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Hermit crabs and their symbionts: reactions to artificially induced anoxia on a sublittoral sediment bottom

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“Every human heartbeat
is a universe of possibilities.”

Gregory David Roberts



Photo: Shannon Rosenberg

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1. Introduction

Hermit crabs inhabit a wide range of environments, from polar to tropical seas and from the supratidal to deep ocean canyons. They play important roles as predators, scavengers, detritivores and even filter-feeders (Schembri, 1982), and their manifold symbioses can enrich the biodiversity of their habitats (Reiss et al., 2003). In the Northern Adriatic Sea, which is characterized by high-biomass macrobenthic assemblages termed multi-species clumps (Fedra et al., 1976), hermit crabs exhibit a high density (1.88 individuals m⁻²). *Paguristes eremita* (Linnaeus, 1767) is the dominant hermit crab species, followed by *Pagurus cuanensis* (Bell, 1845) (Stachowitsch, 1977). According to the crab's size, small *P. eremita* individuals mostly inhabit the shells of *Aporrhais pespelecani* (Linnaeus, 1758), larger individuals shells of *Murex brandaris* (Linnaeus, 1758) and *Hexaplex trunculus* (Linnaeus, 1758) (Stachowitsch, 1980).

Hermit crab-occupied shells are important islands of hard structures for the attachment of epifauna in soft-bottom benthic communities (Brooks and Mariscal, 1986). There, empty shells are likely to be buried in the substrate unless they are used by hermit crabs as protection (Creed, 2000; Stachowitsch, 1977). Hermit crabs are therefore ecosystem engineers: through their use of gastropod shells they affect the abundance and distribution of invertebrates (Gutiérrez et al., 2003; Jones et al., 1994; 1997; Williams and McDermott, 2004). *Paguristes eremita* harbours more than 110 symbionts (in the sense of living together of unlike organisms, without implication of positive or negative influence; De Bary, 1879) including epizoic and endolithic species (Stachowitsch, 1980). The large number, size and diverse assemblage of species (Stachowitsch, 1980; Williams and McDermott, 2004) make it a stable yet mobile microbiocoenosis (Stachowitsch, 1977). Such assemblages influence the period that a shell can function as a hermit crab house due to two simultaneous processes. A constructive process involves species which strengthen and extend the lifespan of a shell, e.g. encrusting forms, ascidians or the sponge *Suberites domuncula* (Olivi, 1792). A deconstructive process weakens the shell and decreases the time it can be utilized, e.g. boring polychaetes, the sponge *Cliona* sp. or the bivalve *Gastrochaena dubia* (Pennant, 1777). This led to a new perspective and classification of hermit crab symbionts based on their function in prolonging or

shortening the period of usefulness of empty gastropod shells as the key resource for hermit crabs. When deteriorated shells are deposited by the hermit crabs, most symbionts survive and grow further: formerly occupied gastropod shells form the basis of many established multi-species clumps and therefore play a crucial role in structuring the overall community (Stachowitsch, 1980).

Coastal shallow seas face the greatest anthropogenic threats due to the impacts of accelerated human activities (Jenkins, 2003). Eutrophication, coupled with water column stratification, has been recognized as one of the gravest threats. This is manifested in low dissolved oxygen levels (Diaz, 2001). Hypoxia (DO concentrations $< 2 \text{ ml l}^{-1}$) and anoxia have spread exponentially since the 1960s and today are a key stressor in shallow marine ecosystems (Diaz and Rosenberg, 2008). The susceptibility of benthic animals to hypoxia varies, but all initially respond with atypical behaviour as well as physiological adaptations (Diaz and Rosenberg, 1995; Gray et al., 2002; Wu, 2002). Lengthier hypoxia and even lower values trigger mass mortalities of the benthic fauna (in the Adriatic; Stachowitsch, 1984), affecting extensive areas and leading to so-called dead zones (Diaz and Rosenberg, 2008). Hypoxia changes not only the structure and function of benthic communities but also has impacts on all scales, from altering biogeochemical processes (Conley et al., 2009) to decreasing the provision of ecosystem services (Sala and Knowlton, 2006). In addition, ocean warming is estimated to reduce survival times of organisms, leading to an increased vulnerability to low DO concentrations (Vaquer-Sunyer and Duarte, 2010a).

The Northern Adriatic Sea is one of nearly 400 recognized dead zones worldwide (Fig. 1). As a shallow, semi-enclosed water body with abundant nutrient discharges, mainly from the Po River, coupled with meteorological and climatic conditions, the Northern Adriatic Sea exhibits most attributes that are associated with the development of low oxygen events (Justić et al., 1993). It can therefore serve as a model for a sensitive ecosystem that is periodically affected by oxygen deficiency (Crema et al., 1991). Due to the difficulty of predicting oxygen depletion events, the EAGU (experimental anoxia generating unit) was developed to simulate anoxia on a small scale and to document behavioural responses, inter- and intraspecific interactions, and mortalities *in situ* (Stachowitsch et al., 2007).

