Inter-specific relationship of size and walking speed in predaceous ladybirds (Insecta: Coleoptera: Coccinellidae)

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Inter-specific relationships of size and walking speed were examined in five species of predaceous ladybird beetles of aphid prey from different habitats. Lengths of legs, weight and volume of body, and walking speed varied significantly among the five species of different sizes that were reared on their preferred prey food in uniform growth conditions. The species are *Menochilus sexmaculata*, *Coccinella transversalis*, *Anisolemnia dilatata*, *Micraspis discolor* and *Scymnus* sp. Lengths of legs and body sizes showed similar growth rates across the five species (isometry), but the giant ladybird species showed significantly higher positive allometry in body volume (allometric coefficient, $\alpha = 6.66$) and significantly lower negative allometry in walking speed relative to body weight ($\alpha = 0.95$) when compared to other species ($\alpha = 3.54$). The unique response by the giant ladybird species in body form and speed may be attributed to its foraging habitat of perennial bamboo forests with large aggregations of non-winged aphid food which seem to favour the evolution of higher body volume and slower speed for giant size when compared to species of smaller sizes which usually forage for short-lived aphid colonies in seasonal and annual habitats of crop plants and weeds. Evidently, size (weight and volume) and speed matter in the evolution of life history attributes of predaceous ladybird beetles.

Keywords: Evolutionary allometry, predaceous ladybirds, size and speed.

BIOLOGICAL diversity is dominated by variations in shape and size. This is most apparent in insects which constitute nearly 1 million species of about 1.65 million extant species of animals so far documented in the world[1]. Variations in shape and size are associated with many of the most fundamental processes of biology, namely metabolism, reproductive rate, movement and evolution[2,3]. From a simple body plan of an insect (head, thorax, abdomen, a pair of antenna, two pairs of wings in many and three pairs of legs) come myriad forms comprising of bees, beetles, bugs, butterflies, fleas and flies. Much of the observed animal diversity is a result of variation in the relative, rather than the absolute, size of the insect body parts. This is also true of other metazoans[4].

Huxley and Tesseir[5] first used the term 'allometry' (literal meaning 'different measures') to describe the relative growth in male fiddler crabs. Since then, this term, in its broadest sense, describes how characteristics of living organisms change with size[6]. Allometry of different kinds has been elaborated which include isometry or static allometry (similar changes in growth rates), ontogenic allometry (changes in relative growth rates during development) and evolutionary allometry (growth rates in characters relative to size across different species of a taxon)[7]. Huxley and Tessier[5] used a linear relationship equation to describe allometry: $y = ax + b$, where y is the organ size, x the body size, a the slope of the relationship and b is the intercept. Since then, a more specific equation is used to describe linear as well as non-linear models of allometry: $y = bx^{\alpha}$, where x and y are the measurements of two given characters respectively[6], b represents rate of proportional growth and α represents the allometric coefficient (product of y/x)[8–10]. When y and x values show the same growth rates, such a relationship is called static allometry or isometry[7], that is, α is 1 or close to 1. Evolutionarily the growth of different structures or characters is not always synchronous. Several characters in development grow at slower or faster rates in relation to body length or body size as a consequence of genetic regulation of development and requirement of adaptations. Environmental factors, among others, also influence variations in growth rates. Such relationships are called negative or hypo allometry ($\alpha < 1$) and positive or hyper allometry ($\alpha > 1$), that is, y and x values scale at different rates. Allometric coefficient values are obtained separately for each individual (within species) or each species (across species) and these are used to describe the relative growth rates within or across species. In comparison, values of intercepts and slopes of regression analysis are used to explain the trend of relationship in the scaling of characters among different individuals within species or across different species[8,11,12]. Both methods are useful in explaining the assumptions of observed allometry.

