

Proceedings in Marine Biology

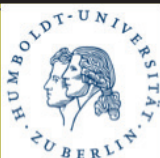
Journal of the Graduate Course of the Humboldt-University and the Museum für Naturkunde at the Station de Biologie Marine de Concarneau



Volume 3

Issue 1

2018



<https://doi.org/10.18452/22969>

Kasper, L. & Raaz, L.V.A.: Beutepreferenz bei *Marthasterias glacialis* (Echinodermata, Asteroidea) in Abhängigkeit von individueller Größe und intraspezifischer Konkurrenz 1-6

Dressler, L.E., Ebel, R. & Ehlers, S.: Protection over mobility? How shell selection in the hermit crab *Clibanarius erythropus* (Paguroidea) is modulated by availability and ecological conditions 7-16

Parsi-Pour, P. & Schaal Moreno, G.: The movement radius of *Patella* sp. around its home scar correlates with duration of water exposure 17-21

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This volume deals exclusively with the results of the research field trip of the Humboldt-University Berlin and the Museum für Naturkunde to the Station de Biologie Marine de Concarneau (France)

from 26.08. - 6.09.2018

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Beutepräferenz bei *Marthasterias glacialis* (Echinodermata, Asteroidea) in Abhängigkeit von individueller Größe und intraspezifischer Konkurrenz

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Abstract

Seastars are opportunistic predators that feed on bivalve molluscs and other invertebrates. In a dynamic system like the sublitoral of the rocky shores near Concarneau (South Brittany, France) there are several parameters possibly influencing the choice of prey like the tides, abundance of seastars as well as abundance of the different prey species. In two different experimental setups (five aquaria with one individual each and two aquaria with about 25 individuals each) we investigated the prey preferences of *Marthasterias glacialis*. We wanted to find out whether there are any prey preferences at all and if so, whether these preferences were depending on individual predator size and on intraspecific competition. The sea stars were offered 6 different prey species: *Magallana gigas*, *Patella spec.*, *Mytilus edulis*, *Phorcus lineatus*, *Littorina obtusata* and *Chthalamus spec.* The results show that *Mytilus edulis* and *Patella spec.* are the most preferred prey species. In addition, our observations suggest that intraspecific competition has an influence on prey choice with a preference for organisms to be subdued and eaten in a shorter amount of time. Concluding we can say that under laboratory conditions the sea star *M. glacialis* shows prey preferences. Those are slightly depending on individual size and intraspecific competition. Preceding work (Gianguzza et al., 2016) supports to expect those findings to be at least in parts applicable to the natural habitat of *M. glacialis*.

Einleitung

Seesterne wie der Eisseestern *Marthasterias glacialis* sind Nahrungsoportunisten, d.h. sie haben ein sehr breites Nahrungsspektrum. Sie ernähren sich unter anderem von Muscheln, Schnecken, Seeigeln, Seepocken und Seescheiden (Penney & Griffiths, 1984). Die Beutearten unterscheiden sich daher nicht nur bezüglich des Nährwerts, sondern auch bezüglich des Kraft- und Zeitaufwands des Seesterns, um die Beute zu öffnen. Die frühesten Fraßexperimente mit *Marthasterias glacialis* wurden schon Ende des 19. Jahrhunderts durchgeführt (Preyer, 1887) und er gilt als lohnendster Versuchsorganismus unter den Seesternen (Valenticic, 1973).

Ihre Verbreitung erstreckt sich im östlichen Atlantik von Island, Norwegen über die Westküste Großbritanniens bis zu den Kapverden, sie kommen aber auch im Mittelmeer und in Südafrika vor (Minchin et al., 1987). Dabei unterscheiden sich die Lebensräume von Weich- bis Hartsubstrat (Penney & Griffiths, 1984). *Marthasterias glacialis* kommt vom Infralitoral, dem obersten Abschnitt des Sublitorals bis

hin zu Tiefen von 180m vor (Mortensen 1927, Madsen 1950). Im Sublitoral des Felswatts bei Concarneau (Südliche Bretagne, Frankreich) leben *Marthasterias glacialis* tagsüber an der Unterseite von Felsen, um dann während der Dämmerung und der Nacht jagen zu gehen und danach meist zu demselben Stein zurückzukehren. Sie verharren dabei einzeln oder in Gruppen unter den Steinen. Nur sehr große Exemplare, ab einem Durchmesser von 20 cm, sind auch tagsüber ungeschützt z.B. an der Kaimauer anzutreffen (persönliche Beobachtungen).

Angepasst an die vorgefundenen natürlichen Bedingungen sowie Möglichkeiten im Labor ergab sich als Zielsetzung für die vorliegende Arbeit, zu testen, ob es bei *Marthasterias glacialis* eine Beutepräferenz gibt und ob diese dann von der Größe des Seesternindividuums und/oder vom intraspezifischen Konkurrenzdruck abhängig ist.

Material & Methoden

Die Versuchstiere wurden im Felswatt in Le Cabellou sowie im Felswatt in Concarneau 0 – 2 m unter Niedrigwasser gesammelt, wenn möglich auch zum Zeitpunkt des Niedrigwassers am Tag. Es wurden alle Individuen der Art *Marthasterias glacialis* (Linnaeus, 1758) mit einem Durchmesser von 5 bis 25 cm gesammelt. Im Labor wurden die Tiere vermessen und auf die Versuchsbecken bzw. Lagerbecken verteilt. Die ursprüngliche Idee, die Versuche auch mit dem Gemeinen Seestern *Asterias rubens* (Linnaeus, 1758) durchzuführen, um mögliche interspezifische Unterschiede zu untersuchen, wurde aufgrund von viel zu geringer Abundanz von *Asterias rubens* verworfen.

Die Beuteorganismen wurden an den gleichen Probestellen gesammelt. Um ein breites Spektrum anzubieten, wurden fünf verschiedene Beutearten ausgewählt: *Magallana gigas* (Thunberg, 1793), *Patella* spec. (Linnaeus, 1758), *Mytilus edulis* (Linnaeus, 1758), *Phorcus lineatus* (da Costa, 1778) und *Littorina obtusata* (Linnaeus, 1758). Auf einigen *Patella*-Individuen sowie auf fast allen *Magallana*-Individuen gab es Bewuchs von *Chthamalus* spec. (Ranzani, 1817) und es stellte sich im Verlauf der Versuche heraus, dass diese den Seesternen auch als Beute dienen, sodass sie in der Auswertung als 6. Beuteart aufgeführt werden. Nicht wie geplant im Experiment als Beutetiere genutzt wurden Seeigel, da an den Sammelorten nicht ausreichend viele Individuen vorzufinden waren.



Abb. 1: Einzelsetup. Ein Individuum *M. glacialis* sowie Beutearten *Patella* spec. (+ *Chthamalus* spec.), *Magallana gigas* (+ *Chthamalus* spec.), *Littorina obtusata*, *Mytilus edulis*, *Phorcus lineatus* auf einem flachen Stein.

Beim Arbeiten mit den Tieren wurde auf kurze Transportzeiten zwischen Probestelle und Labor sowie auf eine ständige Zufuhr von frischem

Meerwasser während der Versuche geachtet.

Seesterne verbringen den Tag unter großen Felsen, die meist von Algen bewachsen sind, sodass sie auch tagsüber in relativer Dunkelheit leben. Um die Bedingungen im Labor anzupassen wurden die Versuchsbecken tagsüber abgedunkelt.