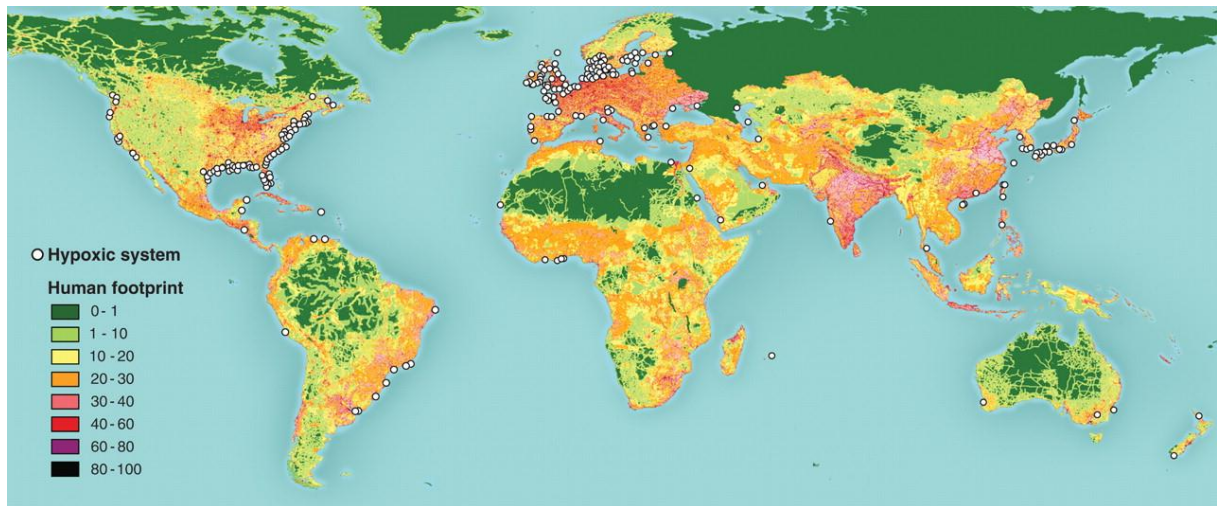


Fig. 1. Worldwide distribution of eutrophication-associated “dead zones”. Affected systems match with the global human footprint (Diaz and Rosenberg, 2008).

First results on selected species and species groups have already been published for the Adriatic (Haselmair et al., 2010; Riedel et al., 2008a; 2008b). Crustaceans are sensitive to anoxia (Vaquer-Sunyer and Duarte, 2008), but our observations indicate that hermit crabs may be somewhat more tolerant. This relative tolerance would have implications for survival of short-term hypoxia and the recolonization of affected areas. Considering the important role that hermit crabs play in this community, only little is known about their responses to hypoxia (Côté et al., 1998; Riedel et al., 2008b; Shives and Dunbar, 2010; Stachowitsch, 1984). The present study is designed to fully document the behaviour of hermit crabs during oxygen crises and to correlate behaviour and mortality with specific oxygen thresholds.

2. Materials and methods

2.1. Study site

The study site is located 2.3 km off Cap Madonna (Piran, Slovenia) in the Gulf of Trieste (45° 32' 55.68'' N, 13° 33' 1.89'' E) close to the oceanographic buoy of the Marine Biology Station Piran at a depth of 24 m (Fig. 2).

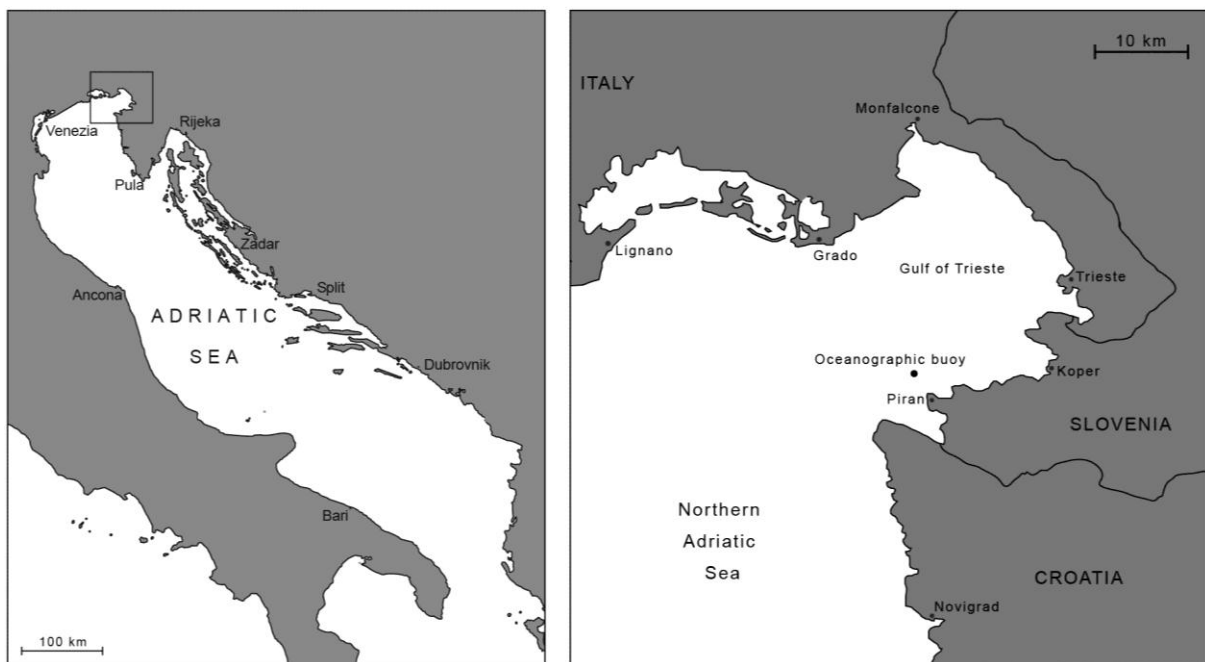


Fig. 2. Overview and detailed map of the study site Piran, Slovenia (from Haselmair, 2008).

The Northern Adriatic Sea is characterized by high biomass epifauna communities, so that it in some respects resembles Paleozoic, stationary suspension-feeding communities rather than modern infauna-dominated assemblages (McKinney, 2007; Zuschin and Stachowitsch, 2009). This can be attributed to a range of factors including productivity, nutrient levels, sediment input and availability of hard substrata.

