



## Shell occupation pattern by the hermit crab *Diogenes alias* McLaughlin & Holthuis, 2001 (Diogenidae) from Mumbai, India

T Nirmal<sup>a</sup>, A Bijukumar<sup>b</sup>, S K Chakraborty<sup>a</sup> & A K Jaiswar<sup>\*,a</sup>

<sup>a</sup>ICAR-Central Institute of Fisheries Education, Panch Marg, Off Yari road Andheri (W), Mumbai – 400 061, India

<sup>b</sup>Department of Aquatic Biology & Fisheries, University of Kerala, Thiruvananthapuram, Kerala – 695 581, India

\*[E-mail: akjaiswar@cife.edu.in]

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The purpose of this study was to ascertain shell occupation patterns by the hermit crab; *Diogenes alias* found inhabiting the subtidal region of Mumbai, northwest coast of India. A total of 385 samples of *D. alias*, occupying different molluscan shells, were collected bi-weekly from trawling operations off Mumbai. The species was found to occupy the shells of 12 gastropods species, of which, the most commonly occupied shells were that of *Tibia curta* (38.7 %) followed by *Indothais lacera* (36.37 %) while the shells of *Rapana rapiformis* and *Turris* spp. were least occupied with 0.26 %. The diversity of shells occupied by male was higher than female and least in ovigerous females. A high correlation was found between the internal volume of shell and weight of hermit crab occupying it. The present study concluded that the shell architecture has influence on the shell occupation by hermit crabs.

[**Keywords:** Anomura, *Diogenes*, Hermit crab, Mumbai, Paguroidea, Shell occupation]

### Introduction

Hermit crabs, anomuran decapods are often found associated with empty shells of gastropods, relating to their vulnerability, due their non-sclerotized abdomen<sup>1</sup>. These portable shelters are known to influence life history traits of hermit crab including fecundity, spawn size, reproduction and population growth<sup>1-3</sup>. The availability of gastropod shell and their fitness to different species of hermit crabs, impact profoundly on hermit crab abundance and its diversity<sup>4</sup>. The relationship between occupancy by the hermit crab and the gastropod shell is not a random choice; the factors such as availability of shells<sup>5</sup>, shell weight<sup>6</sup>, size<sup>2</sup>, shape, internal volume<sup>7</sup>, epibionts, and resistance to predation and desiccation<sup>1</sup> play a decisive role in shell selection.

The shell acquisition behavior starts from the megalopa stage itself as it grows larger, they need increasingly larger shells; this forces them to spend sizable time of their life in constant search for suitable shells<sup>4</sup>. Many studies have been carried out on the shell exchange patterns of different hermit crabs throughout their entire ontogeny<sup>2,8-12</sup>. The hermit crabs are not able to remove live gastropods from their shells, so they have to depend on dead gastropods for a house<sup>13</sup> which is, perhaps, not as abundant as the population of hermit crabs in the

marine environment. These limitations induce them to inter and intraspecific competitive interaction, in terms of niche or resource partitioning and overlap<sup>1,2</sup>.

Currently, 61 valid species are described under the genus *Diogenes*<sup>14,15</sup>, of which, 19 species are reported in Indian waters, excluding the two recently described species (*Diogenes chhapgari* Trivedi, Osawa and Vachhrajani, 2016 and *Diogenes canaliculatus* Komai, Reshmi and Bijukumar, 2013). Among them, *Diogenes alias* McLaughlin and Holthuis 2001 is a tropical subtidal species, mostly restricted to the Indo-West Pacific region. They constitute an abundant portion of trawl landings in Mumbai, India. Perhaps, because of its robust body, they are the single, dominant hermit crab species landing in this region even though they are found co-existing with their congeneric species *Diogenes dubius* (Herbst, 1804) (rarely found in the trawl catch – personal observation).

During the past centuries *D. alias* was misidentified as *Diogenes diogenes* (for a detailed revision on *D. alias* please see McLaughlin & Holthuis<sup>16</sup>), and under this erroneously name a couple of studies were conducted, regarding its larval development<sup>17</sup> and salinity tolerance<sup>18</sup>, despite its abundance and long history, there's a lack of information regarding its biology and ecology. Hence,

the present study was taken up to ascertain the occupation pattern of gastropod shells by *Diogenes alias* and to ascertain the correlation between the hermit crab choices and locally available empty gastropods shell.

