

Synchronized development of gonad and bioluminescent system in pugnose pony fish Secutor insidiator Bloch (Leiognathidae) from Kerala coast

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Abstract

Seasonal and length group based changes in the development of gonad and light organ (LO) were studied in pug-nose ponyfish, Secutor insidiator. The male fishes having larger light organs compared to conspecific females belonging to the same length group. Gonadosomatic Index and Percentage Light organ Weight (PLW) were used to find out the possible synchronization in the gonad and light organ enlargement in both sexes. In males and females mean GSI showed marked increase two times of the year. A prolonged breeding period from June to September with peak in August and another short period from February to March with peak in March. Seasonal changes in the mean PLW in males showed the same trend as that of GSI, whereas the mean PLW in females remained almost same throughout the year. A significant positive correlation was observed between GSI and PLW in males but not in females; it can be suggested that gonad and light organ development correlation is seen in males during the breeding season irrespective of the length of the fish whereas, LO remained almost the same size in all sexually mature females irrespective of the length of the fish and breeding seasons. The result suggested the possible role of bioluminescence in reproduction of this silverbelly species as reported for many other species. .

Keywords: Secutor insidiator, light organ, Gonadosomatic index, percentage light organ weight, bioluminescence.

Introduction

Silver bellies are facultative schoolers inhabiting sandy coastline and mud-bottomed coastal bay and estuarine environments in the tropical and sub-tropical Indo-Pacific Ocean (Jones, 1985). They are capable of emitting bright light from their ventral surface. About 40 species from seven genera are recognized as valid (Froese and Pauly, 2009), and in these small fish, as in several other (but not all) bioluminescent fish, the source of light is a facultative symbiotic marine luminous bacteria, Photobacterium leiognathi (Harvey, 1958; Buchner, 1965; Boisvert, et al., 1967; Reichelt et al., 1977) maintained within an internal structure called a light organ, surrounding and communicating with the oesophagous - which presumably serves as a method of entry and escape of bacteria, though this has never been directly demonstrated (Haneda and Tsuji, 1972, 1976; Mc-Fall Ngai and Dunlap, 1984; Dunlap and Mc-Fall Ngai, 1987). The light organ, which has been welldescribed cytologically (Bassot, 1975) is densely packed with bacteria (Harms, 1928; Haneda, 1940, 1950).

Pony fishes are believed to control the intensity and duration of the bacterial luminescence by coordinating both the light organ and the surrounding tissues [the light organ system (LOS)], including chromatophore rich muscular shutters, the reflecting and transmitting elements in the gas bladder, musculature, bone and the transparent skin of either the anteroventral or flank surface (Hastings, 1971).

Most species of silver bellies possess sexually dimorphic light organ (Mc-Fall-Ngai and Dunlap, 1984; Sparks et al., 2005; Ikejima et al., 2008). Males possess enlarged light organs compared with females, and in some species, the morphological differences in LOS are so extreme that not only the light organ size, but also the area of the transparent skin patch or stripe become distinct in males (Ikejima, et al., 2008). It has thus been postulated, based on these morphological characteristics of the LOS that bioluminescence in leiognathids plays roles in intra and interspecies signaling. In the present study, we investigated Secutor insidiator, distributed along the coastal and estuarine waters along the Kerala coast, for the sexually dimorphic light organ and associated external traits if any. The work is also aimed to test the possible coupling between sexual maturity and secondary development of the light organ. Based on the results, we discussed ecological as well as evolutionary implications of the sexual dimorphism in the light organ of leiognathids.

Material and methods

Monthly collections of specimens were done from the trawl landings at Kollam, Chettuwa, Azhikkode and Cochin along the Kerala coast, from March 2005 to February 2007. 1217 males and 1249 females of *S. insidiator* (males – TL > 71 mm and females - TL > 76 mm) were used in the study. Only sexually mature specimens of *S. insidiator* were used for the estimation of GSI and PLW for a period of two years in a month wise (March 2005 to February 2007) and length group wise (70 -79 mm to 120 -129mm) manner.