There are yet fewer studies on the impact of allometric growth on the relationships with different body parts and behaviour of species within the taxa of several insect groups. Thus, although there is substantial information of positive allometry in long horns of dung beetles[13], butterflies[14] and in many species of ants[15], the limited study on predaceous ladybird beetles (Coleoptera: Coccinellidae) across diverse species is limited to negative allometry of egg size to body size recorded in giant ladybeetles as against the isometry recorded in smaller species[16,17]. Ecologically smaller and giant species of the same taxon (family Coccinellidae) share similar food habits (feed mainly on aphid preys among other soft-bodied insects) and often the same food resource[18,19]. This is relevant for the predaceous giant species of ladybirds, *Anisolemnia dilatata* (Fabricius), in particular, which show food specialization on slow-moving preys[20], and is the largest species in the community of known predaceous ladybird beetles. Adult giant beetles are 3.5 times bigger than the

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next bigger predaceous species, *Coccinella septempunctata* L., commonly found feeding aphid preys (Hemiptera: Aphididae) in vegetable and cereal crops[19]. The aim of this study was to understand the inter-specific relationship or evolutionary allometry for different characters across diverse species of small and large size adult predaceous ladybird species of aphid insect prey found in bamboo habitats and in vegetable crops.

Lengths of the legs and body, live weight and body volume of female beetles (biometrics), and speed of walking (behavioural metric) of starving female beetles were studied. These parameters were selected because of their recognized influences in optimal foraging and reproduction of walking insects[21,22]. Mid-legs were not used in this study because of their perceived role as fulcra in terrestrial insects as opposed to more active roles played by forelegs (triactive function) and hind legs (push forward) during locomotion[11]. Five species of predaceous ladybird beetles of aphid preys used in this study were *Menochilus sexmaculata* (F.), *Coccinella transversalis* (F.), *Micraspis discolor* (F.), *Anisolemnia dilatata* (F.) (the largest species) and *Scymnus* sp. (the smallest species). Hereafter names of these species are used in abbreviations, viz. *Ms*, *Ct*, *Md*, *Ad* and *Scy* respectively. Adults of these species were collected from vegetable crops grown on a farm and from bamboo clusters in a patch of regenerated forest at Ishanchandranagar (23°45.669′N and 91°15.967′E, alt: 34 m) in the vicinity of the Tripura University Campus. *Ms* and *Ct* were collected from bean plants, *Md* from a weed plant *Chromolaena odorata* (L.) King and Robins, and *Ad* and *Scy* were collected from bamboo plants. In the laboratory, two pairs of each of the five species were kept in fresh cylindrical containers (10 cm diameter × 15 cm height) made of acrylic sheet and covered with non-ventilated metal caps at the bottom and ventilated caps at the top. Beetles were offered *ad libitum* supply of live non-winged morph of aphid prey of mixed instars and adults as food, obtained from their respective host plants in fields [*Aphis craccivora* Koch to *Ct* and *Ms*, *Aphis spiraecola* Patch to *Md*, and *Ceratovacuna silvestrii* (Takahashi) to *Ad* and *Scy*]. First generation beetles of these species were obtained following the rearing methods of Agarwala and Majumder[21] and Agarwala *et al.*[23] wherein uniform rearing conditions with respect to physical (temperature, humidity, space) and food parameters (quantity of aphid preys) were provided to all the beetles to ensure uniform growth conditions. Males and under-developed or malformed female beetles, if any, were discarded. Sexes were distinguished either by their sexual behaviour or following the external characters elaborated by Majerus[24]. Age of the laboratory-reared females at the first oviposition was noted and 10 such females of each of the five predaceous species were used to record their biometrics (lengths of body, forelegs and hind legs in mm, body weight in mg and body volume in mm^3 (length × width squared)) and behavioural metric (searching speed measured as the distance covered in mm per second). Body length and body weight of adults were measured following anesthetization with CO_2. Immobile adult females were individually weighed in a microbalance (Mettler Toledo AT20, readability 0.01 mg) followed by measurement of their body lengths from the basal tip of the abdomen to the apical tip of the head by placing individual beetles on a mm graph paper. Walking speed was determined by releasing the 12 h starving individual beetles at the base of 1 cm diameter and 60 cm long pole made of cane wood[21] and recording the distance in mm covered in 60 seconds using a time clock.