## Material and Methods

### Study area

The hermit crab samples were collected twice in a week from the commercial bottom trawl fishing grounds off Mumbai, Northwest coast of India during October 2017 to May 2018. A total of 25 trawl operations of one hour each (Fig. 1) were conducted in the MV Narmada bottom trawl vessel of CIFE during the entire study period. The trawling was conducted at 9 to 17 m depth range with a speed of 2.5-3 knots and cod end mesh size of the net is 35 mm.

### Shell occupation pattern

Hermit crabs, along with shells, were collected and brought to the laboratory, washed and preserved in 70 % alcohol for further studies. Later, the hermit crabs were pulled out of the shells by twisting the animal

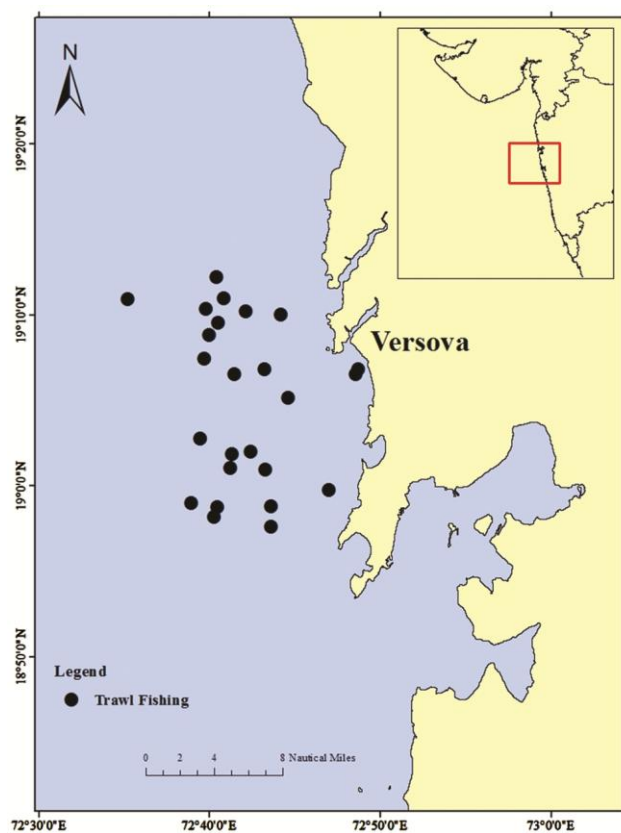


Fig. 1 — Map shows the sampling sites off Mumbai, India

slowly against the direction of shell spiral. The hermit crabs were identified and separated into male (M), female (F) and ovigerous females (OF, females with egg mass adhered to pleopods), based on gonopore position. Cephalothoracic shield length (CSL—from the tip of the rostrum to the V shaped groove at the posterior edge) and wet weight (WW) were recorded for each collected hermit crabs, using vernier calipers and digital balance, respectively.

The inhabited shells were identified to species level using specialized keys<sup>19,20</sup> and various characters of the shells (SL = Shell Length, SW = Shell Width, SAH = Shell Aperture height and SAW = Shell Aperture Width) and Shell Wet Weight (SWW) were measured. In addition, shell internal volume (SIV) was measured by filling the empty shells with fine sand ( $\text{Ø} = 0.25 \text{ mm}^3$ )<sup>21,22</sup>. The voucher specimens were deposited in the museum collections of Fisheries Resource Management Division, CIFE – Mumbai (Catalogue numbers – FRM/HC-1, GS-1 to 12).

### Statistical analysis

The average size of individuals of both sexes was compared by the Mann-Whitney test. The relation between hermit crab variables (CSL and WW) and various shell measurements (SL, SW, SAL, SAW, SIV and SWW) was established for the two most occupied shells and for the different sex categories using correlation coefficient and linear regression. The Chi-square test ( $\chi^2$ ) was employed in pair-wise manner to compare the shell occupancy frequency. All the analysis was carried out using Excel and SPSS.