Zwei verschiedene experimentelle Setups wurden genutzt: 5x Einzelsetup in Kunststoffboxen von 25 x 35 x 15 cm, in denen jeweils ein einzelnes Individuum getestet wurde (Abb. 1). 2x Gruppensetup in Glasbecken von 25 x 50 x 30 cm, in denen zeitgleich jeweils ca. 25 Individuen in einem Becken getestet wurden (Abb. 2). Die Versuchstiere für das Gruppensetup wurden aufgeteilt in Tiere $\leq 8,5$ cm und $> 8,5$ cm. Alle Versuchsbecken wurden mit flachen, möglichst großen Steinen bestückt, um den Versuchstieren halbwegs natürliche Bedingungen und Rückzugsorte zum Akklimatisieren zu bieten. Im Fall von mehreren leeren Gehäusen/Muschelschalen im selben Becken wurden alle gefressenen Individuen dem jeweiligen Seestern zugeordnet. Damit kam es in manchen Fällen zu mehreren Fraßevents von nur einem Individuum. Im Gruppensetup hingegen war es oft schwierig, sämtliche Schnecken unterhalb der Wasseroberfläche und damit erreichbar zu halten.



Abb. 2: Gruppensetup. 25 Individuen *M. glacialis* (v.a. unter dem Stein). Beutearten wie in Abb 1.

Eine Verfälschung der Beutewahl ist dadurch nicht auszuschließen, jedoch sind die Schnecken im natürlichen Lebensraum auch die mobilsten unter den Beutetieren von *Marthasterias glacialis*. Die Versuchsbecken wurden täglich um 9:00, 16:00, 19:00, 22:00 und 01:00 Uhr überprüft. Diese zeitliche Überprüfung war bei gleichzeitig möglichst geringer Störung der Versuchstiere engmaschig genug, da ein einzelnes Fraßevent mehrere Stunden dauert. Die längere Pause zwischen 09:00 und 16:00 Uhr ergab sich aus der Inaktivität der Tiere am Tag sowie der Notwendigkeit mittags neue Versuchstiere zu sammeln. Bei Fraßevents, d.h. beim Beobachten von aktivem Fressen mit ausgestülptem Magen oder der initialen Haltung mit charakteristischem Buckel wurde das entsprechende Versuchstier entnommen und zeitnah ins Meer zurückgebracht, nachdem folgende Daten aufgenommen wurden: Durchmesser des Versuchstiers = Distanz von Spitze des längsten Arms bis Spitze des gegenüberliegenden Arms, Anzahl der Arme, Beuteart. Die entsprechende Beute wurde nachgelegt, sodass jederzeit jede Beuteart ausreichend, aber nie im Überfluss verfügbar war. Bei Vorfinden von leeren Schalen am Morgen wurde die Beuteart gewertet, jedoch kein Tier entnommen, da zumindest beim Gruppensetup nicht auszumachen war, welches Individuum die Beute gefressen hatte.

Im Fall von mehreren leeren Gehäusen/Muschelschalen im selben Becken wurden alle gefressenen Individuen dem jeweiligen Seestern

zugeordnet.

Damit kam es in manchen Fällen zu mehreren Fraßevents von nur einem Individuum. Im Gruppensetup hingegen war es oft schwierig, sämtliche Schnecken unterhalb der Wasseroberfläche – und damit erreichbar – zu halten. Eine Verfälschung der Beutewahl ist dadurch nicht auszuschließen, jedoch sind die Schnecken im natürlichen Lebensraum auch die mobilsten unter den Beutetieren von *Marthasterias glacialis*.

Ergebnisse

Insgesamt wurden 171 Individuen untersucht, die in mehreren Intervallen in die verschiedenen Setups eingesetzt wurden. Dabei kam es zu 229 Fraßevents. Die sich ergebende Diskrepanz zwischen 171 Versuchstieren und 229 Fraßevents trat auf, da einige Schalen von gefressenen Beutetieren erst nach Ende der Nacht aufgefunden wurden, ohne dass der zugehörige Seestern entfernt werden konnte. Wie in Abbildung 3 gut zu erkennen, liegen die Größen der untersuchten Individuen beinahe ausschließlich zwischen 5 cm und 15,5 cm. Hier ist außerdem noch eine Häufung der Größen um den Mittelwert von 8,7 cm zu erkennen. Die Einteilung der Seesterne in zwei Größengruppen ($\leq 8,5$ cm; $> 8,5$ cm) zeigt Beutepräferenzen in Abhängigkeit von der Größe (s. Abb. 4). Zunächst wird deutlich, dass unter allen Individuen die Gemeine Miesmuschel (*M. edulis*) noch vor der Napfschnecke (*Patella spec.*) die am häufigsten gewählte Beute ist.

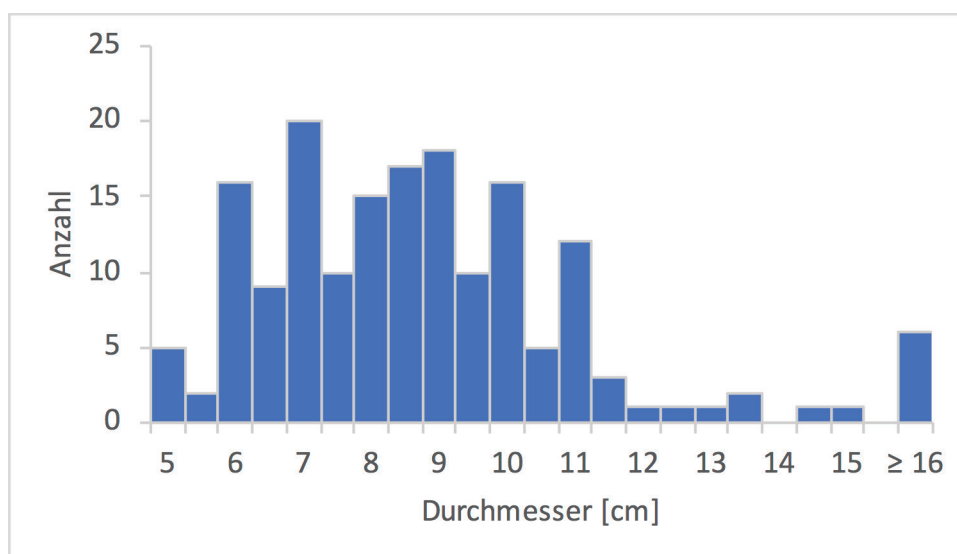


Abb. 3: Größenverteilung (Anzahl gegen Durchmesser in cm) aller untersuchten *Marthasterias glacialis*-Individuen. Individuen mit größerem Durchmesser als 15 cm zusammengefasst.

M. edulis liegt mit 50 % bei den großen bzw. 39,7 % bei kleinen Individuen deutlich über der Wahl von *Patella spec.* (20,2 %; 31,8 %). *Chthamalus spec.* (5,8 %; 1,6%) und *Magallana gigas* (1,0%; 4,8%) hingegen wurden am seltensten gewählt. Bei beiden Gruppen sind zwar die gleichen Trends zu erkennen, jedoch werden von den größeren Individuen häufiger *Patella spec.* sowie *Magallana gigas* gefressen, wohingegen die kleineren Individuen häufiger *Littorina obtusata* und *Chthamalus spec.* gewählt haben.