Data were subjected to one-factor analysis of variance for all measurements and also for interactions between species and different metrics. Mean values of each metric from the five species were compared by Tukey's range test. Raw data of measurements were $\log_{10}$ transformed to increase normality. These were used in regression analysis with best fitted lines (linear or polynomial) to determine the relationship of scales (b) across the five species between leg lengths or body volume or walking speed (y values) and body length and body weight (x values). Origin 50 program was used for statistical analysis. Allometric coefficient α, the product of y/x, was used to compare the allometric gradient among five ladybeetle species of this study. α values of leg length relative to body length and those of body volume and searching speed relative to body weight were determined as these attributes significantly influence the speed of searching and fecundity (body volume in particular) of small and large size female beetles of predaceous species in a competitive environment[16,25]. Females are mostly bigger between the two sexes in ladybirds[26], and discharge the responsibility of bearing fertilized eggs, and laying them in suitable patches to ensure that hatchlings get food nearby[27].

Insect species were identified following the identification keys by Raychaudhuri[28] for aphid prey species, and by Majerus and Kearns[29] and Hodek and Honek[30]. Mounted specimens of these species are preserved in the collections of the Ecology and Biosystematics Laboratories, Department of Zoology, Tripura University with accession numbers provided to each specimen: predaceous ladybird species on insect pins with labels: *Ms* = *Ms*/allometry/01 to 10, *Ct* = *Ct*/allometry/01 to 10, *Md* = *Md*/allometry/01 to 10, *Ad* = *Ad*/allometry/01 to 10, *Scy* = *Scy*/allometry/01 to 10; aphid prey species in mounted glass slides with label: *Aphis craccivora* = *Ac*/allometry/01 to 06, *Aphis spiraecola* = *As*/allometry/01 to 06 and *Ceratovacuna silvestrii* = *Cs*/allometry/01 to 06.

Mean values of lengths of the body, forelegs and hind legs, body weight, body volume (biometrics) and walking speed (behavioural metric) of female adults of the five ladybird species showed significant differences (Table 1). Females of the largest species (*Ad*) were 1.95 times

Table 1. Mean ± SEm values (n = 10) of different parameters measured of five ladybeetle species

	Ladybird species					ANOVA	
Measuring parameters	*Scy*	*Md*	*Ms*	*Ct*	*Ad*	*F* ratio	*P* value
Biometrics							
Body length (mm)	1.89 ± 0.002^{a}	4.07 ± 0.04^{b}	5.01 ± 0.07^{c}	6.17 ± 0.04^{d}	12.05 ± 0.002^{e}	8507.97	0.001
Foreleg length (mm)	1.55 ± 0.01^{a}	3.23 ± 0.03^{b}	3.54 ± 0.08^{c}	5.46 ± 0.16^{d}	8.51 ± 0.12^{e}	746.85	0.001
Hind leg length (mm)	1.72 ± 0.02^{a}	3.61 ± 0.07^{b}	3.94 ± 0.09^{c}	5.44 ± 0.07^{d}	10.51 ± 0.07^{e}	2455.24	0.001
Body volume (mm^{3})	3.69 ± 0.02^{a}	43.36 ± 1.12^{b}	77.22 ± 3.58^{c}	136.27 ± 4.12^{d}	1315.66 ± 45.56^{e}	748.05	0.001
Body weight (mg)	1.23 ± 0.01^{a}	6.58 ± 0.13^{b}	17.86 ± 0.48^{c}	31.09 ± 0.81^{d}	199 ± 2.42^{e}	5147.19	0.001
Behavioural metric							
Walking speed (mm/sec)	4.31 ± 0.07^{a}	8.73 ± 0.15^{b}	10.06 ± 0.21^{c}	14.16 ± 0.36^{d}	11.48 ± 0.41^{e}	180.37	0.001

Different alphabets with mean values in each row as superscripts denote differences between the means by Tukeys' multiple comparison tests. Abbreviations used for the five species of ladybeetles are the same as those used in the text.

