

Protection over mobility? How shell selection in the hermit crab *Clibanarius erythropus* (Paguroidea) is modulated by availability and ecological conditions.

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Abstract

Hermit crabs occupy empty gastropod shells, which have to provide both: mobility and protection. Yet, the process of shell selection and the preference for different architectural traits, such as globose or conical shapes, has not been fully understood. In this study we look into the selection behaviour of *Clibanarius erythropus*. Five gastropod shell types of similar size were offered in a laboratory setup. The results were compared to findings in a natural habitat in Le Cabellou, located on the French Atlantic Coast. Moreover, the radius of movement between consecutive tides was studied to infer how *C. erythropus* obtains shells in the absence of live gastropods. When offered in equal amounts, a vast majority selected a shell of conical shape as a final shelter, either *Tritia reticulata* or, to a lesser extent, *Nucella lapillus*. Consistent with this, these two gastropods provided the shells first selected and occupied the most time during the experiment. A similar preference for a conical shape was observed in the field. Yet, a greater fraction was found to occupy *N. lapillus*. Moreover, after two tides, 47 % of specimens were recovered in close vicinity to their original location. Due to this locational constancy we presume that the population depends on a passive import of certain shells. The different abundance of empty gastropod shells is likely to constitute a limiting factor that modulates shell selection under natural conditions. As a consistent result in the laboratory and the field, a clear preference for a conical shape over globose shells was identified. Although impeding mobility, this architectural trait has been discussed as providing a better protection from predation. Additionally we explain how a conical shape might be beneficial under strong hydrodynamic action, as found at Le Cabellou. Shell preference might therefore be regarded as less species-specific and more of a response to ecological conditions than previously assumed.

Introduction

Arthropods are known for their great diversity, both in ecology and morphology. Within this clade, the Paguroidea (hermit crabs) pursued one of the most unusual evolutionary strategies: a secondary loss of the abdominal exoskeleton and bilateral symmetry in favour of the utilization of gastropod shells for protection (Fig. 1, McLaughlin, 1983). Thereby combining mobility and protection, hermit crabs can be found distributed in almost all marine environments from the intertidal to the deep sea (Hazlett, 1981). While the strong association with the gastropod shell has influenced almost all aspects of their biology (Hazlett, 1981), hermit crabs play an important role as ecosystem engineers within their mobile microhabitat in return (Reese, 1969; McLaughlin 1983).

For several hermit crab species, the intertidal zone provides a continual flux of food from the sea (Reese, 1969). Yet it can be thought of as a demanding ecotone, harbouring the risk of desiccation, abrasion caused by hydrodynamic action and predation by subtidal

fish and shore birds. These challenges have been met by the utilization of gastropod shells for shelter (Reese, 1969). On the other hand, avoiding extreme salinity and temperature is facilitated by the shelter's mobility (Reese, 1969). Although the occupation of shells plays a vital role in the hermit crab's lifestyle, most taxa have not acquired the ability to procure these from living snails (Bertness, 1981). Due to this, hermit crabs have equally evolved mechanisms (e. g. odor detection) to locate deceased gastropods from afar (Rittschoff, 1980; Mesce, 1982; Katz & Rittschoff, 1993) as well as strategies to obtain shells from con- and heterospecifics, e. g. fighting (Hazlett, 1966) and bargaining (Hazlett, 1978). In the course of this, remarkable gatherings of similar sized conspecifics have been observed (Gerhardi, 1994). A mutual benefit from a chain process in shell exchange can be assumed (Gerhardi & Vannini, 1993).