## Results

A total of 385 individuals of *Diogenes alias*, comprised of 233 (60.52 %) males, 84 (21.82 %) females and 68 (17.66 %) ovigerous females were sampled. The mean CSL size of all studied specimens ranged from 2.8 to 12.6 mm ( $7.49 \pm 0.15$ ) for males, 4.2 to 10.9 mm ( $6.79 \pm 0.17$ ) for females, while 4.2 to 10.4 mm ( $7.97 \pm 0.16$ ) for ovigerous females (Table 1). Maximum number of males were recorded in 5.0 - 5.9 mm and 7.0 - 7.9 mm size group, whereas for females and ovigerous females, the dominated size

Table 1 — Carapace shield length values of *Diogenes alias* from the Mumbai, Maharashtra coast, India

Sex	N	Min (mm)	Max (mm)	Mean $\pm$ SD
Male	233	2.8	12.6	$7.49 \pm 0.15$
Female	84	4.2	10.9	$6.79 \pm 0.17$
Ovigerous female	68	4.2	10.4	$7.97 \pm 0.16$

group was 6.0 - 6.9 mm and 7.0 - 7.9 mm, respectively (Fig. 2).

The species was found to inhabit shells of 12 gastropod species in their natural environment (Table 2); out of which, *Tibia curta* (G. B. Sowerby II, 1842) was the most preferred shell (38.7 %) followed by *Indothais lacera* (Born, 1778) (36.37%). The least preferred shell was *Rapana rapiformis* (Born, 1778) and *Turris* spp. (0.26 % both). Out of 385 specimens collected, most of the shells were found to be intact, infested with barnacles and one specimen of *Tonna dolium* found in damaged condition.

Shell occupation pattern was highly influenced by the size of a hermit crab. The shell occupation diversity was more in small sized hermit crabs, as they grew; shell preference diversity is getting reduced (Figs. 3 and 4). Except the first two size classes, *D. alias* of all size preferred the shells of *T. curta*. A higher level of heterogeneity was observed in

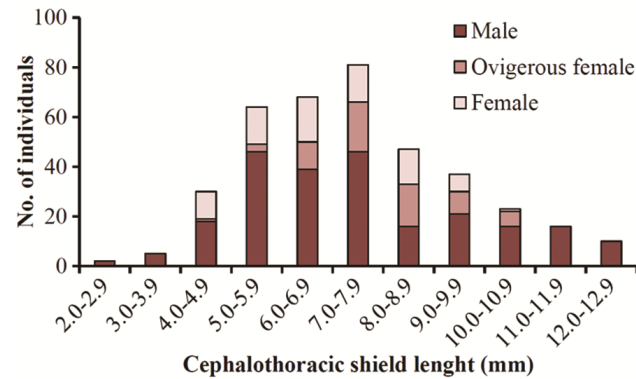


Fig. 2 — Size distribution of different individuals of *D. alias* collected off Mumbai

the case of male hermit crabs and least level of heterogeneity in shell occupancy was shown by ovigerous females. Males and non-ovigerous females were found to occupy 11 and 8 gastropod shell species, respectively (Fig. 5), while ovigerous females occupied only three shells (*T. curta*, *I. lacera* and *B.*

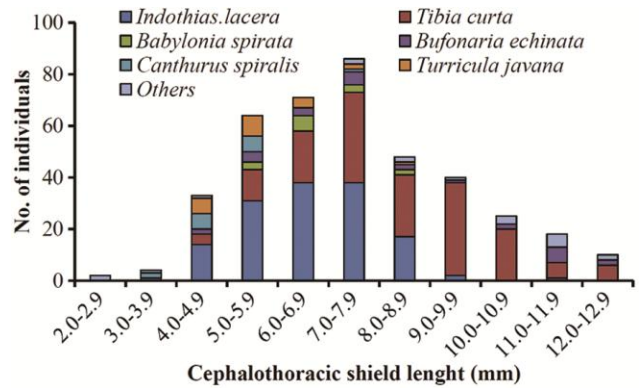


Fig. 3 — Occupation of gastropod shell in relation to size of hermit crab, *D. alias* (CSL = Cephalothoracic shield length).