Specimens were brought to the laboratory on ice and total length (TL, 1mm) and body weight (BW, 0.01 g) of each specimen were measured. The fishes were dissected to note the sex and stage of maturity. The gonads were removed and the circumoesophageal light organ was enucleated with a part of oesophagus, and then oesophageal tissues connecting to the light organ were carefully removed using forceps and dissecting scissors under a binocular microscope. The opaque membrane (melanophore rich muscular shutter) covering the light organ was not removed to avoid making damage and loss of bacterial cells from the light organ. As an operational unit to demonstrate gonad development, Gonadosomatic Index (GSI) was calculated using the equation GSI = 102 (GW/ BW) where, 'GW' is the gonad weight (gm) and 'BW' is the body weight (gm). Percentage of light organ weight to body weight was calculated to depict the secondary development of the light organ by the following equation, PLW = 102 (LW/ BW), where, 'LW' is the light organ weight (gm) and 'BW' is

the body weight (gm). Correlation between both mean GSI and PLW in each sex group was tested with Pearson's correlation. The fishes were grouped into 10 mm length groups and the relationship between monthly mean PLW and GSI for each length group of males and females was tested with Pearson's correlation. One way ANOVA and Post Hoc Test (Tukey) was performed to find out whether the difference in the mean GSI and PLW of various months (months were grouped into 4 ; January to March (group 1-Pre-monsoon), April, May (group 2- Summer), June to September (group 3 - South-west monsoon), October to December (group 4- North-east monsoon) and length groups (four length groups in both sexes; 70-89 mm (group 1), 90-109 (group 2), 110-119 (group 3) and 120-129 (group 4) are significant or not at p = 0.05. The presence of external dimorphism if any in association with the presence of internal light organ was determined by visual observation.

Results and discussion

Sexually mature males and females of *S. insidiator* do not show any external sexually dimorphic features (Fig. 1). But they exhibited internally sexually dimorphic circumoesophageal light organ, with males possessing obviously larger light organ compared to conspecific females belonged to the same length group. The overall general morphology of the light organ is similar in both sexes; they exhibited only the size and volume dimorphism.

Light organ dimorphism in Secutor insidiator





Fig. 1. Externally non- sexually dimorphic male and female S. insidiator

In males and females *S. insidiator*, light organ is a gland like structure seen surrounding the oesophagus. It has two lobes; the right lobe is slightly extended into the air bladder through a small opening. The entire light organ is externally surrounded by a darkly pigmented muscular membrane which leaves window like openings at the tip of the right and left lobes. The gland like part of the light organ, while retracting the muscular membrane was bright fluorescent yellow in colour. The interior of the gas bladder was mostly silver lined and the light emitted from the right lobe of the light organ directly reached into the gas bladder and seems to be reflected and pass outwardly along with the light emitted from the left lobe through the transparent musculature and bone in the anteroventrolateral sides of the body.

Gonad and light organ development

The mean GSI in female showed higher values two times in a year; a prolonged period from June to September with peak in August and another short period from February to March with peak in March. The mean GSI values for males also followed the same pattern. Table 1 shows monthly mean GSI and PLW of males and females of *S. insidiator* for a period of two years.

For males and females, there was a highly significant difference between mean GSI values of various months grouped into four categories according to GSI values (for males: One way ANOVA, F = 20.50, p = 0.01; for females: F = 18.38, p = 0.01). Post Hoc test result further established where exactly the difference was. For males, the mean GSI of group 1 month showed significant difference from group 2 (p = 0.05) and group 4 months (p = 0.01) but not from group 3. Mean GSI of group 1 month showed significant difference from group 1 month of group 2 months showed significant difference from group 3.

(p = 0.05) and group 3 months (p = 0.01) but not from group 4 months. Similarly, the mean GSI of group 3 months are significantly different from group 2 months (p = 0.01) and group 4 months (p = 0.01); but not from group 1 months. Again, mean GSI of group 4 months exhibited significant difference from group 1 (p = 0.01) and group 3 (p = 0.01) months, but not from group 2 months. Females also followed the similar pattern of mean GSI for various month groups like males.