In der zweiten Auswertung wurde von uns zwischen den zwei Setups unterschieden (vgl. Abb. 5). Wie schon bei der Untersuchung der Größenabhängigkeit liegt auch hier die Beutepräferenz

des Durchschnitts bei *M. edulis* und *Patella spec.* Es hat sich jedoch gezeigt, dass im Einzelsetup *Patella* mit 36 % noch vor *M. edulis* mit 28 % als präferierter Beuteorganismus gewählt wurde. Außerdem wurden deutlich mehr *P. lineatus* und etwas mehr *L. obtusata* gefressen. In den Einzelbecken ist es zu keiner beobachteten Wahl von *Chthamalus spec.* oder *M. gigas* gekommen. Wichtig anzumerken ist jedoch, dass im Einzelsetup lediglich 25 Fraßevents gezählt werden konnten. Im Gruppensetup ist es hingegen zu 204 Fraßevents gekommen. Dies ist auch der Grund für die Ähnlichkeit der Gesamtauswertung mit dem Gruppensetup.

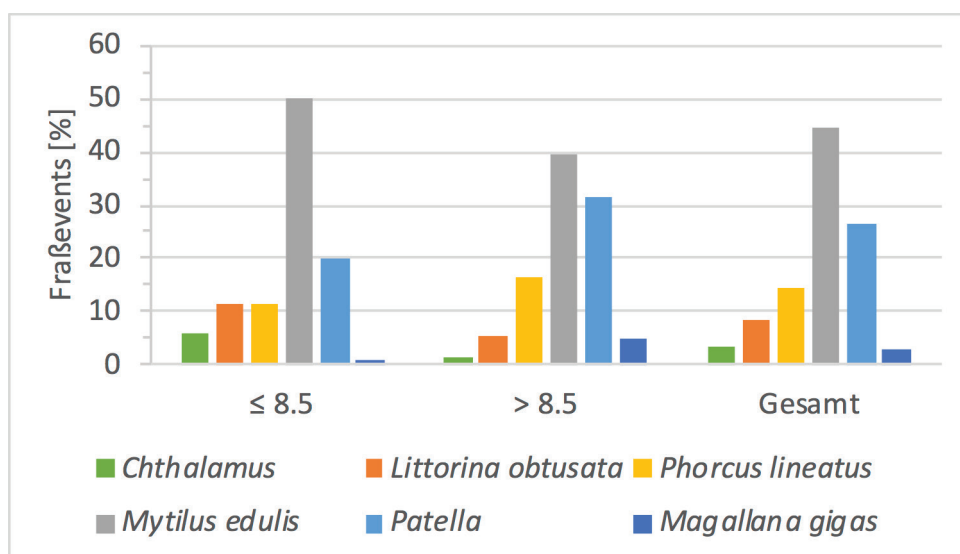


Abb. 4: Beutepräferenz (Verteilung der Fraßevents auf Beutearten) von *Marthasterias glacialis* bzgl. Individuengröße ($\leq 8,5$ cm; $> 8,5$ cm), Gesamtergebnis als Vergleich.

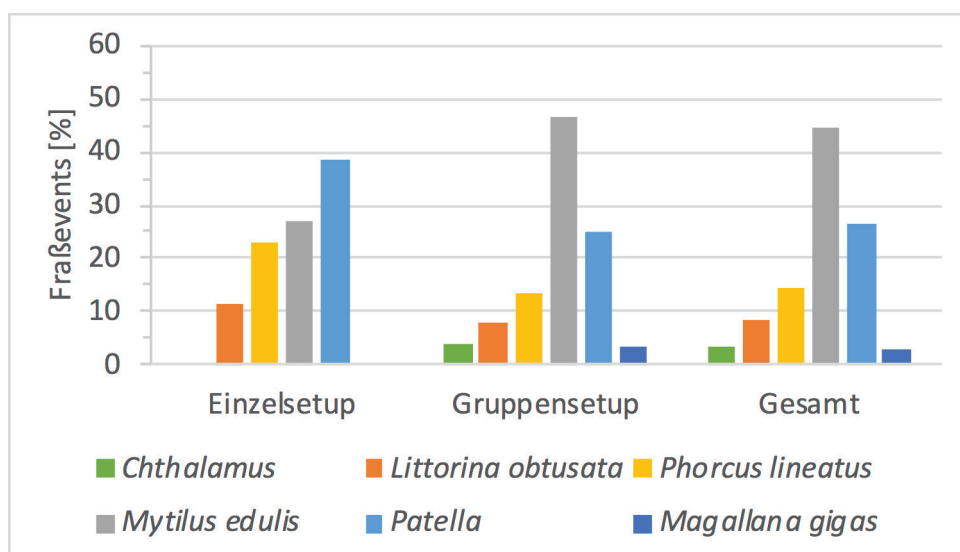


Abb. 5: Beutepräferenz (Verteilung der Fraßevents auf Beutearten) von *Marthasterias glacialis* bzgl. Setup: Einzelsetup (1 Individuum/Becken), Gruppensetup (ca. 25 Individuen/Becken). Gesamtergebnis als Vergleich.

Diskussion

Im Rahmen dieser Arbeit konnten wir zeigen, dass es bei *Marthasterias glacialis* eine deutliche Beutepräferenz sowohl in Abhängigkeit der Größe der Seesterne als auch des Konkurrenzdrucks gibt. Die Individuen haben vorrangig eine Beute gewählt, die mit ihrer jeweiligen Körpergröße korreliert. Die Wahl der Beute war jedoch auch beeinflusst von der An- bzw. Abwesenheit weiterer Individuen von *M. glacialis*.

Die Größenverteilung der untersuchten Individuen ist für *Marthasterias* nicht zwingend repräsentativ, da meist deutlich größere Exemplare von 17 cm bis 30 cm (Gianguzza et al., 2016; Ager, 2008) vorkommen. Es ist also anzunehmen, dass die Untersuchungen entweder an jungen Exemplaren durchgeführt wurden, oder die Individuen aufgrund der Nähe zur Niedrigwasserlinie eine deutlich geringere adulte Körpergröße entwickelt haben. Anlass für diese Vermutung ist das Auffinden von deutlich größeren Exemplaren (> 20 cm) in den tieferen Bereichen (> 3 m Tiefe) derselben Bucht, wie bereits in anderen Studien beschrieben (Verling et al., 2003). Obwohl wir damit die Untersuchung auf eine sehr begrenzte Auswahl an Größenklassen beschränkt haben, kann eine Ausweitung der Ergebnisse auch auf größere Exemplare durch vorherige Forschungsergebnisse gerechtfertigt werden (Gianguzza et al., 2016).

Sowohl in der Auswertung der größenspezifischen Beutewahl als auch in der Setup-Unterscheidung ist deutlich geworden, dass klare Präferenzen bei der Beutewahl zu erkennen sind. *M. edulis* und *Patella spec.* wurden am häufigsten verzehrt. Dies wiederum ist keine wirklich neue Erkenntnis (Branch 1978).