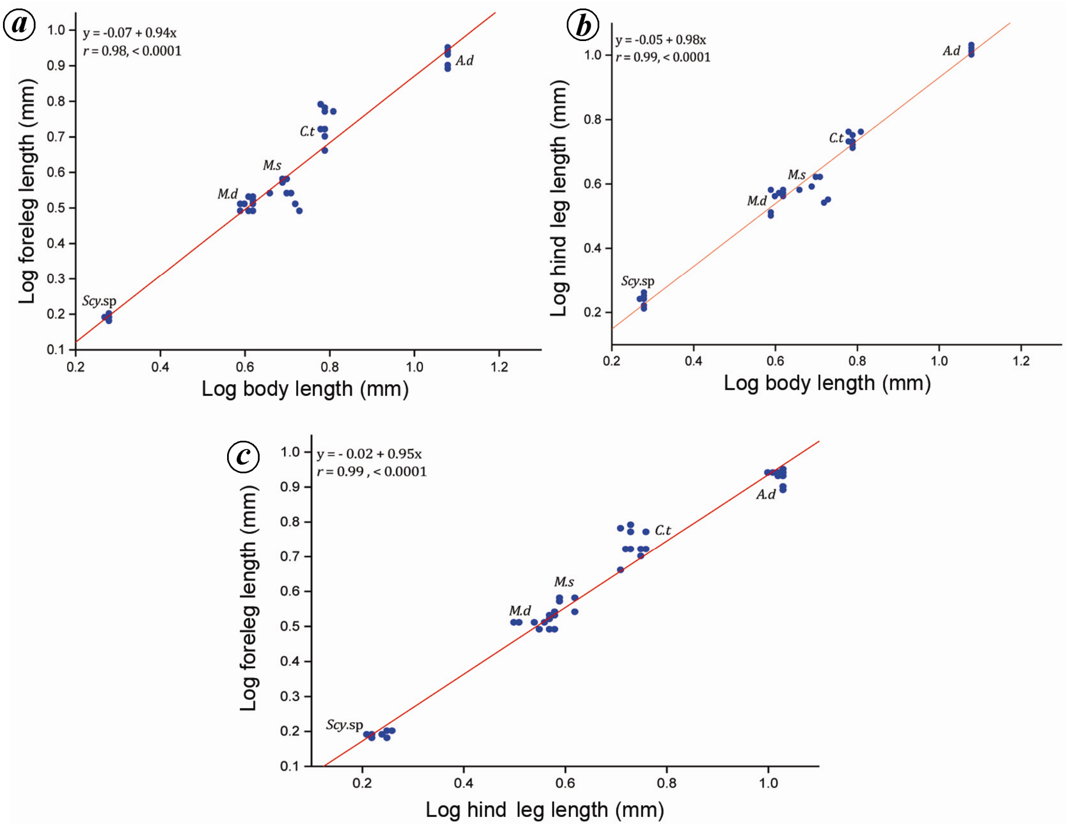

Figure 1. Regression relationship based on log transformed data of liner characters in five species of ladybird species (abbreviations along the regression lines denote names of ladybird species similar to those used in the text): ***a***, between length of foreleg and length of body; ***b***, between length of hind leg and length of body; ***c***, between length of foreleg and length of hind leg.

longer, 6.40 times heavier and 9.65 times larger by volume than the next bigger species *Ct*. In contrast, the walking speed by starving females of beetles was found to be slower (0.81 times) than that of *Ct*.