This sublittoral bottom consists of poorly sorted silty sand with high-biomass aggregations of macrobenthic organisms termed multi-species clumps (Fedra et al., 1976). These multi-species clumps or bioherms are formed by biogenic structures, mainly mollusc shells which serve as a basis for sessile species, mostly serpulid

tubeworms, ascidians, sponges, anemones and bivalves (Zuschin et al., 1999). Multi-species clumps provide a substrate for semi-sessile and vagile species such as the brittle star *Ophiothrix quinque maculata* (Delle Chiaje, 1828), the holothurian *Ocnus planci* (Brandt, 1835) and the sea urchin *Psammechinus microtuberculatus* (Blainville, 1825) as well as crustaceans such as *Pilumnus spinifer* (Milne-Edwards, 1834) and *Pisidia longimana* (Risso, 1816). Filter- and suspension-feeding species dominate. Based on the 3 dominant taxa (*O. quinque maculata*, the sponges *Reniera* spp., and the ascidians *Microcosmus* spp.), this benthic community was named Ophiothrix-Reniera-Microcosmus community (Fedra et al., 1976). The sediment surface between the patchy distribution of multi-species clumps is characterized by a low epifaunal density (Zuschin et al., 1999). This interspace is dominated by predators and deposit feeders such as gastropods, the bivalve *Chlamys varia* (Linnaeus, 1758), the brittle star *Ophiura ophiura* (Linnaeus, 1758) and the hermit crabs *P. eremita* and *P. cuanensis*.

2.2. Experimental design and sampling

The experimental anoxia generating unit (EAGU) is an underwater device designed to artificially create hypoxia and anoxia on a small scale (0.25 m²) on the seafloor. It enables the documentation of the behaviour of macrobenthic organisms to oxygen depletion and increasing H₂S.

The EAGU is composed of a cubic aluminium frame or an interchangeable plexiglass chamber, both measuring 50 x 50 x 50 cm (for more details see Stachowitsch et al., 2007). A separate instrument lid is placed on top of one of these two different bases. This lid houses a time-lapse camera, two flashes and a data logger with sensor array to record DO, H₂S and temperature (Unisense[®]) (Fig. 3). Oxygen was measured 2 and 20 cm above the sediment to capture potential stratification, and the H₂S sensor was located 2 cm above the sediment. PH was measured manually with a WTW TA 197-pH sensor daily during control dives. Photos were taken automatically every 6 min, and sensor data were logged every minute.

The EAGU was deployed in two configurations. First, in the “open” configuration, the aluminium frame was positioned above an aggregation of benthic organisms for 24 h to document behaviour under normoxic conditions. Then, in the “closed” configuration, the aluminium frame was exchanged with the plexiglass chamber and

deployed above the same assemblage to identify responses to decreasing DO concentrations. The chamber allows no water exchange with the water column. Anoxia was induced within 1 – 2 d due to natural respiration rates of the enclosed organisms. The “closed” configuration was maintained for another 1 – 2 d to detect the reactions of more tolerant species. Remaining organisms (living and dead) were then collected for preservation in a 4 % formalin:seawater solution, and species and biomass were determined. The fieldwork was conducted in September 2005 and from July to October 2006.

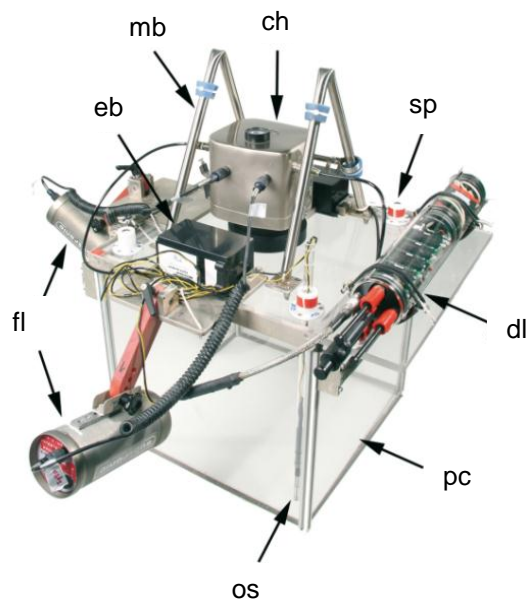


Fig. 3. Experimental anoxia generating unit (EAGU) consisting of a plexiglass chamber and the instrument lid atop. ch: camera housing, dl: datalogger, eb: external battery, fl: flashes, mb: metal brackets, os: oxygen sensor, pc: plexiglass chamber, sp: sensor port. (Photo: Gregor Eder; Stachowitsch et al., 2007).

Transects (30 m long, 0.5 m on each side) were laid in September 2010 to determine the abundance of hermit crabs. Either one or both sides of the transects were evaluated, yielding a total of 9 transects of 0.5 m width covering an area of 135 m². Pagurids were collected by hand using scuba diving techniques along transects. The samples were transported to the laboratory in 1 mm² mesh bags placed into buckets with fresh seawater. The lengths and species of the occupied shells (± 0.1 mm) were measured. The hermit crabs were then released into the sea.

2.3. Data analysis

This study focused on the behaviour of the hermit crab *P. eremita* (formerly named *P. oculatus*) by evaluating two deployments in the open configuration. Eight deployments were evaluated in the closed configuration.

Overall, 6705 images were evaluated yielding a documentation time of 670.5 h (45.5 h open, 625 h closed configuration). Behaviour was analysed image by image and recorded in categories (Tab. 1). In the open configuration, all visible individuals within the camera's field (inside and outside of the aluminium frame) were evaluated. In the closed configuration, hermit crabs were evaluated only inside the plexiglass. If 4 or fewer hermit crabs were present in an experiment, all were evaluated. If more individuals were present, those 4 individuals that were visible throughout the experiment were selected. Additional criteria for selection included range of sizes, occupied shell species and symbionts. Three housing categories are distinguished: small crabs in *A. pes-pelecani* shells; large crabs in *M. brandaris* or *H. trunculus* shells; crabs occupying the sponge *S. domuncula* (crabs of various sizes).