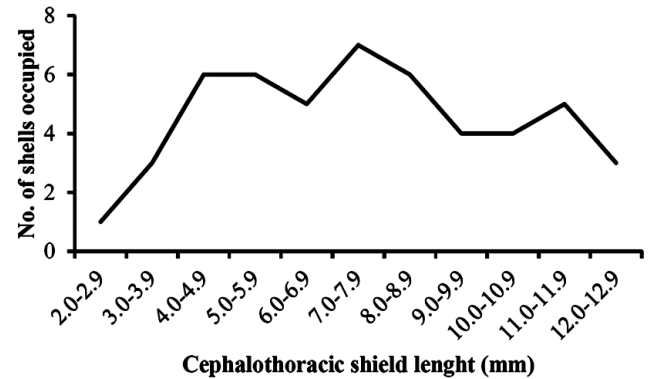


Fig. 4 — Number of species of gastropod shell occupied as a function of hermit crab size, *D. alias*

Table 2 — List of gastropod shells occupied by *Diogenes alias* off Mumbai waters, Northwest coast, India

Species	Total	%	Males		Non-ovigerous females		Ovigerous females	
			N	%	N	%	N	%
<i>Babyloniaspirata</i> (Linnaeus, 1758)	14	3.63	11	4.72	3	3.57	0	0.00
<i>Bufonaria echinata</i> (Link, 1807)	26	6.75	21	9.01	2	2.38	3	4.41
<i>Cantharus spiralis</i> Gray 1839	15	3.89	6	2.57	9	10.71	0	0.00
<i>Gyrenium natator</i> (Roding, 1798)	3	0.78	2	0.86	1	1.19	0	0.00
<i>Volegalea cochlidium</i> (Linnaeus, 1758)	4	1.04	2	0.86	2	2.38	0	0.00
<i>Indothais lacera</i> (Born, 1778)	140	36.4	88	37.8	30	35.71	22	32.35
<i>Tanea lineata</i> (Roding, 1798)	9	2.34	9	3.86	0	0.00	0	0.00
<i>Rapana rapiformis</i> (Born, 1778)	1	0.26	1	0.43	0	0.00	0	0.00
<i>Tibia curta</i> (G. B. Sowerby II, 1842)	149	38.7	73	31.3	33	39.28	43	63.23
<i>Tonna dolium</i> (Linnaeus, 1758)	2	0.52	2	0.86	0	0.00	0	0.00
<i>Turris</i> spp.	1	0.26	1	0.43	0	0.00	0	0.00
<i>Turricula javana</i> (Linnaeus, 1767)	21	5.45	17	7.29	4	4.76	0	0.00
<b>Total</b>	<b>385</b>		<b>233</b>		<b>84</b>		<b>68</b>	

*echinata*). Male hermit crabs had a tendency to occupy rare shells.

In females x ovigerous females relationship, the occupation frequency were only significant for shells of *C. spiralis* and *T. javana*, being both more used by non-ovigerous females. In males x females relationship, significant difference were observed in the occupation frequency of shell *B. spirata*, *B. echinata*, *I. lacera*, *T. lineata*, *T. curta* and *T. javana*. In males x ovigerous females relationship, significant

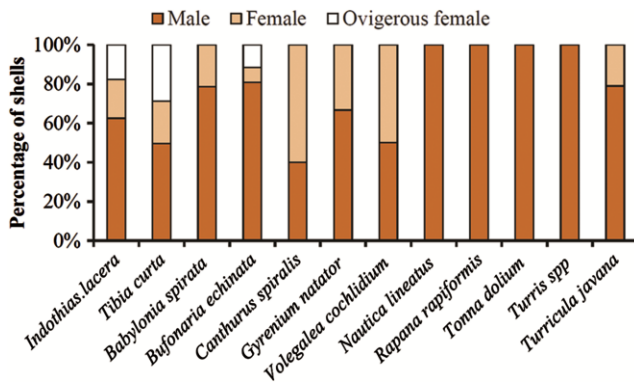


Fig. 5 — Frequency of gastropod shell occupation by male, female and ovigerous female of *D. alias*

differences were observed in *C. spiralis* in addition to those shells shown significance in male-female relation.