Allometric coefficients (α) of forelegs and hind legs relative to body lengths showed significant differences across five species (Table 2). Regression analysis of these parameters showed direct relationship (slope values: forelegs = +0.94 mm growth/1 mm growth of body length, Figure 1 *a*; hind legs = +0.98 mm growth/1 mm growth of body length, Figure 1 *b*; between fore and hind legs = +0.95, Figure 1 *c*). Within species, forelegs of the five ladybird species were longer compared to the hind legs.

Allometric coefficients of body volume relative to body weight in the five ladybird species showed higher measures of body volumes with body volume being the highest (α = 6.66) in giant ladybirds compared to a much lower value (α = 3.03) recorded in the smallest species (*Scy*). Regression analysis of scaling between body volume (y) and body weight (x) showed a curvilinear

Table 2. Mean ± SEm values ($n = 10$) of allometric coefficients (α) of different parameters measured as relative growths in five ladybeetle species.

	Ladybird species					ANOVA	
Allometric coefficients	*Scy*	*Md*	*Ms*	*Ct*	*Ad*	*F* ratio	*P* value
Biometrics							
Fll/Bl (mm/mm)	1.89 ± 0.002^a	4.07 ± 0.04^b	5.01 ± 0.07^c	6.17 ± 0.04^d	12.05 ± 0.002^e	8507.97	0.001
Hll/Bl (mm/mm)	1.55 ± 0.01^a	3.23 ± 0.03^b	3.54 ± 0.08^c	5.46 ± 0.16^d	8.51 ± 0.12^e	586.65	0.001
Fll/Hll (mm/mm)	1.72 ± 0.02^a	3.61 ± 0.07^b	3.94 ± 0.09^c	5.44 ± 0.07^d	10.51 ± 0.07^e	1235.64	0.001
Bv/Bw (mm^3/mg)	3.03 ± 0.01^a	6.56 ± 0.70^b	4.28 ± 0.46^c	4.37 ± 0.22^c	6.66 ± 1.28^d	436.26	0.001
Behavioural metric							
Ws/Bw (mm per second/mg)	3.54 ± 0.03^a	1.29 ± 0.05^b	0.56 ± 0.01^c	0.45 ± 0.02^d	0.95 ± 0.001^e	1056.82	0.001

Different alphabets with mean values in each row as superscripts denote differences between the means by Tukeys' multiple comparison tests. Abbreviations used for the five species of ladybeetles are the same as those used in the text but that of the parameters are: Fll, Foreleg length; Hll, Hind leg length; Bl, Body length; Bv, Body volume; Bw, Body weight; Ws, Walking speed.

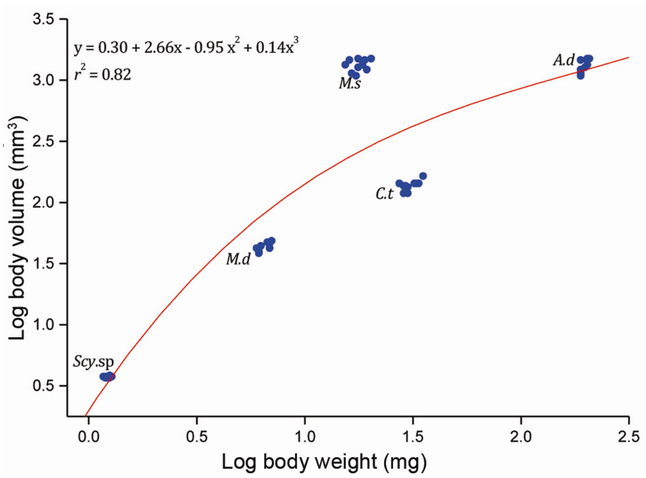

Figure 2. Regression relationship (best fitted curve) based on log transformed values of body volume and body weight in the five species of ladybird species. Abbreviations along the regression line denote names of ladybird species similar to those used in the text.