Bei der Größenunterscheidung hat sich gezeigt, dass größere Individuen häufiger *Patella* gewählt haben als die der kleineren Gruppe. Beim Aufbau der Experimente mussten wir feststellen, dass für *Patella* aufgrund ihrer Größe im Vergleich zu *M. edulis* mehr Kraft zum Öffnen/Anheben benötigt wird. Ein weiterer Hinweis darauf, dass größere *M. glacialis* auch schwerer zu öffnende Beute wählen, ist die häufigere Wahl von *M. gigas*. Zwar ist in den beschriebenen Fällen die benötigte Energie zum Öffnen deutlich höher als bei den kleinen Beutetieren, jedoch steigt auch der Nährwert deutlich an. Dieser Zusammenhang stellt zwar eine mögliche Erklärung für die Beobachtungen dar, unklar ist jedoch, woher der einzelne Seestern „weiß“, ob sich der energetische Aufwand für seine jeweilige Körpergröße „lohnt“ bzw. ob er den Kampf überhaupt gewinnen kann.

Die Untersuchung der zwei Setups hat ergeben, dass in den Einzelbecken entgegen der anderen

Beobachtungen *Patella spec.* bevorzugt wurde. Da es sich bei *M. glacialis* zumindest in der Nähe der Niedrigwasserlinie um opportunistische Räuber handelt (Verling et al., 2003), könnte durch unser Gruppensetup in erster Linie die Konkurrenz zu einer Bevorzugung der leichter zu öffnenden Spezies geführt haben. Dies würde erklären, warum die Individuen in den Einzelbecken häufiger die schwerer zu lösenden, jedoch größeren *Patella* gewählt haben, welche auch im natürlichen Habitat zur bevorzugten Beute gehören (Branch, 1978). Da die Gesamtzahl der angegriffenen *M. gigas* sehr gering war, reicht unser Probenumfang nicht aus, um zu sehen, ob sich die beschriebene Tendenz auch bei der größten angebotenen Beute, *M. gigas*, zeigt. Die häufige Wahl der Gehäuseschnecken *P. lineatus* und *L. obtusata* kann hingegen vor allem darauf zurückgeführt werden, dass diese häufig so schnell und unbemerkt gefressen wurden, dass der Seestern noch ein weiteres Beutetier wählen konnte. Es wurde jedoch auch bereits mehrfach gezeigt, dass *M. glacialis* im opportunistischen Stil sein Jagdverhalten den Gegebenheiten anpasst und auch auf Meeresschnecken ausweicht (Branch, 1978; Gianguzza et al., 2016; Verling et al., 2003).

Insgesamt ist gut zu erkennen, dass es deutliche Präferenzen bei der Beutewahl von *M. glacialis* gibt, die nichtsdestotrotz die Charakteristik eines opportunistischen Jagdstils zeigen. Weitere Untersuchungen könnten sich zum Beispiel darauf spezialisieren, das Verhalten in natürlicherer Umgebung in Kombination mit statistisch auswertbaren Daten zu untersuchen. In unserem Fall war eine statistische Auswertung leider nicht möglich, da die Etablierung des Versuchsaufbaus zu viel Zeit in Anspruch genommen hat. Es ist von großem Interesse, weiterführende Untersuchungen mit einem verbesserten Setup durchzuführen. Hierfür wäre es denkbar, eine habitatgetreuere Situation zu simulieren, indem etwa 10 Becken mit jeweils 3-5 Individuen und der entsprechenden Beute bestückt werden. Zusätzlich sollten natürliche Habitatbestandteile wie Steine und Bewuchs vorhanden sein. So ließe sich ein ausreichender Durchsatz von Individuen mit einem naturgetreueren Aufbau kombinieren.

Literaturverzeichnis

- Ager, OED. (2008). *Marthasterias glacialis* Spiny starfish. In Tyler-Walters H. and Hiscock K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [online]
- Branch, GM. (1978). The responses of South African patellid limpets to invertebrate predators. *Zool Africana*. 1978;13(2):221-232.
- Gianguzza, P., Di Trapani, F., Bonaviri, C., Agnetta, D., Vizzini, S., Badalamenti, F. (2016). Size-dependent predation of the mesopredator *Marthasterias glacialis* (L.) (Asteroidea). *Marine Biology* 163:65
- Gosselck, F., Darr, A., Jungbluth, JH., Zettler, ML. (2009). Trivialnamen für Mollusken des Meeres und Brackwassers in Deutschland (Polyplacophora, Gastropoda, Bivalvia, Scaphopoda et Cephalopoda). *Mollusca*. 2009;27(1):3-32.
- Madsen, FJ. (1950). The echinoderms collected by the Atlantide expedition 1945–46. 1. Asteroidea. *Atlantide Rep 1*: 167–222
- Minchin, D. (1987). Sea-water temperature and spawning behaviour in the seastar *Marthasterias glacialis*. *Marine Biology* 95. p. 139-143
- Mortensen, T. (1927). *Handbook of the echinoderms of the British Isles*. Oxford University Press London.
- Penney, AJ. & Griffiths, CL. (1984). Prey selection and the impact of the starfish *Marthasterias glacialis* (L.) and other predators on the mussel *Choromytilus meridionalis* (Krauss). *Journal of Experimental Marine Biology and Ecology* 75. p. 19-36
- Preyer, W. (1887). Über die Bewegungen der Seesterne. *Mitt. zool. Stn Neapel* 7: 27-127, 191-233.
- Valentincic, T. (1973). Food finding and stimuli to feeding in the sea star *Marthasterias glacialis*. *Netherlands Journal of Sea Research* 7. p. 191-192
- Verling, E., Crook, AC., Barnes, DKA., Harrison, SSC. (2003). Structural dynamics of a sea star (*Marthasterias glacialis*) population. *J Mar Biol Assoc UK*. 2003;83(3).

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

& Costa, 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 ($\chi^2=90.1$, $df=4$, $p<0.001$).

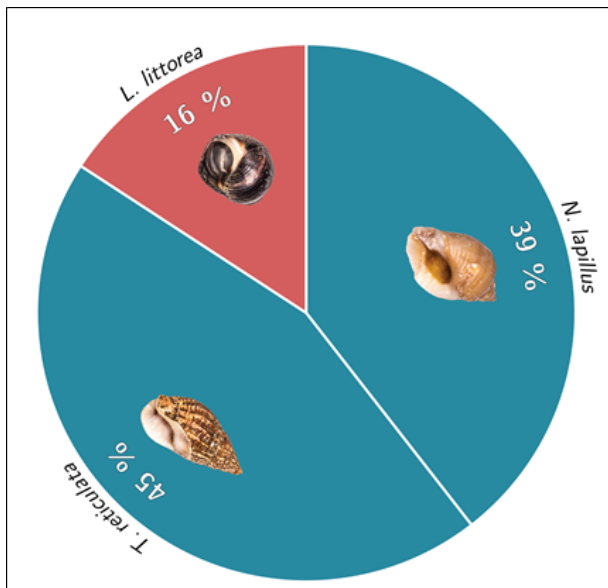


Fig. 6: The results of the shell selection under equal supply show a pronounced preference for a conical shape (blue) in *C. erythropus*. After 60 min the greatest fraction selected *T. reticulata*. Only a minor fraction occupied a shell of globose shape (red). No shells of *P. lineatus* and *S. umbilicalis*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

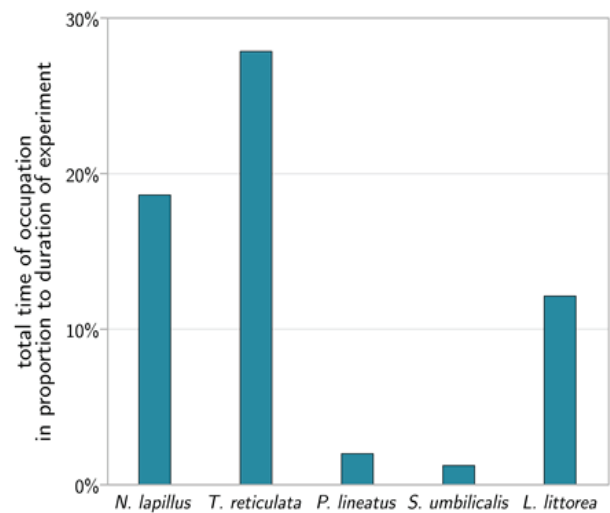












Fig. 7: The total time spent in different shell types during the experiment is consistent with the final shelter selected by *C. erythropus*. Careful considerations in the selection process can be inferred. Total of occupation time given in proportion to duration of experiment.