Regression analysis was carried out for the most preferred shell under field conditions (for *T. curta* and *I. lacera*) to correlate the shell and animal variables (CSL, WW and SL, SW, SAW, SAH, SWW and SIV). The higher coefficients of determination were obtained between WW x SIV followed by CSL x SIV for both the occupied shells (Table 3). Similarly, regression analysis was carried out between different categories of hermit crab (male, female and ovigerous female) and shell variables of the two most occupied shells. A strong correlation was found between SIV and WW in the case of female and male, and for ovigerous female, the best fit was obtained on CSL x SWW (Table 4).

**Discussion**

*Diogenes alias* occupied shells of 12 gastropod species in which *T. curta* was the most preferred shell. The number of species of gastropod shells, used by *D. alias*, was less as compared with other congeners<sup>23-27</sup>, which indicated that either the hermit crabs had

Table 3 — Regression equations of different morphological measures of *Diogenes alias* (CSL = Cephalothoracic Shield Length and WW = hermit crab Wet Weight) and the two most occupied species of shells (SL = Shell Length; SW = Shell Width; SAL = Shell Aperture Length; SAW = Shell Aperture Width; SWW = Shell Wet Weight; SIV = Shell Internal Volume). [N = number of individuals; rs = Spearman correlation coefficient].

Species	Variables	N	Y= a X <sup>b</sup>	Ln Y = Ln a + b Ln X	r <sub>s</sub>	
<i>Tibia curta</i> (G. B. Sowerby II, 1842)	CSL x SL	149	SL = 31.68 CSL <sup>0.51</sup>	ln SL = 3.46 + 0.51 ln CSL	0.59*	
	CSL x SW	149	SW = 12.27 CSL <sup>0.47</sup>	ln SW = 2.51 + 0.47 ln CSL	0.59*	
	CSL x SAL	149	SAL = 11.5 CSL <sup>0.51</sup>	ln SAL = 2.44 + 0.51 ln CSL	0.41*	
	CSL x SAW	149	SAW = 5.37 CSL <sup>0.43</sup>	ln SAW = 1.68 + 0.43 ln CSL	0.39*	
	CSL x SWW	149	SWW = 1.43 CSL <sup>1.35</sup>	ln SWW = 0.36 + 1.35 ln CSL	0.61*	
	CSL x SIV	149	SIV = 0.27 CSL <sup>1.63</sup>	ln SIV = - 1.31 + 1.63 ln CSL	0.62*	
	WW x SL	149	SL = 70.61 WW <sup>0.13</sup>	ln SL = 4.26 + 0.13 ln WW	0.50*	
	WW x SW	149	SW = 26.01 WW <sup>0.11</sup>	ln SW = 3.26 + 0.11 ln WW	0.46*	
	WW x SAL	149	SAL = 25.32 WW <sup>0.14</sup>	ln SAL = 3.23 + 0.14 ln WW	0.36*	
	WW x SAW	149	SAW = 10.22 WW <sup>0.12</sup>	ln SAW = 2.32 + 0.12 ln WW	0.36*	
	WW x SWW	149	SWW = 11.81 WW <sup>0.36</sup>	ln SWW = 2.47 + 0.36 ln WW	0.52*	
	WW x SIV	149	SIV = 2.83 WW <sup>0.52</sup>	ln SIV = 1.04 + 0.52 ln WW	0.64*	
	<i>Indothais lacera</i> (Born, 1778)	CSL x SL	140	SL = 14.74 CSL <sup>0.56</sup>	ln SL = 2.69 + 0.56 ln CSL	0.66*
		CSL x SW	140	SW = 11.64 CSL <sup>0.51</sup>	ln SW = 2.45 + 0.51 ln CSL	0.60*
CSL x SAL		140	SAL = 10.58 CSL <sup>0.48</sup>	ln SAL = 2.36 + 0.48 ln CSL	0.60*	
CSL x SAW		140	SAW = 5.33 CSL <sup>0.55</sup>	ln SAW = 1.67 + 0.55 ln CSL	0.51*	
CSL x SWW		140	SWW = 0.68 CSL <sup>1.52</sup>	ln SWW = - 0.39 + 1.52 ln CSL	0.62*	
CSL x SIV		140	SIV = 0.16 CSL <sup>1.79</sup>	ln SIV = - 1.83 + 1.79 ln CSL	0.67*	
WW x SL		140	SL = 31.34 WW <sup>0.21</sup>	ln SL = 3.44 + 0.21 ln WW	0.72*	
WW x SW		140	SW = 22.92 WW <sup>0.20</sup>	ln SW = 3.13 + 0.20 ln WW	0.67*	
WW x SAL		140	SAL = 20.41 WW <sup>0.17</sup>	ln SAL = 3.02 + 0.17 ln WW	0.61*	
WW x SAW		140	SAW = 11.35 WW <sup>0.20</sup>	ln SAL = 2.43 + 0.20 ln WW	0.54*	
WW x SWW		140	SWW = 5.36 WW <sup>0.54</sup>	ln SWW = 1.68 + 0.54 ln WW	0.65*	
WW x SIV		140	SIV = 1.45 WW <sup>0.81</sup>	ln SIV = 0.37 + 0.81 ln WW	0.88*	