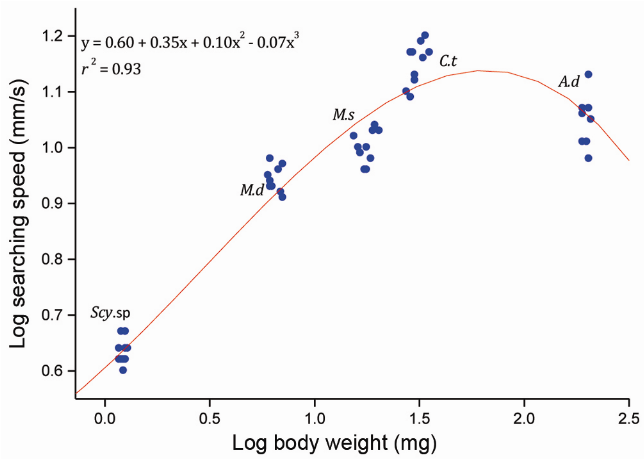

Figure 3. Regression relationship (best fitted curve) based on log transformed values of walking speed and body weight in the five species of ladybird species. Abbreviations along the regression line denote names of ladybird species similar to those used in the text.

relationship across the five species. A higher body volume relative to body weight recorded in the smallest species (*Scy*: slope = $+2.66x$) was followed by lower volumes relative to body weights in *Md*, *Ms* and *Ct* (slope = $-0.95x^2$), and a positive allometry in the giant ladybirds (*Ad*) (slope = $0.14x^3$) (Figure 2).

Allometric coefficients of walking speed of starving females relative to their body weights varied significantly across the five species. The smallest species (*Scy*) searched for a prey at an average speed of 3.54 mm/second as against a much slower speed of 0.95 mm/second by the giant ladybirds (Table 2). The other two bigger species, *Ms* and *Ct*, also showed negative allometry in walking speeds relative to their body weights. Regression analysis of scaling between walking speed and body weight showed nonlinear relationship across the five species, from an initial higher rate of speed in the smallest species (*Scy*: slope = $+0.35x$) (Figure 3) to decreasing rates of speed in bigger species (*Md*, *Ms* and *Ct*: slope = $+0.10x^2$) (Figure 3); however, the lowest rate was recorded in the giant ladybeetles (*Ad*: slope = $-0.07x^3$) (Figure 3).

A majority of studies on the inter-specific relationships in insects, beetles in particular, demonstrate that the most measurable aspects of morphological characters co-vary with body size[31,32]. Positive allometry and negative allometry have evolved independently in several insects[33]. Males of two seed beetles (family Bruchidae) show longer antennae as a ratio of their body sizes that enhances their mating success than individuals having shorter antennae[34]. Among dung beetles, males with longer and stronger horns access females with a greater success in mating. Individuals with relatively shorter and weaker horn are excluded[13]. Results suggest that individuals within populations of a species and those between species of a taxon often display nonlinear allometry in functional attributes that contribute to their life history fitness[35,36].