Previous studies have presented heterogeneous explanations for the preference of a certain shell type in hermit crabs. On one hand, there are

indications for a species-specific preference (Reese 1962, Grant 1963, Orians & King, 1964; Völker, 1967). Meeting different morphological requirements, occupying differently shaped shell types allows a sympatric coexistence of hermit crab taxa by sharing the resources (Reddy & Bisewar, 1993). On the other hand, shell size appears to have a great influence: smaller individuals (and species) occur in a greater variety of shells (Jackson, 1913; Reese, 1969), while in larger hermit crabs a full withdrawal of the carapace is not provided for in smaller shelters (Orians & King, 1964). Furthermore, shell size is known to limit growth rate and reproductive output (clutch size), effecting the individual fitness as well as the demographic structure of the population (Reese 1969, Bertness 1980). To meet these criteria with a certain efficiency, a desirable shell has often been described as voluminous but lightweight (e. g. Bertness, 1981; Reddy & Bisewar, 1993). These qualities are conjunct in globose shells, which have been shown to enable a faster movement while foraging (Benvenuto, Satoni & Gherardi, 2003). In opposition to this, other species have been shown to prefer conical shells (Orians & King, 1964; MacKay, 1945). It has been argued that this architectural trait, although not favourable for mobility, provides a better protection from predation, particularly due to thick walls and narrow apertures (Gerhardi, 1994). Regardless of the outcome, it can be assumed that hermit crabs engage in an active selection process (Conover, 1978), which, in natural populations, would be limited by the abundance of empty gastropod shells (Kellogg, 1976; Bertness, 1980; Bertness, 1981; Reddy & Bisewar, 1993). This could explain why usually the most abundant gastropod in a habitat provides the shell type most often occupied by the local hermit crab population (Bollay, 1964; Völker, 1967). On the other hand, it appears likely that a certain hermit crab species is more abundant in habitats where their preferred shells are available.

In opposition to species-specific explanations, different shell preferences have been noted for populations of *Clibanarius erythropus* (Latreille, 1818) (Fig. 1), a common hermit crab in the Atlantic and Mediterranean intertidal zones (Zariquiey Alvarez, 1968). Generally, crab size and the size of the occupied shell have been found to correlate (Botelho & Costa, 2000), but while in the Mediterranean a preference for globose shells has been described (Gherardi, 1991; Benvenuto, Satoni & Gherardi, 2003), in the Atlantic *C. erythropus* is assumed to select shells of conical shape in greater proportions (Botelho

& Coasta, 2000; Southward & Southward, 1977). To shed some light onto the shell preference in *C. erythropus*, we investigated a population of the intertidal on the French Atlantic Coast. At Le Cabellou (Fig. 2) *C. erythropus* lives in a complex three-dimensional environment on hard substrate and faces strong tidal amplitudes. We looked at shell preference under equal supply in laboratory experiments. Moreover we carried out field studies to compare our findings with the shell distribution under a natural supply of shells. Doing this, we were testing the following hypotheses: 1) There is a preference: providing an equal abundance of different gastropod shell types, the individual selection results in an unequal distribution. 2) The selection is modulated by shell supply: under the assumed influence of a different abundance of empty shells in a natural population the selection results in an unequal distribution that differs from (1). 3) With respect to pronounced hydrodynamic action and hard substrate in the habitat, preferences for a certain architectural trait should reflect the requirements for protection more than those for mobility. In both (1) and (2) the distribution of occupied shell types will therefore be in favour of a conical shape.



Fig. 1: *C. erythropus* shows typical morphological adaptations of a hermit crab: a secondary loss of the abdominal exoskeleton and bilateral symmetry, associated with the utilization of and dependency on empty gastropods shells as a shelter.

Material and Methods

Field Collection

Our field studies and experiments were carried out on the Breton coast in Le Cabellou in France (47° 51' 18.5" N, 3° 54' 56.2" W, Fig. 2) between the 28th of August and the 3rd of September 2018. The field collection was undertaken at low tide following three transects from the low water line to the shore in an approximate distance of 200 m to another. Overall 664 hermit crabs were collected. The shells occupied by the specimens were then identified and counted. All crabs were held in a 60 l tank filled with aerated seawater, some sediment, stones and algae to provide food and a near-natural environment.