Monthly mean GSI and PLW of sexually mature specimens of males and females of S. insidiator are shown in Table 2 and 3. The mean GSI of males belonging to various length groups classified into 4 categories did not show any significant difference whereas, females showed significant difference (one way ANOVA, F = 4.35, p = 0.05); between group 1 (70-89) mm) and group 3 (110-119 mm) individuals. In all the other groups, the difference in the mean GSI was not significant. These results and observations on the ova diameter measurements clearly indicated that S. insidiator along the coastal waters off Kerala (South west coast of India) has two definite breeding seasons ie, group 1 months (January, February and March) and group 3 months (June, July, August and September) and a period of quiescence in group 2 months (April, May) and group 4 months (October, November and December). This is similar to the breeding period of *S. insidiator* reported from the South - east coast of peninsular India (James, 1973; Jayabalan and Ramamoorthy, 1985; Abraham et al., 2011).

Seasonal changes in the mean PLW in males followed exactly the same pattern as observed for the mean GSI; with highly significant difference between month groups (F=45.63, p=0.01). The Post Hoc test result also exhibited very similar trends to that of mean GSI. But mean PLW did not show any significant

Table 1. Monthly Gonadosomatic Index (GSI) and Percentage Light Organ Weight (PLW) (mean ± Sd) of sexually mature males and females of S. insidiator

Month	No. of fis	h examined	GSI (r	nean)	PLW		
	Male	Female	Male	Female	Male	Female	
March	89	76	1.32 ± 0.23	2.1±0.56	1.42 ± 0.05	0.28 ± 0.16	
April	125	126	0.73 ± 0.06	0.81 ± 0.06	0.32 ± 0.06	$0.28 {\pm} 0.18$	
May	96	79	$0.98\!\pm\!0.08$	1.08±0.23	0.48 ± 0.06	0.31 ± 0.08	
June	76	65	1.02 ± 0.23	1.75 ± 0.25	1.52 ± 0.25	$0.30 {\pm} 0.08$	
July	106	125	1.25 ± 0.06	2.48 ± 0.63	1.62 ± 0.78	0.29 ± 0.09	
August	136	126	1.33 ± 0.03	$2.6\pm$ 0.56	1.23 ± 0.03	0.27 ± 0.08	
September	109	152	1.10 ± 0.04	1.82 ± 0.24	$0.80\!\pm\!0.05$	$0.26 {\pm} 0.08$	
October	83	75	$0.81\!\pm\!0.03$	$0.87 {\pm} 0.06$	0.43 ± 0.06	$0.28 {\pm} 0.03$	
November	81	93	$0.71\!\pm\!0.06$	0.83 ± 0.05	0.48 ± 0.05	$0.26 {\pm} 0.02$	
December	68	120	0.82 ± 0.06	$0.95\!\pm\!0.08$	0.51 ± 0.03	$0.24 {\pm} 0.06$	
January	123	105	1.07±0.35	1.62±0.05	0.86 ± 0.69	0.25 ± 0.05	
February	125	107	1.21 ± 0.98	1.89±0.56	1.51 ± 0.06	0.27±0.06	

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Table 2. Mean GSI and PLW of sexually mature specimens of male S. insidiator belonging to various length groups

Month	Length groups (mm)											
	70-79		80-89		90-99		100-109		110-119		120-129	
	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW
March	1.09	1.02	1.41	1.52	1.23	1.36	1.42	1.56	1.20	1.62	1.56	1.64
April	0.56	0.63	0.83	1.06	0.96	0.46	0.22	1.03	0.82	1.06	1.02	1.23
May	0.76	0.71	0.98	0.85	1.02	0.56	0.58	0.86	1.56	0.85	1.36	0.93
June	1.03	1.26	1.22	1.36	1.26	1.23	1.62	1.36	1.23	1.65	1.45	1.26
July	1.25	1.56	1.45	1.45	1.52	1.56	1.71	1.58	1.86	1.83	1.26	1.35
August	1.36	1.63	1.53	1.65	1.53	1.35	1.23	1.25	1.43	1.96	1.75	1.85
September	1.45	1.25	1.20	1.03	1.46	1.96	0.61	1.63	0.81	1.63	1.03	1.91
October	1.02	0.92	0.61	0.65	1.02	1.10	0.33	1.26	0.73	1.23	.82	1.03
November	0.81	0.56	0.71	0.81	0.86	0.74	0.48	0.35	0.92	0.56	0.65	.096
December	0.95	0.45	0.82	0.91	0.75	0.56	0.54	0.45	1.06	0.63	0.75	0.85
January	1.26	1.23	1.36	1.26	0.71	1.26	0.86	1.35	1.21	1.35	1.23	1.26
February	1.01	1.26	1.31	1.35	1.22	1.42	1.34	1.41	1.48	1.51	1.32	1.62