\*Statistically significant, p < 0.01

Table 4 — Regression equations of different morphological measures of *Diogenes alias* (CSL = Cephalothoracic Shield Length and WW = hermit crab Wet Weight) and different categories of hermit crabs occupying the two most occupied species of shells (SL = Shell Length; SW = Shell Width; SAL = Shell Aperture Length; SAW = Shell Aperture Width; SWW = Shell Wet Weight; SIV = Shell Internal Volume). [N = number of individuals; rs = Spearman correlation coefficient].

Species	Variables	N	Y = a X <sup>b</sup>	Ln Y = Ln a + b Ln X	r <sub>s</sub>	
Male	CSL x SL	161	SL = 5.73 CSL <sup>1.19</sup>	ln SL = 1.75 + 1.19 ln CSL	0.72*	
	CSL x SW	161	SW = 14.02 CSL <sup>0.40</sup>	ln SW = 2.64 + 0.40 ln CSL	0.63*	
	CSL x SAL	161	SAL = 7.97 CSL <sup>0.66</sup>	ln SAL = 2.08 + 0.66 ln CSL	0.71*	
	CSL x SAW	161	SAW = 10.06 CSL <sup>0.16</sup>	ln SAW = 2.31 + 0.16 ln CSL	0.17**	
	CSL x SWW	161	SWW = 0.54 CSL <sup>1.70</sup>	ln SWW = - 0.61 + 1.70 ln CSL	0.61*	
	CSL x SIV	161	SIV = 0.14 CSL <sup>1.88</sup>	ln SIV = - 1.94 + 1.88 ln CSL	0.77*	
	WW x SL	161	SL = 34.63 WW <sup>0.34</sup>	ln SL = 3.54 + 0.34 ln WW	0.63*	
	WW x SW	161	SW = 25.74 WW <sup>0.11</sup>	ln SW = 3.25 + 0.11 ln WW	0.55*	
	WW x SAL	161	SAL = 21.45 WW <sup>0.19</sup>	ln SAL = 3.07 + 0.19 ln WW	0.63*	
	WW x SAW	161	SAW = 12.55 WW <sup>0.06</sup>	ln SAW = 2.53 + 0.06 ln WW	0.19**	
	WW x SWW	161	SWW = 7.15 WW <sup>0.48</sup>	ln SWW = 1.97 + 0.48 ln WW	0.64*	
	WW x SIV	161	SIV = 2.12 WW <sup>0.62</sup>	ln SIV = 0.75 + 0.62 ln WW	0.78*	
	Female	CSL x SL	63	SL = 6.28 CSL <sup>1.17</sup>	ln SL = 1.84 + 1.17 ln CSL	0.64*
		CSL x SW	63	SW = 9.78 CSL <sup>0.59</sup>	ln SW = 2.28 + 0.59 ln CSL	0.69*
CSL x SAL		63	SAL = 11.38 CSL <sup>0.46</sup>	ln SAL = 2.43 + 0.46 ln CSL	0.30**	
CSL x SAW		63	SAW = 6.2 CSL <sup>0.41</sup>	ln SAW = 1.82 + 0.41 ln CSL	0.39*	
CSL x SWW		63	SWW = 0.26 CSL <sup>2.13</sup>	ln SWW = - 1.35 + 2.13 ln CSL	0.73*	
CSL x SIV		63	SIV = 0.08 CSL <sup>2.18</sup>	ln SIV = - 2.55 + 2.18 ln CSL	0.84*	
WW x SL		63	SL = 28.19 WW <sup>0.51</sup>	ln SL = 3.34 + 0.51 ln WW	0.72*	
WW x SW		63	SW = 21.35 WW <sup>0.24</sup>	ln SW = 3.06 + 0.24 ln WW	0.73*	
WW x SAL		63	SAL = 20.51 WW <sup>0.20</sup>	ln SAL = 3.02 + 0.20 ln WW	0.33**	
WW x SAW		63	SAW = 10.65 WW <sup>0.16</sup>	ln SAW = 2.37 + 0.16 ln WW	0.41*	