Fig. 2: The field study was carried out at Le Cabellou, located on the French Atlantic coast. Altered after Wikimedia Commons CC-ASA-4.0.

In addition, empty gastropod shells were collected at Le Cabellou. The five most abundant shell types in the field were utilized for the following behavioral experiments (Fig. 3): *Nucella lapillus* (Linnaeus, 1758), *Tritia reticulata* Linnaeus, 1758, *Phorcus lineatus* (da Costa, 1778), *Steromphala umbilicalis* (da Costa, 1778) and *Littorina littorea* (Linnaeus, 1758). All shells used in the experiment were measured in length, width and height with a caliper gauge. To ensure a comparable size of the shells offered, larger specimens of *N. lapillus* and *P. lineatus* as well as smaller specimens of *S. umbilicalis* were excluded. In size, the shells utilized in the experiment roughly resembled our preselected reference specimens (Fig. 3). Moreover, we determined the structural volume of each shell type utilized in the experiment by measuring the



Fig. 3: To ensure a similar size of the five offered shell types, all shells used in the experiment were measured and compared to these reference specimens: 1 = *N. lapillus*, 2 = *T. reticulata*, 3 = *P. lineatus*, 4 = *S. umbilicalis*, 5 = *L. littorea*.

volume of water that was displaced by 16 specimens in a 50 ml Falcon tube. In advance, each shell was filled with water to exclude the interior volume from our consideration. This volume was then divided by the number of specimens to determine the average volume of a single shell. Analogously, the weight of 16 specimens was measured utilizing an analytical precision scale ($\Delta = 0.1$ mg) to infer the average mass of a single shell.

In our collection of empty gastropod shells we were predominantly short of *T. reticulata*. Consequently, crabs occupying this shell type had to be removed from their shells. Therefore several empty shells of different species and sizes were offered for a voluntary exchange. While this strategy turned out to be successful with a great number of specimens, we only occasionally had to facilitate the process with a fresh water treatment (30°C for a maximum of 2 min) to induce the abandonment of the occupied shell. Non of the crabs that passed through these procedures were further employed for the behavioural study. All crabs collected were set free after the completion of the experiment.

Experimental Setup

All experiments were carried out at La station marine de Concarneau, France. A setup was developed to clarify the shell preference in *C. erythropus*, when offered in equal abundance. The trials were carried out in separate plastic containers of 500 ml volume (diameter: 14 cm at the top, 11.5 cm at the bottom, colour: white) filled up with sea water to a level of 3 cm. A thin layer of natural sediment served as substrate to prevent distortions of the results due to sub-

strate colour and to provide a better grip. One crab per container, usually withdrawn in its shell, was inserted centrally for a duration of 60 min. Laterally, in equal distance to another, five empty gastropod shells were positioned, one each of the aforementioned species (Fig. 4). The original shell was removed immediately after being abandoned for the first time. No further shells were removed after consecutive shell exchanges. For each exchange, the origin and target shell type was recorded, as well as the duration of stay within each shell type. The shell occupied after 60 min was considered the final choice. For repeated trials with other specimens the order of the offered shells was randomized. In total the tests were carried out with 50 specimens, in equal proportions initially occupying the five examined shell types. Each crab was only used once in a single experiment.



Fig. 4: Setup of the selection experiment under equal supply: a plastic container was filled up with sea water to a level of 3 cm. Natural sediment served as substrate. 0 = *C. erythropus* in its original shell (here as an example *N. lapillus*), alternative shells offered: 1 = *N. lapillus*, 2 = *T. reticulata*, 3 = *P. lineatus*, 4 = *S. umbilicalis*, 5 = *L. littorea*. Positions of shell types were exchanged several times during the experiment.