Table 3. Mean GSI and PLW of sexually mature specimens of female S. insidiator belonging to various length groups

Month	Length groups (mm)											
	70-79		80-89		90-99		100-109		110-119		120-129	
	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW	GSI	PLW
March	1.06	0.21	1.82	0.31	2.06	0.28	2.98	0.25	3.12	0.26	3.45	0.26
April	0.96	0.23	1.36	0.34	1.56	0.26	2.01	0.26	1.25	0.24	1.02	0.24
May	1.25	0.26	0.45	0.32	2.85	0.24	2.15	0.24	2.25	0.21	2.26	0.23
June	1.26	0.21	1.56	.201	2.46	0.19	2.65	0.26	2.78	0.23	2.35	0.24
July	1.96	0.20	1.98	0.26	2.72	0.16	2.73	.024	3.16	0.25	2.96	0.31
August	2.05	0.26	2.56	0.25	3.12	0.23	2.45	0.25	3.56	0.25	2.98	0.24
Sept.	2.16	0.25	2.89	0.21	2.01	0.24	1.56	0.26	2.98	0.31	2.31	0.24
October	1.02	0.30	1.31	0.20	1.42	0.29	1.23	0.25	1.26	0.31	1.56	0.29
November	1.09	0.29	1.23	0.25	1.21	0.24	1.05	0.31	1.09	0.26	1.06	0.28
December	1.01	0.25	1.03	0.23	0.65	0.27	1.03	0.23	1.35	0.25	1.26	0.27
January	1.26	0.26	1.56	0.26	0.85	0.31	2.15	0.31	2.45	0.24	1.36	0.25
February	1.15	0.24	1.89	0.21	2.15	0.35	2.74	0.31	2.68	0.21	2.86	0.23

difference between various length groups. At the same time, difference in the mean PLW in various month groups (seasonal) as well as length groups were not significant in females.

A significant strong positive correlation was found only in males (r = 0.83, p = 0.01). Analysis of correlation between monthly mean GSI and PLW of males belonged to various length classes indicated a positive correlation and a weak negative correlation for females (Table 4). From the above results, it can be suggested that correlation in gonad and light organ development is seen only in males but in females light organ size did not increase with gonad development. Male light organ showed an overall increase in the size of the light organ in synchronization with the gonad development during

the breeding seasons irrespective of the length of the fish. But the size of the light organ remained almost similar in all sexually mature females irrespective of the length of the fish and breeding season. However, enlargement of light organ in males did not show any external modification in the form of clear patch in the flank region.

Since the discovery of sexually dimorphic light organ in pony fishes many functions have been postulated. Earlier studies shows that pony fishes uses ventral luminescence to counter illuminate the down welling ambient light to obscure their silhouette (Nealson and Hastings, 1979; Jayabalan and Ramamoorthi, 1979; 1982; McFall- Ngai and Morin, 1991). Earlier study shows that other ecological functions attributed to

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Length group (mm)	'r'	р	significance	'r'	р	Significance
	Males		Females			
70-79	0.96	0.05	Significant	-0.25	-	Not significant
80-89	0.92	0.01	Significant	-0.35	-	Not significant
90-99	0.71	0.05	Significant	-0.48	-	Not significant
100-109	0.57	0.05	Significant	-0.25	-	Not significant
110-119	0.40	0.05	Significant	-0.13	-	Not significant
102-129	0.68	0.05	Significant	-0.11	-	Not significant

Table 4. Correlation between monthly mean GSI and PLW of males and females of S. insidiator belonging to various length classes (Pearson's correlation)

luminescence is assistance in feeding avoidance of predation, startling display or alarm signal (McFall- Ngai and Dunlap, 1983).