The hermit crabs themselves are typically only partially visible (i.e. antennae, eyestalks). Thus, the image evaluation was based on the locomotion and/or position changes of the shell. Shell locomotion was equated with crab locomotion. Displacement (i.e. major/minor locomotion) in small and large crabs was equated to shell displacement. For individuals in large *S. domuncula*, it was equated to estimated crab length. When a hermit crab left its shell, the evaluation was based solely on the animal's behaviour. Behaviours were documented as long as living organisms were visible and clearly identifiable, i.e. until mortality or until poor visibility due to decomposition of other benthic organisms. Mortality was recorded 2 h after the last observed locomotion or body movement. "Hours after hypoxia and anoxia" refer to the total time span measured between 2 ml l⁻¹ DO (mild hypoxia) and the evaluated behaviour, whereby the anoxia component is provided separately (time between 0 ml l⁻¹ DO (anoxia) and the behaviour). Day and night were defined according to sunrise and sunset of the corresponding day of the deployment. Deployment 11 was chosen to graphically depict the sensor and hermit crab data because it was one of the longest experiments and it was also used for evaluations in the open configuration (Fig. 4).

Tab. 1. Behaviours and reactions of hermit crabs investigated, including categories and sub-categories.

Category/sub-category	Criteria
Visibility	
<i>visible</i>	Hermit crab, its shell or parts thereof visible. This includes shell largely covered by other organisms (e.g. crab under brittle star aggregation, i.e. outline recognizable, no exit tracks).
<i>non-visible</i>	Neither crab nor its shell or parts thereof visible (e.g. hidden behind a multi-species clump).
Location	
<i>on sediment</i>	Crab/shell located on sediment or on bivalve shells on sediment.
<i>elevated</i>	Crab/shell on multi-species clump (no contact with sediment).
Horizontal locomotion	
<i>no locomotion</i>	No displacement.
<i>minor</i>	Displacement <1 shell length or <1 body length (if crab outside shell).
<i>major</i>	Displacement ≥1 shell length or ≥1 body length (if crab outside shell).
<i>turn</i>	Turning movement without displacement.
Body movement	Crab movement without displacement (retraction into or stretching out of shell; appendage movements: chelipeds/legs; slight shell movements if crab not visible).
Body posture	
<i>normal</i>	Biologically normal body postures. One or more of the following visible: eyes, cheliped(s), leg(s), antennae. If crab not visible, shell aperture slightly elevated (i.e. not flat on sediment surface).
<i>extended</i>	Soft (posterior) part of carapace (and occasionally also anterior part of abdomen) visible.
<i>out</i>	Crab fully emerged/shell abandoned.
Shell position	
<i>upright</i>	Aperture facing down.
<i>overturned</i>	Aperture facing up.
Interaction	Visible interaction of crab, its shell, or a symbiont with another organism. Includes: <ul style="list-style-type: none"> • organism on top of shell, • hermit crab on organism that shows reaction, • interaction not directly visible but reconstructed based on track and/or reactions between two images. <p>Excludes organisms used by crab solely as a substrate, e.g. crab climbs up on or over a sponge or ascidian.</p>

2.4. Statistical analysis

The behavioural categories were assigned to dissolved oxygen categories: normoxia (≥ 2.0 ml l⁻¹), mild hypoxia (2.0 – 1.0 ml l⁻¹), moderate hypoxia (1.0 – 0.5 ml l⁻¹), severe hypoxia (0.5 – 0.01 ml l⁻¹), and anoxia (0 ml l⁻¹).

The non-parametric Kruskal-Wallis test was used to determine behavioural reactions due to declining oxygen concentrations. The Mann-Whitney *U*-test was performed to compare a behaviour between different oxygen categories (for significances see Appendix 1: Tab. 2 – 6). To detect differences in behavioural responses between day- and night phases, cross tables were computed and the Pearson Chi-square test was performed (for significances see Appendix 1: Tab. 7). To identify which factor (length of the closed configuration, duration of hypoxia and anoxia, and development of H₂S,) affected mortalities and survivorship, linear regressions were used. H₂S concentrations were transformed using a log ($x + 1$) transformation (for significances see Appendix 1: Tab. 8). For statistical analyses the software package SPSS 17.0 was used.

3. Results

3.1. Sensor data

During the normoxia phase of the deployments (open configuration), DO values varied from 2.6 to 5.6 ml l⁻¹ on the bottom (2 cm above the sediment) and from 2.8 to 8.9 ml l⁻¹ 20 cm above the sediment. The values were typically higher 20 cm above the sediment (exceptions: deployments 6, 7, 9, 11). DO curves at the two heights intersected in deployments 9 and 11. In all deployments, the subsequent closed configuration caused an immediate and constant decrease in DO concentrations (Fig. 4). Anoxia was generated within 1 to 3 d. It was induced faster in deployments 7, 8, 10 and 11 (after 17.4 to 33.5 h) and slower in deployments 9, 12 and 13 (after 51.7 to 69.8 h). In deployment 2 an intermediate oxygen peak developed. H₂S was created in all deployments: in those with short anoxia (8, 9, 10, 12), concentrations increased up to 21 μmol l⁻¹; when anoxia lasted for at least 2 d (2, 7, 11, 13) the values rose up to 304 μmol l⁻¹. The temperature remained constant in each deployment (range across deployments: 18.5 to 21.4 °C) and bottom water salinity was 38 ‰ (for more details see Haselmair et al. 2010).