Radius of Movement

To assess the possible radius of movement in *C. erythropus* under natural conditions, we chose six different gathering spots within the intertidal at Le Cabellou (Fig. 5). Five of them were located on hard substrate. Only the north-western most spot provided soft substrate with pebbles, stones and a rich growth of macrophytes. At low tide, in each spot, we marked 30 hermit crabs' occupied shells with water resistant lacquer. After two tides, the surroundings were searched for marked specimens. The number of hermit crabs recovered within a radius of 7 m from the original location was recorded.



Fig. 5: Six different gathering spots within the intertidal of Le Cabellou were selected to assess the radius of movement in *C. erythropus* (spots marked with red circles). They were only accessible at low tide and mostly located on hard substrate (as indicated by the colours in sketch).

Post-Processing

All data has been processed with Microsoft office 365 (©2019 Microsoft Corporation) and LibreOffice 6.1.3.2 (©2000-2018 LibreOffice-Beitragende). Statistic tests were carried out with RStudio 1.1.463 (© 2009-2018, Rstudio Inc.) utilizing R 3.5.1 (©2018, The R Foundation for Statistical Computing). Images were processed with gIMP 2.8.16 (© S. Kimball & P. Mattis), Adobe Photoshop Lightroom 6 (©2007-2016, Adobe Systems Incorporated) and Inkscape 0.91 (©2015, Free Software Foundation).

Results

Behavioural Experiments

The specimens ($n=50$) entered the experiment in an equal distribution of occupied shell types. The experiment aimed to investigate a shell selection preference under equal abundance of empty gastropod shells. 84 % of all tested hermit crabs were found to choose either *N. lapillus* or *T. reticulata* as their final shelter. Moreover, 16 % were found in *L. littorea*. Neither *P. lineatus* nor *S. umbilicalis* were chosen as a final shelter by any specimen (Fig. 6). A Chi-Square-Test confirmed a significantly unequal distribution after the completion of the experiment ($\chi^2=90.1$, $df=4$, $p<0.001$).

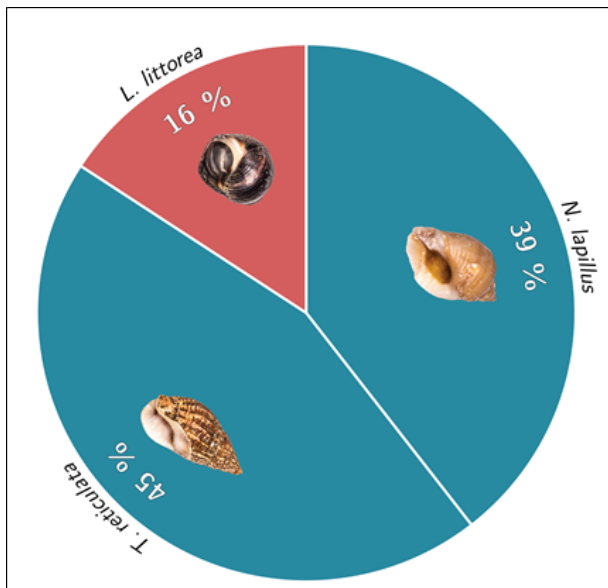


Fig. 6: The results of the shell selection under equal supply show a pronounced preference for a conical shape (blue) in *C. erythropus*. After 60 min the greatest fraction selected *T. reticulata*. Only a minor fraction occupied a shell of globose shape (red). No shells of *P. lineatus* and *S. umbilicalis* were selected as a final shelter. $n=50$.

Moreover, this finding is consistent with the total time spent in the different shell types during the experiment. The total occupation time of each shell type in proportion to the duration of the experiment (50 h) differed significantly from an equal distribution (Fig. 7, $\chi^2=42.4$, $df=4$, $p<0.001$). Most time was spent in *T. reticulata* (28 %), *N. lapillus* (19 %) and *L. littorea* (12 %). *P. lineatus* and *S. umbilicalis* were occupied for only minor portions of time (2 % respectively 1 %). The remaining time was predominantly spent in the original shelter.