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		2	2	2	1	5	12
		2	3	2	5	3	15
		0	0	0	0	0	0
		0	0	1	1	0	2
		1	0	4	2	2	9
	Σ abandoned	5	5	9	9	10	

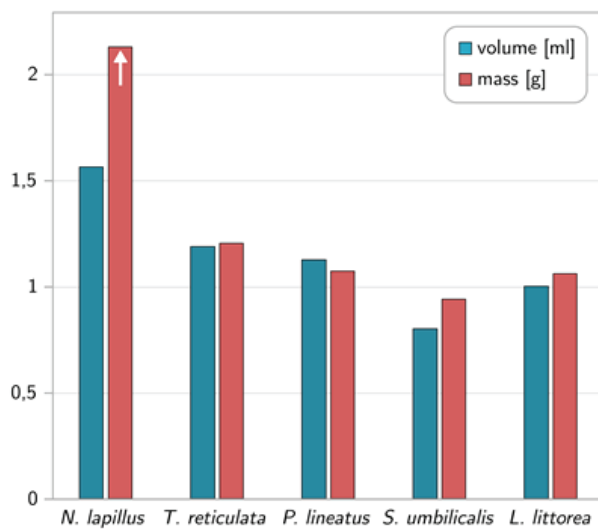


Fig.8: *N. lapillus* has a significantly ($p = 0.05$) greater mass per specimen than other gastropod shells (as indicated by arrow). No significant differences were found among the other shell types. The outer volume does not differ significantly between the shell types employed in our behavioural experiment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

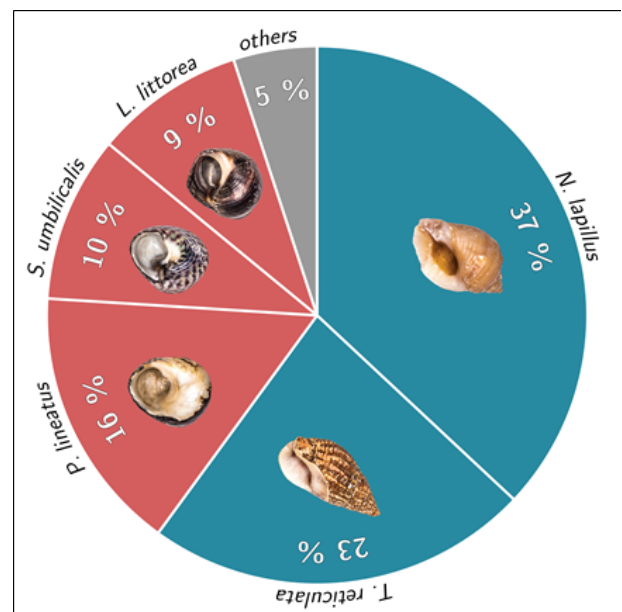


Fig. 9: The distribution of shells occupied by *C. erythropus* in a natural habitat indicates a modulation of shell preference by availability. Yet, the greatest fraction was found in a shell of conical shape (blue). Globose shells constituted a minor fraction (red). Others include *C. zizyphinum* (3 %), *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 (Oriens & 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.

References

- Arce, E., & Alcaraz, G. (2011). Shell use by the hermit crab *Calcinus californiensis* at different levels of the intertidal zone. *Scientia Marina*, 75(1), 121-128.
- Benvenuto, C., Sartoni, G., & Gherardi, F. (2003). Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore. *Journal of the Marine Biological Association of the United Kingdom*, 83(3), 457-461.
- Bertness, M. D. (1980). Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *Journal of Experimental Marine Biology and Ecology*, 48(1), 1-16.
- Bertness, M. D. (1981). The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana*, 40(2), 197-205.
- Bollay, M. (1964). Distribution and utilization of gastropod shells by the hermit crabs *Pagurus samuelis*, *Pagurus granosimanus*, and *Pagurus hirsutiussculus* at Pacific Grove, California. *Veliger*, 6(suppl).

- Botelho, A. Z., & Costa, A. C. (2000). Shell occupancy of the intertidal hermit crab *Clibanarius erythropus* (Decapoda, Diogenidae) on São Miguel (Azores). In *Island, Ocean and Deep-Sea Biology* (pp. 111-117). Springer, Dordrecht.
- Briffa, M., & Austin, M. (2009). Effects of predation threat on the structure and benefits from vacancy chains in the hermit crab *Pagurus bernhardus*. *Ethology*, 115(11), 1029-1035.
- Conover, M. R. (1978). The importance of various shell characteristics to the shell-selection behavior of hermit crabs. *Journal of Experimental Marine Biology and Ecology*, 32(2), 131-142.
- Etter, R. J. (1988). Physiological stress and color polymorphism in the intertidal snail *Nucella lapillus*. *Evolution*, 42(4), 660-680.
- Fraaije, R. H. (2003). The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. *Palaeontology*, 46(1), 53-57.
- Gherardi, F. (1991). Relative growth, population structure, and shell-utilization of the hermit crab *Clibanarius erythropus* in the Mediterranean. *Oealia*, 17(NS), 181-196.
- Gherardi, F., & Vannini, M. (1993). Hermit crabs in a mangrove swamp: proximate and ultimate factors in the clustering of *Clibanarius laevimanus*. *Journal of Experimental Marine Biology and Ecology*, 168(2), 167-187.
- Gherardi, F., Zatterri, F., & Vannini, M. (1994). Hermit crabs in a mangrove swamp: the structure of *Clibanarius laevimanus* clusters. *Marine Biology*, 121(1), 41-52.
- Grant Jr, W. C. (1963). Notes on the ecology and behavior of the hermit crab, *Pagurus acadianus*. *Ecology*, 44(4), 767-771.
- Hazlett, B. A. (1966). Social behavior of the Paguridae and Diogenidae of Curacao. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 23(1), 1-143.
- Hazlett, B. A. (1967). Interspecific shell fighting between *Pagurus bernhardus* and *Pagurus cuanensis* (Decapoda, Paguridea). *Sarsia*, 29(1), 215-220.
- Hazlett, B. A. (1978). Shell exchanges in hermit crabs: aggression, negotiation, or both?. *Animal behavior*, 26, 4. Pp 1278-1279
- Hazlett, B. A. (1981). The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics*, 12(1), 1-22.
- Hazlett, B. A. (1987). Information transfer during shell exchange in the hermit crab *Clibanarius antillensis*. *Animal behaviour*, 35(1), 218-226.
- Jackson, H. G. (1913). *Eupagurus*. LMBC Memoirs no. 21. *Proc. Trans. Liverpool Biol. Soc.* vj, 493-573.
- Katz, J. N., & Rittschof, D. (1993). Alarm/investigation responses of hermit crabs as related to shell fit and crab size. *Marine & Freshwater Behaviour & Phy*, 22(3), 171-182.
- Kellogg, C. W. (1976). Gastropod shells: a potentially limiting resource for hermit crabs. *Journal of experimental marine Biology and Ecology*, 22(1), 101-111.
- MacKay, D. C. (1945). Notes on the aggregating marine invertebrates of Hawaii. *Ecology*, 26(2), 205-207.
- McLaughlin, P. A. (1983). Hermit Crabs—Are They Really Polyphyletic?. *Journal of Crustacean Biology*, 3(4), 608-621.
- Mesce, K. A. (1982). Calcium-bearing objects elicit shell selection behavior in a hermit crab. *Science*, 215(4535), 993-995.
- Orians, G. H., & King, C. E. (1964). Shell selection and invasion rates of some Pacific hermit crabs.
- Ramsey, M. Shell Preferences in Hermit Crabs., Bsc(Hons) Conservation Biology, University of Lincoln
- Reddy, T., & Biseswar, R. (1993). Patterns of shell utilization in two sympatric species of hermit crabs from the Natal coast (Decapoda, Anomura, Diogenidae). *Crustaceana*, 65(1), 13-24.
- Reese, E. S. (1961, January). Interspecific and intraspecific dominance relationships of sympatric species of intertidal hermit crabs. In *American Zoologists* (Vol. 1, No. 3, pp. 382-382). 1041 New Hampshire St, Lawrence, KS 66044: Amer Soc Zoologists.
- Reese, E. S. (1962). Shell selection behaviour of hermit crabs. *Animal Behaviour*, 10(3-4), 347-360.
- Reese, E. S. (1969). Behavioral adaptations of intertidal hermit crabs. *American Zoologist*, 9(2), 343-355.
- Rittschof, D. (1980). Chemical attraction of hermit crabs and other attendants to simulated gastropod predation sites. *Journal of Chemical Ecology*, 6(1), 103-118.
- Rittschof, D., Sarrica, J., & Rubenstein, D. (1995). Shell dynamics and microhabitat selection by striped legged hermit crabs, *Clibanarius vittatus* (Bosc). *Journal of Experimental Marine Biology and Ecology*, 192(2), 157-172.
- Schade, H., Kunz, E., Kameier, F., & Paschereit, C. O. (2013). *Strömungslehre*. Walter de Gruyter.