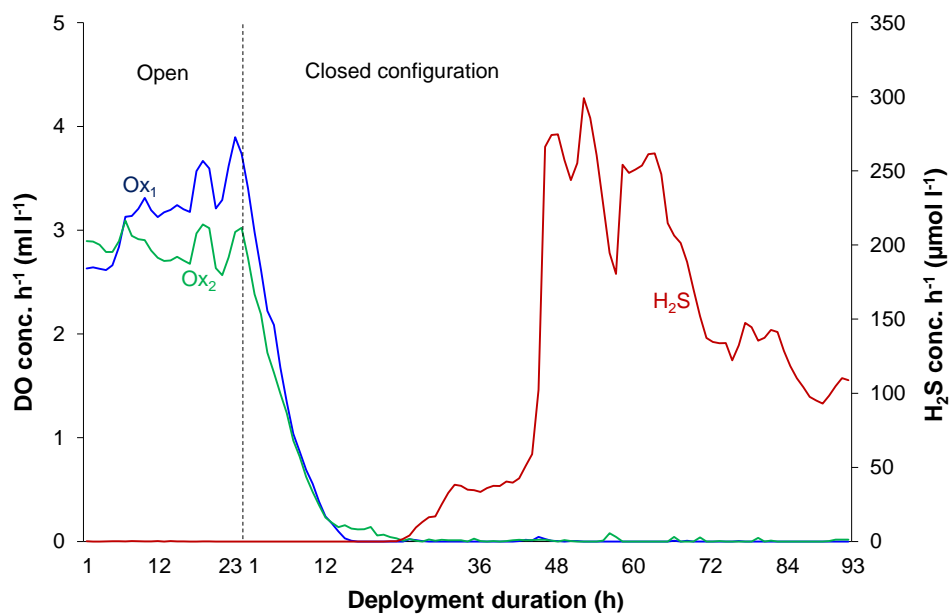


Fig. 4. Sensor data of deployment 11. Ox₁ (blue): oxygen sensor on the bottom, Ox₂ (green): oxygen sensor 20 cm above the sediment, H₂S (red): hydrogen sulphide concentrations. Note that lower sensor had higher DO values here (atypical) but that bottom layer water became hypoxic first.

3.2. Hermit crab abundance

3.2.1. Transects

Transects covering 135 m² contained 330 hermit crabs, yielding an average of 2.4 individuals 1 m⁻². The dominating species was *P. eremita* (n = 296; 90 %), followed by *P. cuanensis* (n = 24; 7 %). The remaining 3 % (n = 10) consisted of *Pagurus prideaux* (Leach, 1815) and unidentified individuals. Most *P. eremita* (smaller individuals) occupied shells of *A. pespelecani* (n = 176; 60 %), with larger individuals in *M. brandaris* (n = 24; 8 %) and *H. trunculus* (n = 37; 13 %). The remaining crabs inhabited 20 *Cerithium* sp. (7 %), 20 *Gibbula* sp. (7%), 9 *Fusinus* sp. (3 %) and 10 unidentified shells (3 %). Of the latter, 9 shells were completely covered by the sponge *S. domuncula* and not identifiable.

3.2.2. Normoxia (open EAGU configuration)

The two deployments evaluated in the open configuration yielded 25 and 26 hermit crabs (deployment 9 and 11, respectively), i.e. a total of 51 individuals entered the camera's field (inside and outside of the aluminium frame) at some point.

3.2.3. Rapidly sinking values/hypoxia/anoxia (closed EAGU configuration)

In the closed configuration, eight deployments were evaluated. The density of hermit crabs varied from 0 to 11 individuals (only one deployment contained no crabs). Twenty-five individuals were evaluated (see selection criteria above): 9 inhabited *A. pespelecani*, 11 *M. brandaris* or *H. trunculus*, 3 *S. domuncula*-covered shells and 2 unidentified shells. In certain cases, differentiation between *M. brandaris* and *H. trunculus* was not possible due to damaged shells and/or to dense symbiont cover.

3.3. Behaviour during normoxic conditions

During the open configuration, the normal behaviour of hermit crabs was observed. Crabs were mainly located on the sediment (85 % of observations) between multi-species clumps or partly hidden under their edges. Typically their shells were positioned upright (96 %) and they exhibited a normal body posture, i.e. some extremities – eyes, chelipeds, legs and antennae – were visible (92 %). Locomotion occurred in 23 % of observations. While during the day, slightly more major than minor locomotion occurred (17 and 14 %, respectively), during the night minor locomotion (9 %) dominated over major locomotion (5 %). More locomotion was documented during the day than during the night (total, including turns: 33 and 15 %, respectively). Body movements were recorded in 22 %. In the open configuration, interactions (both inter- and intraspecific; see 3.4.8.) were documented in 49 %. The number of interactions differed between day and night (36 and 58 %, respectively).

After switching to the closed configuration, certain behavioural patterns decreased or increased rapidly, although oxygen concentrations were still normoxic. These behavioural changes are attributed to the exchange of the open aluminium frame with the plexiglass chamber, which altered the water currents. During the initial, closed configuration, hermit crabs were on multi-species clumps more frequently during the day and especially the night (32 and 45 % of observations versus 11 and 18 % during the open configuration). Total locomotion during the initial, closed EAGU remained at the same value (23 %) as during the open configuration, but the distribution of minor and major locomotion changed. During the day, the initial, closed EAGU triggered a small increase of major locomotion (from 17 to 21 %) and a slight decrease of minor locomotion (from 9 to 7 %). Total locomotion was 30 % during the day and 12 % at night; the diurnal rhythm persisted. Interactions during the day remained similar in the initial, closed configuration (38 %), but during the night they increased to 73 % (from 58 %).