Furthermore, the first shell exchange undertaken during the experiment corresponds with these findings. While only 50 % of specimens

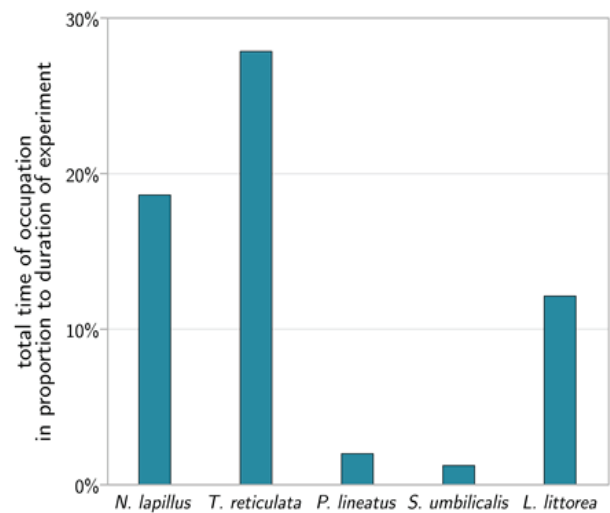












Fig. 7: The total time spent in different shell types during the experiment is consistent with the final shelter selected by *C. erythropus*. Careful considerations in the selection process can be inferred. Total of occupation time given in proportion to duration of experiment.

occupying *N. lapillus* ($n=5$) and *T. reticulata* ($n=5$) decided to abandon their initial shelter, an exchange from *L. littorea* (100 %, $n=10$), *S. umbilicalis* (90 %, $n=9$) and *P. lineatus* (90 %, $n=9$) was observed more frequently. On the other hand, most specimens (71 %, $n=27$), that decided to exchange their shelter, chose either *N. lapillus* (32 %, $n=12$) or *T. reticulata* (39 %, $n=15$) as their first alternative, resulting in a significantly unequal distribution ($\chi^2=21.7$, $df=4$, $p<0.001$). A slightly smaller fraction (28 %, $n=9$) chose *L. littorea* during the first exchange, while *S. umbilicalis* was only selected twice (7 %). No specimen changed into *P. lineatus* as a first alternative shelter (Tab. 1). While 12 specimens decided not to abandon their initial shells, for the majority that did so (68 %, $n=24$), the first alternative shelter became their final choice for the duration of the experiment.

During the entire experiment we were able to observe a strongly stereotypical selection behaviour, which steps were followed consequently and repeatedly: a palpation of the aperture, a palpation of the exterior surface from all sides, an inspection of the accessible interior and its cleaning and the testing for mobility of the shelter by moving it around. When an exchange is finally undertaken, the original shelter is usually held in close proximity. A return into the original shell has frequently been observed.

To gain further insight into physical parameters that could possibly induce a preference for a certain shell type, the average volume and mass were measured. Our specimens of

Tab.1: The first shell exchange undertaken by *C. erythropus* during the experiment indicates a clear preference for the conical *N. lapillus* and *T. reticulata*, as well as careful considerations in the process. 93 % of specimens initially occupying a globose shell decided to exchange their shelter. Out of these, 64 % moved into a conical shell. Only 50 % of specimens initially occupying a conical shell decided to leave their shelter. Out of these, only 10 % moved into a globose shell. List of first shell exchanges undertaken (n=38), including origin and target shells, excluding specimens without a shell exchange (n=12).

