characteristic as a means of adaptation.

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