- Southward, A. J., & Southward, E. C. (1977). Distribution and ecology of the hermit crab *Clibanarius erythropus* in the western Channel. *Journal of the Marine Biological Association of the United Kingdom*, 57(2), 441-452.
- Tallmark, B. (1980). Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. *Mar Ecol Prog Ser*, 3(1), 51-62.
- Tricarico, E., Breithaupt, T., & Gherardi, F. (2011). Interpreting odours in hermit crabs: a comparative study. *Estuarine, Coastal and Shelf Science*, 91(2), 211-215.
- Trussell, G. C., Johnson, A. S., Rudolph, S. G., & Gilfillan, E. S. (1993). Resistance to dislodgement: habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Marine ecology progress series*, 135-144.
- Völker, L. (1967). Zur Gehäusewahl des Landeinsiedlerkrebse *Coenobita scaevola* Forskal vom Roten Meer. *Journal of Experimental Marine Biology and Ecology*, 1(2), 168-190.
- Wikimedia Commons, Blank Map of Europe, [https://commons.wikimedia.org/wiki/File:Blank_map_of_Europe_\(without_disputed_regions\).svg](https://commons.wikimedia.org/wiki/File:Blank_map_of_Europe_(without_disputed_regions).svg), CC-ASA-4.0, 19.02.2019, 13:25
- Zariquey Alvarez, R. (1968). *Crustáceo Decápodos Ibéricos*. *Investigacion Pesquera*, 32. Barcelona

The movement radius of *Patella spec.* around its home scar correlates with duration of water exposure

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Abstract

With its extraordinary ability of orientation enabling home fidelity the limpet *Patella* has been of high interest for scientists during the last two centuries. To assess possible correlations between limpet behaviour and distance to the low water line it is useful to observe their active movement range from one low tide to the next low tide and also from day to night. By comparing photographs taken each day and night over the test duration we determined a degree of home fidelity of 94.2% at the rocky shores of the Breton Atlantic coast. We also observed a positive correlation between the proximity of the limpet's home scar to the low water line and its movement radius. We present an adequate strategy as uninvasive as possible for similar studies.

Introduction

The behaviour of intertidal organisms changes in close correlation with the tides (Fingerman 1957). Members of the marine gastropod genus *Patella* inhabit rocky shores between the border of the sublittoral zone and the upper shore line where they are constantly exposed to the influences of the tides (Davis & Fleure 1903). During high tides and low tides at night they graze on the rocks feeding on algae. During the day ebb tide forces them to return to their home scars, that perfectly match their shell margins using chemical and olfactory orientation (Edelstam & Palmer 1950; Funke 1968). Exposed to air with a high risk of predator attacks they remain at their home scars where they adhere themselves firmly to the ground using their shell muscles (Funke 1968). Since Lukis studied *Patella* for the first

time in 1831 there have been many studies trying to solve the mystery of the limpet's orientation mechanisms and activity (Davis & Fleure 1903; Villet & Groody 1940; Edelstam & Palmer 1950; Kohn 1961; Funke 1968; Maier & Mielke 2016). However, little has been done to characterise correlations between the animal's movement activity and their geographical position in the tidal zone. The aim of this study is to (i) re-assess *Patella*'s site fidelity and (ii) test for correlations between individual moving ranges and home scar positions along a transect from the low to high water lines. By observing the limpets in their natural habitat we were able to deploy methods which in contrast to previous studies did not interfere with the animal's chemical orientation.

Material and Methods

Test sites and organisms

Two different areas were used for the experiments. Both selected areas were rocky intertidal zones of the Atlantic coast. The first area was in front of the Marinarium in Concarneau (France) and the second area was in Le Cabelou (France), south of the fort. Each area was subdivided in 3 zones (1, 2 and 3 in Concarneau and 4, 5 and 6 in Le Cabelou). The areas 1 and 4 were approximately at LWL + 177 cm, 2 and 5 approximately at LWL + 237 cm and 3 and 6 approximately at LWL + 297 cm. It was made sure, that the zones were composed by coherent areas without gaps and that they were easily accessible from above to take pictures and to observe all individuals. 120 Individuals belonging

to the genus *Patella* were observed, 20 in each zone. The chosen individuals were marked with nail polish on top of their shell to be distinguished from the other individuals in the nearby area.

Sampling

For a total of five days the presence and site fidelity of the individuals and their range of motion were monitored. Sampling was done at ebb tide ± 90 minutes, both during the day and night. Initially each zone was photographed (e. g. Fig. 1). To calculate the reference size of each zone the distance between the two individuals that were furthest apart was measured at the beginning of the trial. A reference size was calculated with

with these distances.

The individuals were counted at the site each time sampling was done. The site fidelity was monitored by comparing the pictures taken during the day to the reference. Individuals, that were not at their home scar at least once were counted. The distance between the two individuals that were the furthest apart was measured every time sampling was done at night. These measurements were used to calculate the size of this area at the time of sampling. In further calculations, the daily measured sizes were compared to the reference size single handedly.