		INITIALLY OCCUPIED SHELL					Σ of target shells
							
	FIRST TARGET SHELL	<i>N. lapillus</i>	<i>T. reticulata</i>	<i>P. lineatus</i>	<i>S. umbilicalis</i>	<i>L. littorea</i>	
	<i>N. lapillus</i>	2	2	2	1	5	12
	<i>T. reticulata</i>	2	3	2	5	3	15
	<i>P. lineatus</i>	0	0	0	0	0	0
	<i>S. umbilicalis</i>	0	0	1	1	0	2
	<i>L. littorea</i>	1	0	4	2	2	9
Σ abandoned		5	5	9	9	10	

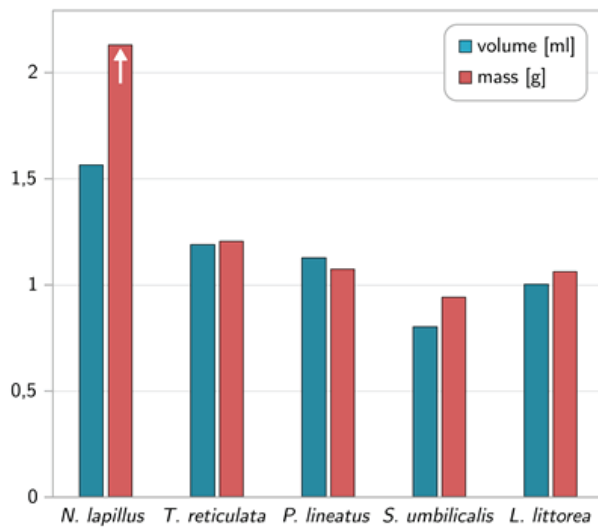


Fig.8: *N. lapillus* has a significantly ($p = 0.05$) greater mass per specimen than other gastropod shells (as indicated by arrow). No significant differences were found among the other shell types. The outer volume does not differ significantly between the shell types employed in our behavioural experiment since specimens of comparable sizes were utilized.

L. littorea had a volume of 1.0 ml and a weight of 1.06 g, while *S. umbilicalis* only reached 0.8 ml and 0.94 g. In *P. lineatus* we recorded a volume of 1.1 ml and a mass of 1.07 g, whereas *T. reticulata* displaced 1.2 ml and

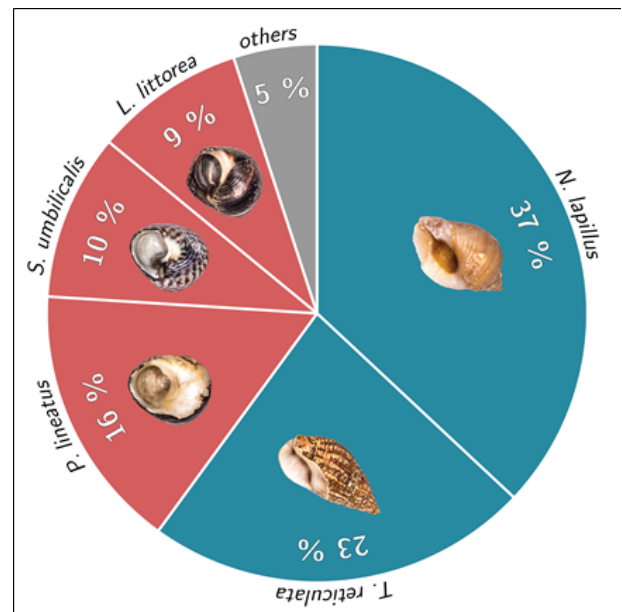


Fig. 9: The distribution of shells occupied by *C. erythropus* in a natural habitat indicates a modulation of shell preference by availability. Yet, the greatest fraction was found in a shell of conical shape (blue). Globose shells constituted a minor fraction (red). Others include *C. zizyphinum* (3 %), *O. erinacea* (1 %) and *L. obtusata* (1 %). specimens (n=664) collected at Le Cabellou, France.

weighed 1.20 g. In *N. lapillus* the greatest volume was measured, reaching 1.6 ml. Its mass was determined to be 2.18 g. While no indication for an unequal distribution of the volumes was found ($\chi^2=3.1$, $df=4$, $p=0.54$), this did not apply for weight ($\chi^2=79.4$, $df=4$, $p<0.001$), since the mass of *N. lapillus* exceeded a confidence interval of 95 % around the arithmetic mean (Fig. 8).