In the following section the statistics performed for normoxia include all evaluations $>2 \text{ ml l}^{-1} \text{ DO}$ (i.e. both in open and initial, closed configuration).

3.4. Responses to decreasing dissolved oxygen concentrations

Decreasing DO values triggered a sequence of altered and atypical behaviours in hermit crabs.

3.4.1. Location changes

During normoxia, hermit crabs were located on the sediment in 76 % of all observations (Fig. 5a; for all significances see Appendix 1: Tab. 2). Hypoxia triggered avoidance, i.e. migration to the higher multi-species clumps (Fig. 6). At mild hypoxia, the crabs (47 % of all observations) moved up to such clumps. A similar percentage (48 %) was on the clumps during moderate hypoxia. This value fell to 39 % during severe hypoxia and anoxia (Fig. 5a).

The responses differed considerably according to the type of the occupied housing (large shells, small shells, *S. domuncula*). The three categories differed in the time spent on the respective substrates (sediment/multi-species clumps) in each oxygen category (for all significances see Appendix 1: Tab. 3 – 6). Initially, small crabs were located on the sediment (64 % of all observations) during normoxia (Fig. 5b). During mild hypoxia, those on multi-species clumps highly significantly increased (56 %). Slightly less than half (46 %) spent their time on clumps during moderate hypoxia, rising to 52 % during severe hypoxia and decreasing to 39 % during anoxia. Large crabs, in contrast, spent most of the time on the sediment in all oxygen categories. During normoxia, they were almost exclusively on the sediment (94 % of observations; Fig. 5c). Mild hypoxia triggered some movement onto clumps (19 %), with a peak during moderate hypoxia (30 %), followed by a continuous decrease (15 and 9 % during severe hypoxia and anoxia, respectively). During normoxia, crabs in *S. domuncula* remained mostly on the sediment (70 %; Fig. 5d). Mild hypoxia caused movement onto clumps in 97 %, a value that remained constant during moderate hypoxia. This value fell somewhat during severe hypoxia (93 %) and anoxia (85 %), but these animals spent most time on elevated substrate.

Housing-related differences were also detected in the number of vertical up and down movements (i.e. movement from sediment onto elevated substrate or vice versa, not vertical locomotion on elevated substrate). Most crabs in small shells (7 of 9) spent some time on multi-species clumps. In contrast, 5 of 11 large crabs remained exclusively on the sediment throughout a deployment. The remaining large

individuals moved up and down at most 2 times per deployment. All 3 crabs in *S. domuncula*, however, climbed on multi-species clumps, and 2 of them remained there through anoxia until the end of the deployment.

Finally, the location at the end of the evaluation differed according to housing. Most small (9 of 10 individuals) and large crabs (9 of 11) returned to the sediment. Two of 3 individuals in *S. domuncula*, however, remained on multi-species clumps until the end of the deployments.

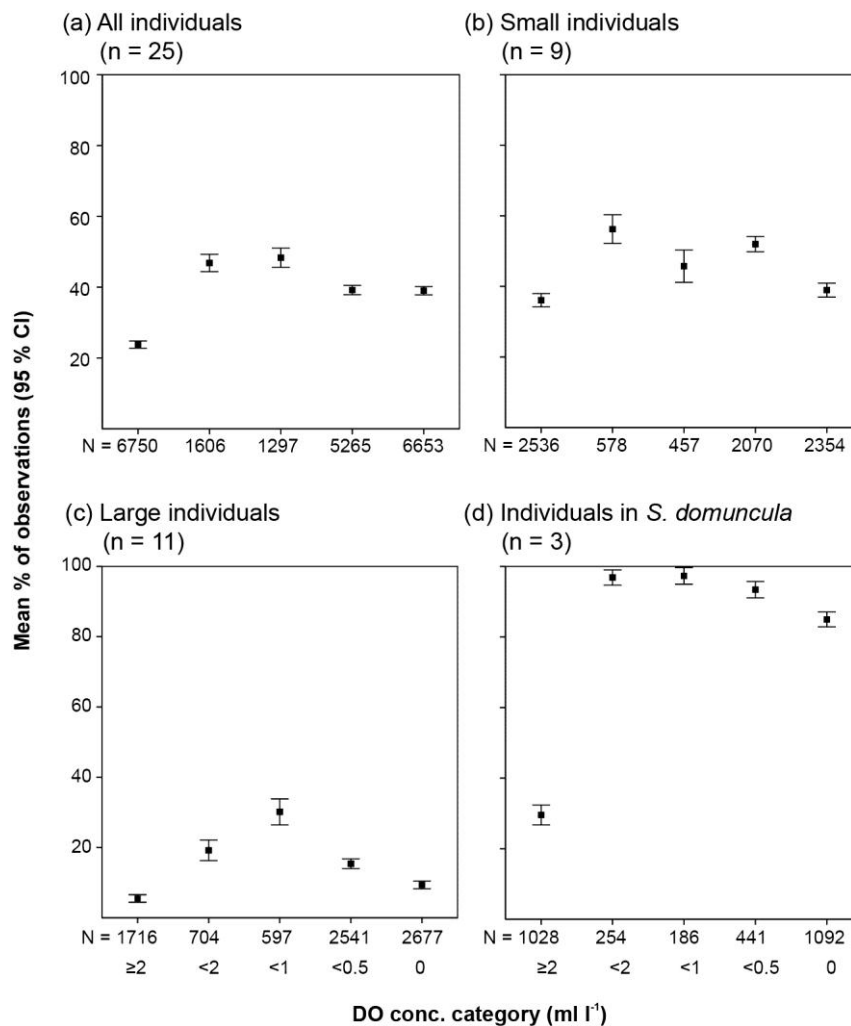


Fig. 5. Hermit crabs on multi-species clumps (mean percentage) related to five oxygen thresholds: (a) all individuals, (b – d) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