In the present study, predaceous ladybirds show isometry in linear characters of size (lengths of legs and body) across different sizes of diverse species, but giant ladybirds showed positive allometry in body volume relative to body weight when compared to smaller species. There is a strong explanation for such a relationship. The smallest species, *Scy*, and its congeneric (*Pseudoscymnus*, *Cryptolaemus*, *Nephus* among others) of the tribe Scymnini possess fewer ovarioles (2–12)[37], lay eggs singly[38], lay fewer (per day fecundity: 03.12 ± 0.014 eggs, $n = 10$ females) and small sized eggs (fresh weight of eggs: mean ± SEm = 0.121 ± 0.002 mg, $n = 40$ eggs from 10 females), and forage in low prey density[38] compared to giant ladybeetles (*Ad*) which possess 84–92 ovarioles, lay bigger eggs (fresh weight of eggs: mean ± SEm = 0.832 ± 0.002 mg, $n = 40$ eggs from 10 females), and show much higher reproductive potential (mean ± SEm per day fecundity: $Ad = 34.56 \pm 2.08$ eggs, $n = 10$ females)[23]. Although there is no study on the volumes of eggs of these beetles, it could be assumed that the egg volume to body volume ratio should co-vary across diverse species. That is, females of smaller species with fewer ovarioles producing smaller and fewer eggs should require smaller space for gonads in the abdomen to store mature eggs than by larger species. Higher numbers of ovarioles and higher numbers of larger eggs are directly related to their body size, weight in particular[16]. The higher than normal slope of the body volume in relation to body weight in *Ad* could be a response to its specialized habitat, and higher functional and numerical responses to long-lived large aggregates of aphid colonies of bamboos and sugar canes[23]. These plants occur in abundance in the hot and humid climate of tropics of the old world[20]. In comparison, smaller ladybird predators are polyphagous and visit patchy habitats of annual herbs, including seasonal crop plants, are less abundant, and support short-lived aphid colonies[39,40]. Negative allometry in the walking speed relative to body weights in the three bigger species of this study, however, may be related to spending less energy/unit time in the search for food by starving females possibly to avoid exhaustion when compared smaller species. Allometric coefficients of metabolic rates relative to body mass are found to show negative allometry across diverse taxa[12,41]. This is mainly explained as conservation of energy for basic needs in larger animals[12].

This study brings out interesting features of interspecific relationship between size and walking speed of ladybird predators. Linear sizes of morphology follow isometry in ladybirds of different sizes, but the giant ladybird species show unique feature of positive allometry in the body volume. Negative allometry in walking speed relative to body weight in bigger species including the giant ladybirds vindicates the larger role of metabolic rates in an unpredictable environment. Further study using metabolic and developmental parameters in these and more species of ladybirds would better explain the underlying mechanism for size differences in these insects.

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Population structure and reproductive biology of selected sciaenid species along the fishing grounds of Goa, west coast of India

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The present hypothesis on reproductive migration pattern between two species of sciaenids is based on the data collected with the help of the single-day commercial trawl with a fishing effort of 181 h along the fishing grounds of Goa, west coast of India. The observations on abundance revealed that between the two species (*Johnius borneensis* and *Otolithes ruber*) that formed bulk of the catch, a significant inverse trend in catch was observed. The pattern of migration based on the examination of female gonadal status suggested *J. borneensis* to be a continuous spawner and was evidenced by continuous occurrence of gravid and spent females and their juveniles. On the other hand, the rare occurrences of gravid females of *O. ruber* from the study area suggest that the species spawns away from the coast or might migrate to some potential spawning grounds. Further, an assessment of fecundity and the ova distribution pattern propounded higher fecundity in *O. ruber* compared to *J. borneensis* with multiple spawning in both the species.

Keywords: Fecundity, population, spawning, Sciaenidae.

THE fishing grounds off Goa support an array of vertebrate and invertebrate fauna[1,2]. Of these, the sciaenids are one of the most diverse and commonly occurring teleostean faunal groups contributing to around 10% of the total demersal catches of Goa[3]. Published literature from this region[2] revealed that these constituted 18% and 23% of the demersal fish assemblages of Marmugao and Aguada bay respectively, in terms of their abundance. In recent years, the demersal fishery of the region is subjected to increased fishing pressure through bottom trawlers for commercial exploitation. Moreover, large-scale mortality of juveniles owing to the use of reduced mesh sizes in trawl net influences the occurrence and abundance of commercially important demersal fauna.

Reproduction and recruitment is a species-specific biological process crucial for the continued existence and proliferation of population. Studies pertaining to reproductive biology and spawning behaviour are essential for a complete understanding of population dynamics[4,5]. Moreover, reproductive rate determines the resilience

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