Calculations

The ratio of animals that was found back at the homescar during daytime and the animals that were missing or at another spot throughout the trial was calculated in percent. To determine

differences of the ranges of motion between the different zones, we compared the sizes of the zones to the respective reference. To approach the daily range of motion, we calculated the size of the zones as circular shaped surfaces. The measured distances were used as the diameter of the area. The range of motion was then calculated as the factor between the sizes of the zones at night compared to the reference as: Range of motion = SIZE (Sample X) / SIZE (Sample 1). The average for each zone was calculated. Furthermore, we used a double-sided T-Test using R Studio (Version 1.1.419 – © 2009-2018 RStudio, Inc.) to compare the zones with each other. Comparisons were made between the zones along the transects at both sites (e.g. zones 1, 2 & 3) as well as between the corresponding zones of both collection sites (e.g. zones 1 & 4, 2 & 5 etc.).

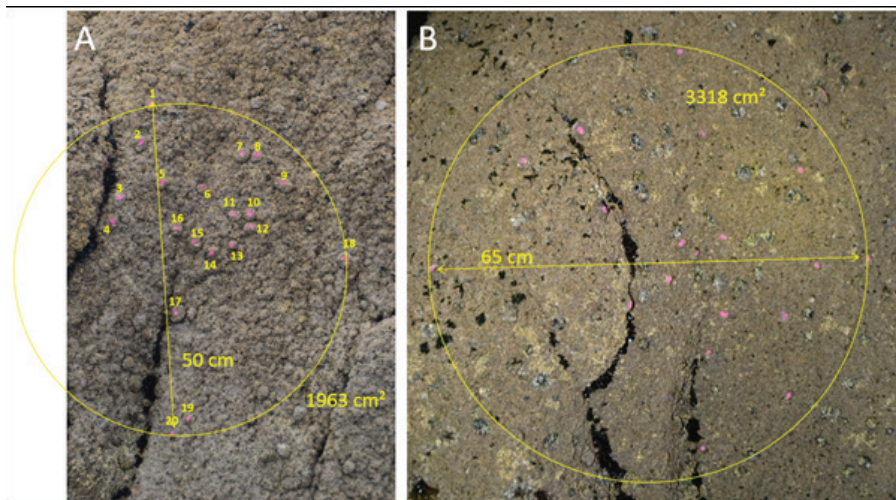


Fig. 1: Zone 2 (Concarneau); A) shows *Patella* spec. during the day (first sampling). B) shows the same specimens during the night (second sampling). To approach the daily range of motion, we calculated the area of the zones as circular shaped surfaces. To calculate the area of each zone the distance between the two individuals that were the furthest apart was measured.

Results

Patella shows a high rate of home fidelity

To determine the home fidelity of *Patella* spec. we calculated the ratio of animals that returned to their home scar every day versus the animals that had been found at a different spot or missing at least once. 94.2% of the animals were found at the respective home scar during each day. 5.8% of the specimens were not found at the home scar at least once (7 out of 120). One individual could not be found (Zone 2, 7th sampling) and did not reappear. The same individual had been found at a surprisingly large distance from the respective zone (6th sampling).

Limpets closest to the LWL show the highest movement radius

To investigate the range of motion of *Patella*

spec., we calculated the sizes of the zones and compared them to each other. Fig. 2.2.1 shows the range of motion of the animals in the zones 1, 2 and 3 (Concarneau). The animals in zone 1 present a significantly larger range of motion than the animals in the other two zones (2.08 ± 0.39). The animals in zone 2 show a higher range of motion than the ones in zone 3 (1.84 ± 0.35 and 1.44 ± 0.30 respectively), although the differences are not significant (Fig. 2.2.1). Fig. 2.2 shows the zones 4, 5 and 6 (Le Cabellou). The animals in zone 4 present the highest range of motion (5.22 ± 1.09), the animals in zone 5 the lowest (1.74 ± 0.30). The animals in zone 6 had a range of motion of 2.20 ± 0.16 . The differences are significant in all three zones (Fig. 2.2).

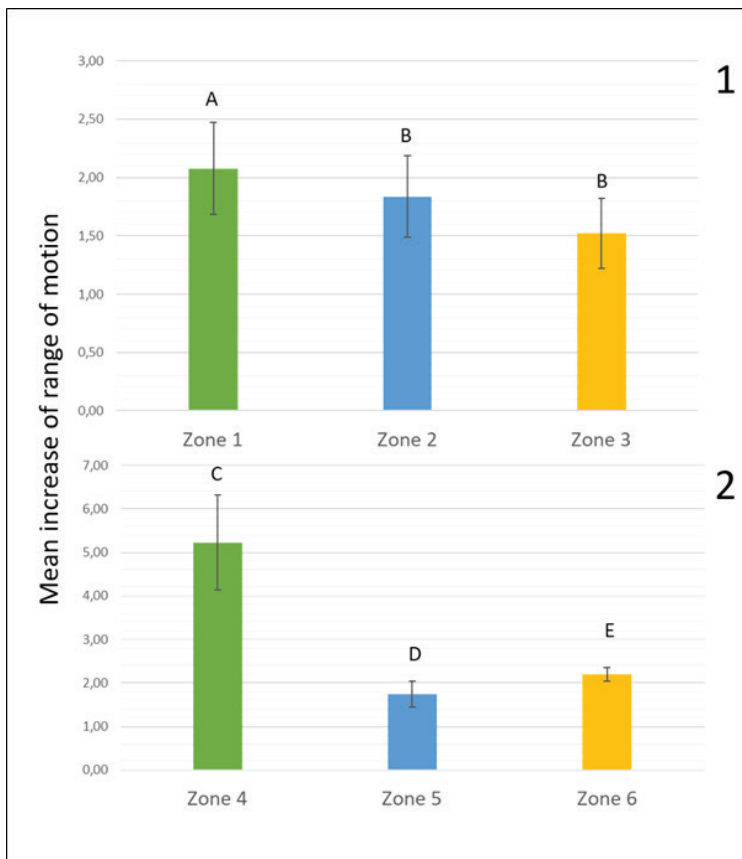


Fig. 2: Mean increase of range of motion of *Patella* spec. in 1) Concarneau and 2) Le Cabellou in different distances from the low water line from close (Zones 1 and 4) to far (zone 3 and 6). Significant differences are marked by different letters.

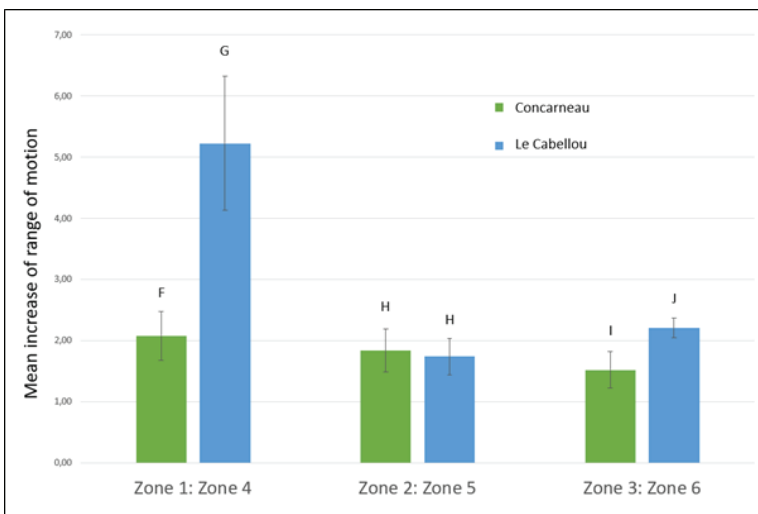


Fig. 3: Comparison of the mean increase of range of motion of *Patella* spec. in Concarneau (green) and Le Cabellou (blue) in different distances from the low water line from close (Zones 1 and 4) to far (zone 3 and 6). Significant differences are marked by different letters.