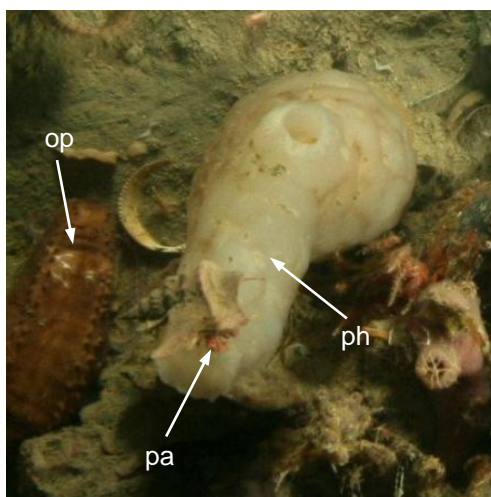


Fig. 6. *Paguristes eremita* (pa) in *Aporrhais pespelecani* shell on top of ascidian *Phallusia mammilata* (ph) at 13.6 h after anoxia ($18.3 \mu\text{mol l}^{-1} \text{H}_2\text{S}$) in deployment 11. The holothurian *Ocnus planci* (op) on left.

3.4.2. Decreased locomotion

Most horizontal locomotion was observed during normoxic conditions (23 %; Fig. 7a). Mild hypoxia caused a decrease (14 %). Locomotion further decreased during severe hypoxia (4 %), with very low values throughout anoxia (5 %).

Locomotion in crabs in *S. domuncula* was lower in all oxygen categories compared to crabs in shells (Fig. 7c). The decrease from normoxia (17 % of all observations) to severe hypoxia (1 %) was constant and steep, and during anoxia this value remained the same (1 %).

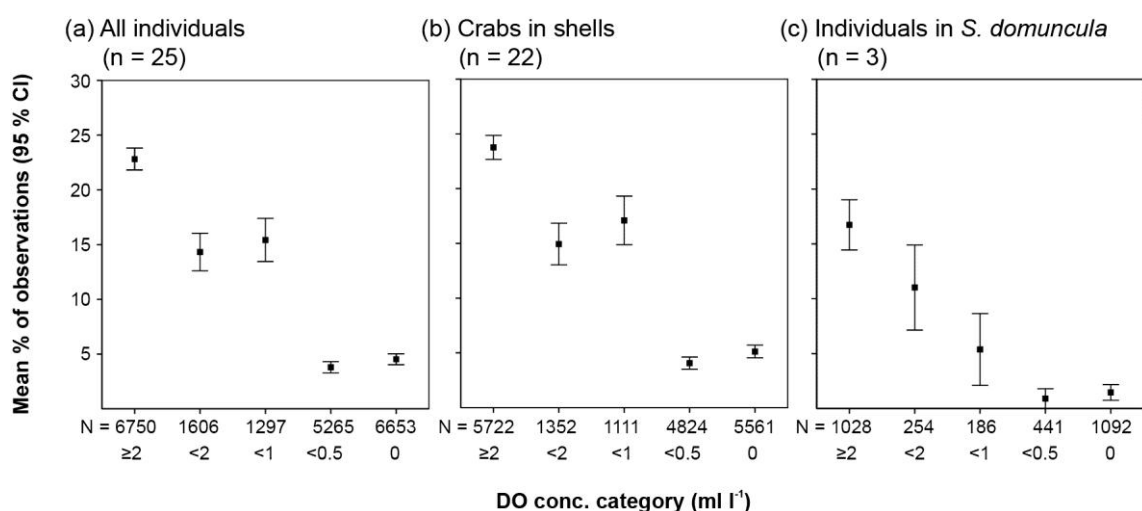


Fig. 7. Total locomotion (mean percentage) of hermit crabs related to five oxygen thresholds: (a) all individuals, (b/c) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

3.4.3. Altered activity pattern

Locomotion occurred in episodes, reflecting activity peaks. Initially, more locomotion was recorded during the day than at night. Oxygen depletion reduced these episodes, which is represented in a smaller activity peak during early anoxia (Fig. 8). All crabs that emerged from their shells (except for one individual; see below), however, moved around shell-less on the sediment or multi-species clumps. This is reflected in an increase in the last activity peak (Fig. 8). This last phase of locomotion was initiated directly at or shortly after emergence, after a mean of 55 h (SD = 9.4) of combined hypoxia and anoxia (mean anoxia duration = 26.9 h; SD = 14.2). The duration of this phase ranged from a single change of location (minutes) to 13.9 h (mean = 3.7 h; SD = 4.1). Within this period a mean of 15 changes of location occurred (range: 1 to 40).

A diurnal activity pattern was observed during normoxia, with highly significantly different numbers of locomotion during the day and night (Appendix 1: Tab. 7). During mild hypoxia, no difference in locomotion was recorded between the day and night. During moderate and severe hypoxia a diurnal pattern was present, again with significant differences between day- and night phases. At anoxia, no diurnal rhythm was detected.