WW x SWW		63	SWW = 4.02 WW <sup>0.91</sup>	ln SWW = 1.39 + 0.91 ln WW	0.82*	
WW x SIV		63	SIV = 1.45 WW <sup>0.85</sup>	ln SIV = 0.37 + 0.85 ln WW	0.87*	
Ovigerous female		CSL x SL	65	SL = 7.56 CSL <sup>1.16</sup>	ln SL = 2.02 + 1.16 ln CSL	0.61*
		CSL x SW	65	SW = 11.95 CSL <sup>0.50</sup>	ln SW = 2.48 + 0.50 ln CSL	0.54*
	CSL x SAL	65	SAL = 7.39 CSL <sup>0.73</sup>	ln SAL = 2.00 + 0.73 ln CSL	0.62*	
	CSL x SAW	65	SAW = 7.67 CSL <sup>0.31</sup>	ln SAW = 2.04 + 0.31 ln CSL	0.30**	
	CSL x SWW	65	SWW = 0.32 CSL <sup>2.09</sup>	ln SWW = - 1.13 + 2.09 ln CSL	0.76*	
	CSL x SIV	65	SIV = 0.41 CSL <sup>1.46</sup>	ln SIV = - 0.90 + 1.46 ln CSL	0.45*	
	WW x SL	65	SL = 38.28 WW <sup>0.35</sup>	ln SL = 3.64 + 0.35 ln WW	0.48*	
	WW x SW	65	SW = 22.39 WW <sup>0.19</sup>	ln SW = 3.11 + 0.19 ln WW	0.51*	
	WW x SAL	65	SAL = 19.57 WW <sup>0.25</sup>	ln SAL = 2.97 + 0.25 ln WW	0.54*	
	WW x SAW	65	SAW = 11.71 WW <sup>0.10</sup>	ln SAW = 2.46 + 0.10 ln WW	0.24 <sup>ns</sup>	
	WW x SWW	65	SWW = 4.67 WW <sup>0.75</sup>	ln SWW = 1.54 + 0.75 ln WW	0.70*	
	WW x SIV	65	SIV = 1.19 WW <sup>0.90</sup>	ln SIV = 0.17 + 0.90 ln WW	0.72*	

\*Statistically significant, p < 0.01, \*\* p < 0.05 and <sup>ns</sup> not significant

specific requirements or the diversity of shells in the study area was insufficient. Hermit crabs were highly selective in preference to certain size range of shells<sup>4,28</sup>. The shell selection varied according to the type of habitat and the size of hermit crab. The small size class (2.0-4.0 mm CSL) occupied smaller shell, such as that of *Gyrenium natator* and *Turris* spp., while larger hermit crabs (10-12 mm CSL) occupied larger shells of *Tonna dolium*, *Rapana rapiformis*, *Nautica lineatus* and *Volegalea cochlidium*. The diversity of shells utilized by smaller hermit crabs was found to increase with their growth and, after reaching threshold size, the number of shells utilized by larger hermit crabs was reduced. Thus, it can be

inferred that the availability of smaller gastropod shells was higher in the study area; moreover, the smaller hermit crabs were opportunistic in selecting shells while larger hermit crabs aimed at fitness. This finding indicated that a considerable change in shell preference and diversity of shell occupation has been common in hermit crabs at different stages of life. Many authors<sup>29,30</sup> have reported similar conclusions.