Field collection and radius of movement

In our field collection at Le Cabellou *C. erythropus* was found to occupy eight different gastropod shell types (Fig. 9), of which 95 % were represented by *L. littorea* (9 %, n=63), *S. umbilicalis* (10 %, n=67), *P. lineatus* (16 %, n=105), *T. reticulata* (23 %, n=152) and *N. lapillus* (37 %, n=244). In consistency with our behavioural experiments, 60 % alone were found to occupy the latter two shell types (n=396), resulting in a significantly unequal distribution ($\chi^2=87.7$, $df=7$, $p<0.001$). To a minor extent *Calliostoma zizyphinum* (Linnaeus, 1758, 3 %, n=19), *Ocenebra erinacea* (Linnaeus, 1758, 1 %, n=8) and *Littorina obtusata* (Linnaeus, 1758, 1 %, n=6) were occupied. Furthermore, the distribution of the five most abundant shell types was found to differ significantly between the field and the results obtained in the laboratory ($\chi^2=50.0$,

df=4, $p < 0.001$).

At low tide, 180 specimens of *C. erythropus* found around six gathering spots within the intertidal of Le Cabellou were marked with lacquer. After two tides, we were able to recover an average of $47 \% \pm 13 \%$ of the marked specimens in close vicinity to their original

Discussion

A clear preference for *N. lapillus* (39 %) and particularly *T. reticulata* (45 %), when offered in equal amounts, was observed in *C. erythropus*. The unequal distribution of this result confirms hypothesis (1). Moreover, the total time spent within these shells during the selection process and the first selected shell were consistent with this finding. From this, we infer that the selection process follows careful considerations and is only undertaken if the preceding examination of the shell indicates that the benefits of an exchange outweigh the possible dangers. In particular, the vulnerability during the process and a possible loss of the original shell need to be mentioned. Still, our findings seem to partly contradict the natural distribution of occupied shells at Le Cabellou. While a similar proportion of shells originated from *N. lapillus* (37 %), only 23 % of *C. erythropus* were found to occupy *T. reticulata* in the field. Yet, the most remarkable difference was found in the greater proportion of *P. lineatus* and *S. umbilicalis* occupied in the field. Due to these significant differences in distribution hypothesis (2) is confirmed.

It could be argued that a greater range in size within the specimens collected in the field might have resulted in a greater heterogeneity of occupied shells (see Reese, 1969). Yet, a pronounced deviation in shell distribution can hardly be explained without considering the influence of an unequal and limited abundance of vacant shells. We presume that these natural conditions modulate the outcome of the selection process. Since no great number of empty gastropod shells were found anywhere at Le Cabellou, a lack of availability is likely to have induced an opportunistic behaviour in favour of *P. lineatus*, *S. umbilicalis* and *L. littorea*. During sample collection we were able to confirm a sufficient occurrence of these gastropods directly within the intertidal, while living *T. reticulata* and *N. lapillus* were not encountered. For the latter, a nocturnal lifestyle might serve as an explanation for its absence during our study, which was carried out at daytime. *T. reticulata*, on the other

location. While most of the specimens were found within a diameter of less than a metre, none were reported in a distance greater than 7 m from the original position. Moreover, in a minor number of specimens, we found indications of them having lost their markers.

hand, is known to live in subtidal soft sediment (Tallmark, 1980). For this reason, it must be assumed that their shells are locally harder to obtain than others. Yet, our findings contradict the established perception, that shell distribution in hermit crabs relates proportionally to the abundance of live gastropods (Bollay, 1964; Völker, 1967). Indeed, the comparably frequent occupation of *T. reticulata* - even in the absence of their live gastropods in the closer surroundings - suggests that this shell type must appeal to the local hermit crab population in particular. However, only further research on gastropod abundance could elucidate the extent of its influence on the selection process.