The reproductive roles and /or sex specific intra - species communication in this family of fishes have been postulated by in Photoplagios elongatus and P. rivulatus (Haneda and Tsuji, 1976). Jayabalan and Ramamoorthi (1982) and Jayabalan (1985) worked with light organ dimorphism in some leiognathids and suggested the possible role of sex specific luminescence in attracting opposite sex. Past result strongly supports the functional coupling between reproduction and bioluminescence in this species of leiognathids. They also reported the presence of a male specific rectangular flank patch for the emission of light which act as an externally sexually dimorphic trait (Azuma et al., 2005; Sparks et al., 2005; Ikejima et al., 2008).

From the present study it is clear that male and female S. insidiator has an internally dimorphic light organ with males exhibiting greatly enlarged light organ compared to conspecific females belong to same length group. The result is in agreement with that of Haneda and Tsuji (1976), Dunlap and McFall-Ngai (1984), McFall -Ngai and Dunlap (1984), Jayabalan (1985), Kimura et al. (2003), Sparks and Dunlap (2004) and Ikejima et al. (2008). Further, male specific external modification in association with the internal light organ is lacking in S. insidiator which is in consistent with observations in Leiognathus fasciatus and L. nuchalis where males have moderately enlarged light organ compared to similarly sized conspecific females though they lack any external clear skin patch in association with the internal light organ (Ikejima et al., 2004; Sparks and Dunlap, 2004). Although the mode of bioluminescent behavior during spawning of these two species is yet to be clarified, this result points to the possible involvement of bioluminescence in mating behavior even in this leiognathid species which lacks any external sexual dimorphism of the light organ. McFall-Ngai and Dunlap (1984) observed that out of 14 species of pony fishes, two species showed only internal volume dimorphism which is in agreement with the present observation in S. insidiator.

Leiognathids, because of their wide distribution can be suggested as an excellent system in which to address the guestions on ecology and evolution of bioluminescent sexual dimorphism in marine teleosts. In this context, we would like to point out that, attracting a mate with luminescence has some other drawbacks that an animal hoping to lure a mate may attract a predator by mistake (Young, 1983). Unfortunately, we were unable to evaluate any of these risk factors. Further our observation revealed that *S. insidiator* move to deeper waters for spawning, as the mature specimens were obtained from trawl catches operated in deeper waters along the Kerala coast which is in agreement with the observation of Jayabalan and Ramamoorthi (1985). From this it can be postulated that, they may prefer greater depths for spawning where background bioluminescence is low and predators are few. A similar sort of behaviour was reported in a cranchiid squid Leachia pacifica, where females develop a photogenic organ at the tip of the third arm and it moved near-surface waters to depths greater than 1,200m in order to avoid predator risk while producing brighter luminescence for attracting the mates (Young, 1975). Contrasting life history pressures and temporal shift in ecology can exert a strong influence on the evolution of sexual dimorphism (Reimchen and Nosil, 2004). Sexual selection for species specific luminescence signaling presumably plays a key role in generating and maintaining species diversity within leiognathidae. In addition, leiognathids inhabit turbid coastal waters with poor visibility and are often captured in mixed assemblages of several species (Sparks et al., 2005), it can be inferred from the present result that the internally sexually dimorphic light organ and synchronization occurs in the gonad and light organ enlargement in *S. insidiator* provide compelling evidence for an assortative mating scheme in which males use species - specific patterns of luminescence signaling to attract mates, and that this system functions to maintain reproductive isolation in these turbid coastal environments. We postulate that light organ sexual dimorphism has permitted a number of morphologically similar forms to coexist and maintain species fidelity, especially in habitats with extremely poor visibility. The intensity of a sexual display (visual) has been hypothesized to be a character on which females exhibit choice, and has been found to be important

in a wide variety of organisms including fireflies (Cratsleyand Lewis, 2003). Further research is needed in this regard which would give opportunity to expand our understanding of the mating behavior in marine organisms that utilize luminescence for courtship and in fishes in general.

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