Even though there was little difference in the size distribution of different sexes of hermit crab, males of *D. alias* showed slightly higher average CSL than female and ovigerous counterparts. This may related to the differential energy utilization by the hermit crab (male used their energy for growth and female toward



reproduction). Resource partitioning has been reported as important in the case of inter-specific competition between species and between the different size groups of the same species<sup>31</sup>. Higher heterogeneity in the usage of shell was found in the males followed by the females and then ovigerous females. Usually, males were larger in size, hence, they are dominant in fighting for shells and food. Retaining maximum clutch size and for incubation of eggs was the prime necessity for ovigerous females and, for that reason, they prefer only selected shells which were giving maximum internal space. Difference in shell occupation between sexes was reported earlier, as well<sup>6,22, 32,33</sup>. Sexual dimorphism, competitive ability or reproductive behaviour was also described as reasons for difference in shell occupation exhibited by different sexes<sup>21,34,35</sup>.

Occupying intact shells by hermit crab reduced the chance of being evicted by other congeners or by predators and desiccation<sup>36</sup>. Hermit crabs occupy damaged or drilled shells only when intact shells were not available in enough numbers<sup>37,38</sup>. In the present study, only one case of damaged shell occupancy (*Tonna dolium*) by large sized *D. alias*, was recorded. This indicates there is enough number of larger and intact shells available for the hermit crabs to occupy in Mumbai waters. Further, the hermit crabs were not sufficiently capable of removing neither live gastropods nor dead animals from their shells; therefore, they had to wait for the dead meat present in the shell to disintegrate or to be removed by predators. In the process, there was a chance of the gastropod shell being deposited under the sand, which made the shell acquisition process more complicated for hermit crabs<sup>39</sup>.

Many studies have reported a correlation between characteristics of hermit crab and shell occupation<sup>1,40</sup>. The internal volume of gastropods has been found to be the major factor influencing the crab in shell selection<sup>4,21,41-44</sup> compared to other variables, such as shell aperture length and width. In the present study, a strong correlation between internal volume and wet weight of shell and hermit crab was an indication of need of more internal volume for males and females for body growth and to retain a larger number of eggs, in the case of ovigerous females<sup>45</sup>.

The shell of *T. curta* was the heaviest among all shells occupied by *D. alias*. According to the energy saving hypothesis<sup>44</sup>, occupying a heavy shell required more energy in terms of locomotion, which negatively

affects the growth and reproduction of hermit crabs. Semi-terrestrial hermit crab shell occupation patterns may vary from aquatic hermit crabs in one sense: the animal tries to save energy because the entire weight must be carried by the occupier, which causes it to select a lighter shell, providing protection from predators<sup>44, 47</sup>. But in the case of aquatic hermit crabs, such as *D. alias*, buoyancy in water reduced the shell weight, so they can afford to select larger and heavier shells, which provided increased benefits of resistance against the predator and dislodgement from tidal action. They have also shown preference towards heavier shells, thereby creating more resistance against dislodgement, similar to the observation made by Hahn<sup>48</sup>. *D. alias* had the ability to discriminate between different species of shells based on shell architecture. Similar findings were reported by Bundhitwongrut<sup>46</sup>.

The gastropod shells were an indispensable resource for the hermit crab, which affected their biology. Availability of shell in the locality played a major role in shell occupation behavior of the hermit crab. We have characterized the shell occupation pattern of hermit crab *D. alias* along the Mumbai coast. From this study, it is concluded that *Tibia curta* is the most occupied shell by the hermit crab and shell internal volume was the most important factor in the selection of shells under field conditions. This result would help in understanding any change in shell occupation behavior in the future relating to an anthropogenic stress and will also act as an indicator species for that change. This in turn, helps fish managers to understand the particular ecosystem's health status as well as to undertake decisions relating to mitigation/conservation measures.

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### Conflict of Interest

The authors declare there is no conflict of interest.

### Author Contributions

TN carried out sampling, data analysis and wrote the manuscript with support from AKJ and AB. SKC

helped in the interpretation of results. All authors discussed the results and contributed to the final manuscript.

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