The movement radius of the limpets in Le Cabellou is higher than in Concarneau

To investigate possible differences in range of motion between Le Cabellou and Concarneau, We compared the corresponding zones of both sites (Fig. 3). We found a significant difference in the lower zones (1 and 4), where the range of motion is higher in the limpets at Le Cabellou than in Concarneau (5.22 ± 1.09 and 1.63 ± 0.39 respectively, Fig. 3). In the upper shore (Zones 3 and 6) the tendency was quite similar and the limpets at Le Cabellou showed to have a larger range of motion than Concarneau as well (2.20 ± 0.16 and 1.52 ± 0.30 respectively, Fig. 3). In the middle shore (Zones 2 and 5) no significant difference could be found between Le Cabellou

and Concarneau (1.74 ± 0.30 and 1.84 ± 0.35 respectively, Fig. 3).

Overall a tendency of a higher range of motion close to the LWL was observed (Fig. 3). Additionally, we pooled the zones 1 to 3 and 4 to 6 and compared the average range of motions of both areas in general. The overall average range of motion for Le Cabellou showed to be significantly higher than in Concarneau (3.06 ± 1.72 and 1.81 ± 0.40 respectively). This can be due to numerous reasons that we did not monitor with sufficient detail, like differences in the terrain or differences in direct sunlight radiation. Further experiment to investigate the influence of site properties should be done in the future.

Discussion

Home fidelity in *Patella* spec. in the field has already been observed in 1903 (Davis und Fleure 1903) as well as under laboratory conditions (Funke 1968; Edelstam und Palmer 1950). This behaviour is a powerful mechanism to lower the risk of predation as they are able to adapt their shell perfectly to their subsoil over time by actively rasping the substrate off their home scars with their goethite teeth (Funke 1968; Lowenstam 1962) minimizing the risk of predation, once the shell perfectly matches the subsoil. In the tidal zone of Concarneau and Le Cabellou we determined a high percentage of home fidelity of 94.2% (113 out of 120). Only a few (seven out of 120) specimens did not return to their home scars regularly during the experimental period although they were all found in the surrounding area except one specimen. It cannot be ruled out that sites we determined as home scars are actually the home scars as they can leave or change their home scars over several weeks or months (Funke 1968). One of the specimens got lost after 2 nights after it was seen unusually far away from its home scar the previous night. We can only speculate about a reason for that but there is a possibility of predation.

Observing the range of motion in relation to the distance to the low water line showed variation between the zones. Specimens closer to the LWL present a significantly larger range of motion than the ones further away both in Concarneau and Le Cabellou (Fig. 2). Those specimens are exposed to water for a longer period of time and thus have more time to return to their home scars with lower risk of drying out. The further away the limpets are from the LWL the more irrelevant the differences between the zones become. High on the shore, where space becomes more and more limiting, competition over the best spots enhances territorial behaviour of *Patella* (Branch 1975). With less appropriate places the limpets have been observed to mark their territory and thus cut off their competitors' way with their individually smelling mucus trace (Funke 1968) resulting in lower range of motion.

Outlook

Our results suggest, that the observation of more zones in one area might improve the results. Also, sectioning the upper shore of an area into more than two zones might provide crucial information about the importance of air exposure time and the influence of other factors in relation to it. Our results don't provide enough information to make precise assumption about

The differences of air exposure become less relevant as the territorial pressure gives priority to other factors like the characteristics of the area. Here, features like gradient angle and thus shadiness and moistness are the limiting factors of the range of motion. Therefore in Concarneau the middle and the upper zone show no significant differences whereas in Le Cabellou in the zone furthest from the LWL the limpets move more than in the middle zone.

Moreover, there were significant differences between the zones when comparing the two sites with each other. The limpets in Le Cabellou presented a significantly larger movement radius than the ones in Concarneau (Fig. 3). The site properties were very different between Le Cabellou and Concarneau. The limpets in the middle and upper zones in Concarneau were sitting on a significantly steeper angle than the limpets in the respective zones in Le Cabellou. Different properties that might differ in the two beaches could influence the activity of *Patella* like food supply, the angle of inclination, the presence of Balanidae or the species composition (Davis und Fleure 1903). Observing and quantifying these differences could be an interesting approach for future studies that might deal with the surface quality of the two areas.

It is worth mentioning that interspecific variation has not been considered in this study. Detaching the limpets is necessary to identify them to species level. Therefore, we deliberately did not do this to guarantee that all individuals were not harmed in the process of the experiment. Furthermore, it has been shown to be difficult to detach the animals from the ground without damaging them (Davis und Fleure 1903), which is not in our interest. For the same reason, we refrained from individually marking the specimens and their location, as their sensitive coatactles, which are responsible for their orientation, could be disturbed by the distinctive colour odour (Funke 1968). It is shown that the behavior of *Patella* can be studied adequately without invasive measures.

these specific parameters. Additionally, zones with comparable properties may increase the precision of the results, as the site properties appear to be crucial to the behavior of the limpets. Variations of the angle, the moisture and shadiness may influence the range of motion and therefore should be further explored. Additionally, more detailed information about the indivi-

dual range of motion could be useful for more specific conclusions. Better results might be obtained by placing cameras photographing the zones in regular intervals. These could be either submergible to leave them installed during the experiment or markings could help to place them on the same position every time sampling is done. Individual locomotion patterns could be analyzed and reveal potential correlations of range of motion and size or population density.

References

- Branch, G. M. (1975): Mechanisms Reducing Intraspecific Competition in *Patella* spp.: Migration, Differentiation and Territorial Behaviour. *The Journal of Animal Ecology* 44 (2), S. 575.
- Davis, James Richard Ainsworth; Fleure, H. J. (1903): *Patella*, the common limpet / by J.R. Ainsworth Davis and H.J. Fleure. London: Williams & Norgate.
- Edelstam, Carl; Palmer, Carina (1950): Homing Behaviour in Gastropodes. *Oikos* 2 (2), S. 259.
- Fingerman, Milton (1957): Lunar Rhythmicity in Marine Organisms. *The American Naturalist* 91 (858), S. 167–178.
- Funke, Werner (1968): Heimfindevermögen und Ortstreue bei *Patella* L. (Gastropoda, Prosobranchia). *Oecologia* 2 (1), S. 19–142.
- Kohn, Alan J. (1961): Chemoreception in Gastropod Molluscs. *American Zoologist* 1 (2), S. 291–308.
- Lowenstam, H. A. (1962): Goethite in Radular Teeth of Recent Marine Gastropods. *Science* (New York, N.Y.) 137 (3526), S. 279–280.
- Maier, H. und Mielke, M. (2016): Die Schalenmorphologie von *Patella* spp. an der bretonischen Atlantikküste ist standortabhängig. *Proceedings in Marine Biology* (11).
- Villee, C. A.; Groody, T. C. (1940): The Behavior of Limpets with Reference to Their Homing Instinct. *American Midland Naturalist* 24 (1), S. 190.