In the field, 47 % of *C. erythropus* were recovered within close proximity of their original positions after two consecutive tides. We are therefore presuming a relatively small radius of movement within the local population of *C. erythropus* at Le Cabellou. As an explanation for the observed locational constancy, we presume a social clustering for mutual benefits from a chain process in shell exchange, as described for different hermit crab species (Gerhardi & Vannini, 1993; Gerhardi, 1994). Yet, the question for a possible supply with vacant *T. reticulata* remains unsolved. It is known that *Clibanarius* finds shells subtidally, if they are not supplied in the intertidal zone (Botelho & Coasta, 2000). Nonetheless, long-distance travel has hitherto only been observed on soft sediment (Rittschof, Sarrica & Rubenstein, 1995). Additionally, a great fraction of hermit crabs at Le Cabellou occupies conical shells, of which an inhibiting influence on mobility has been shown (Benvenuto, Satoni & Gherardi 2003). Therefore it is questionable if *C. erythropus* is capable of obtaining shells through long-distance movement in a complex three-dimensional substrate, as found in Le Cabellou. In consequence, an active procurement of vacant *T. reticulata* from the subtidal appears unlikely. We therefore think that the population might predominantly rely on the import of vacant *T. reticulata* through tides and currents.

Protection over Mobility?

The pronounced preference for a conical shell, as observed in the field and in the laboratory, confirms hypothesis (3). Our finding appears to be consistent with observations in other Atlantic populations of *Clibanarius* (Botelho & Costa, 2000; Southward & Southward, 1977). This architectural trait has previously been discussed to be beneficial for protection (Gherardi, 1994). *T. reticulata* offers a smaller aperture, impeding the intrusion of predators, while *N. lapillus* is characterised by a significantly greater weight per volume, presumably providing thicker walls. The latter appears particularly relevant under strong hydrodynamic action and on a hard substrate (Arce & Alcaraz, 2011), both of which are present in Le Cabellou. A trade-off between mobility and protection appears likely (Orians & King, 1964). Furthermore, the intrinsic advantages of a conical shape need to be considered, since elongated bodies provide less hydrodynamic resistance than globose structures (Schade et al., 2013). While such adaptations have previously been found to occur in live gastropods (Trussel et al., 1993), further research could shed some light on the question if strong hydrodynamic action induces the preference for an elongated shape in the

subsequent occupants as well. Moreover, it needs to be questioned if these aspects are responsible for a contradicting preference, which has been observed in the Mediterranean populations of *C. erythropus* (Gherardi, 1991; Benvenuto, Sartoni & Gherardi, 2003).

Methodical Aspects

Hitherto shell selection experiments involved invasive means that forced hermit crabs out of their shells. Thermal and osmotic stress or mechanical destruction of the shell have frequently been applied (for an example see Hazlett, 1987; Ramsey, 2013). However, besides the risk of harming the subject, we presume that a risky shell exchange is rarely undertaken in the presence of vital threats. We therefore consider it unlikely to obtain results representing natural behaviour after such procedures. For this reason no hermit crabs were utilized in our experiments, that had previously been forced out of their shells. We found that a great fraction of specimens voluntarily changed shells if not disturbed for a sufficient time and adequate alternatives were provided. We recommend this method for further studies.

Conclusion

The distribution of shells selected by *C. erythropus* at Le Cabellou differs from its preference, when supplied in equal amounts. Our findings indicate a modulation caused by the availability of empty gastropod shells under natural conditions. Overall, our results show that a conical shape is preferred over other architectural traits, while *T. reticulata* appears to be the most appealing shell type. To obtain these shells, *C. erythropus* probably relies on

import through tides and current. We believe that a need for protection is the predominant reason for this preference. The pronounced hydrodynamic action at Le Cabellou might serve as an explanation. Future research should elucidate if shell-selection is more plastic within species than previously assumed. Rather, it might be considered as a response to different ecological conditions.

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