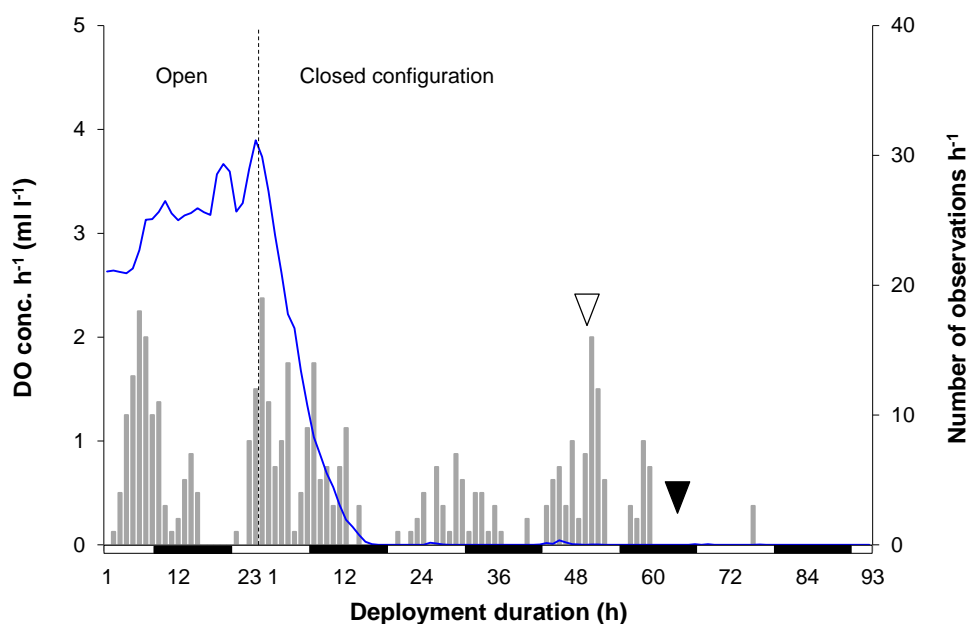


Fig. 8. Average number of locomotions per hour during deployment 11. $n = 3$ crabs in open, $n = 4$ in closed configuration. White and black bars represent day and night, respectively. White and black arrowheads show emergence from shell and death, respectively (50 % of individuals).

3.4.4. Changes in body movements

Initially, during normoxia, locomotion and body movements accounted for a similar percentage of observations (23 and 26 %, respectively; Fig. 7a and 9a). At mild hypoxia, locomotion decreased but body movements started to increase highly significantly (51 % of observations) and reached a peak at moderate hypoxia (68 %; Fig. 9a). Then, body movements continuously dropped at severe hypoxia and anoxia (42 and 34 %, respectively). At anoxia, in contrast, locomotion amounted to only 5 % of observations (Fig. 7a). In most crabs (20 of 25 individuals) body movements lasted longer than locomotion (mean = 25.2 h; SD = 24.1; range: 18 min to 81.4 h). The remaining 5 crabs moved around shell-less on the substrate, and locomotion ceased at about the same time as body movements.

Whereas the pattern in sponge-inhabiting individuals was the same as for hermit crabs in shells, mild hypoxia triggered a steeper increase of body movements (70 % of observations) and a higher peak during moderate hypoxia (91 %, Fig. 9c).

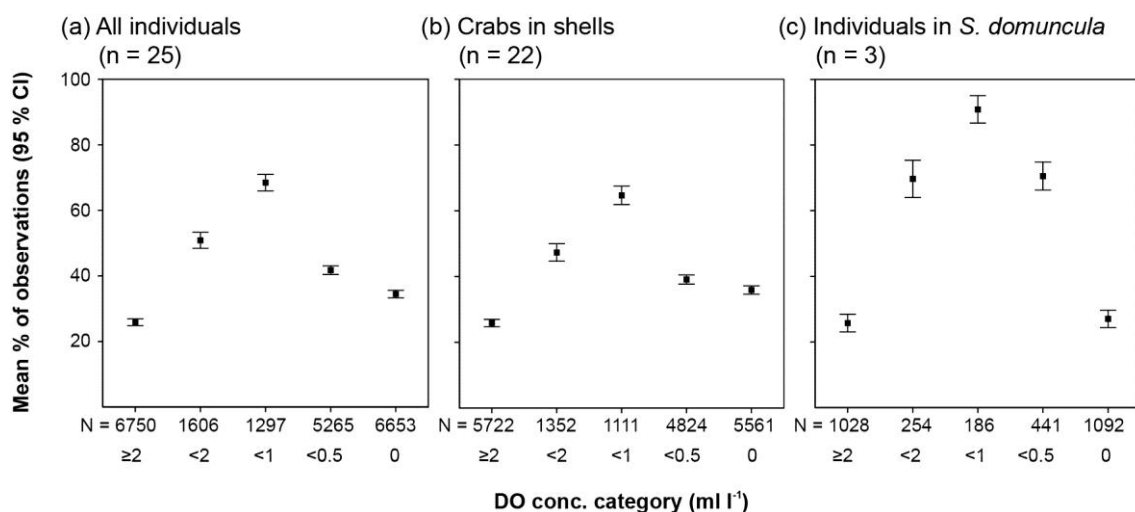


Fig. 9. Hermit crab body movements (mean percentage) related to five oxygen thresholds: (a) all individuals, (b/c) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

3.4.5. Atypical body posture: extension from shell

During normoxia, the normal body posture (e.g. eyes and antennae, occasionally chelipeds, visible from above) was documented in 93 % of observations. Extension from the shell and other atypical postures were rare (7 %; Fig. 10a). Eight individuals were extended 19 times for a short period (maximum 9 images) while examining the sediment or empty, damaged shells. Interactions (both inter- and intraspecific) caused 3 individuals to stretch out of their shell towards the opponent (maximum 2 images). With decreasing DO concentrations, extension continuously increased until anoxia (44 % of observations), with a first jump at mild and a second major jump at moderate hypoxia (15 and 34 %, respectively; Fig. 10a).

This pattern was more distinct in crabs inhabiting *S. domuncula*: values were higher during moderate hypoxia (57 %) and anoxia (55 %; Fig. 10c), but the major jump also occurred at moderate hypoxia.

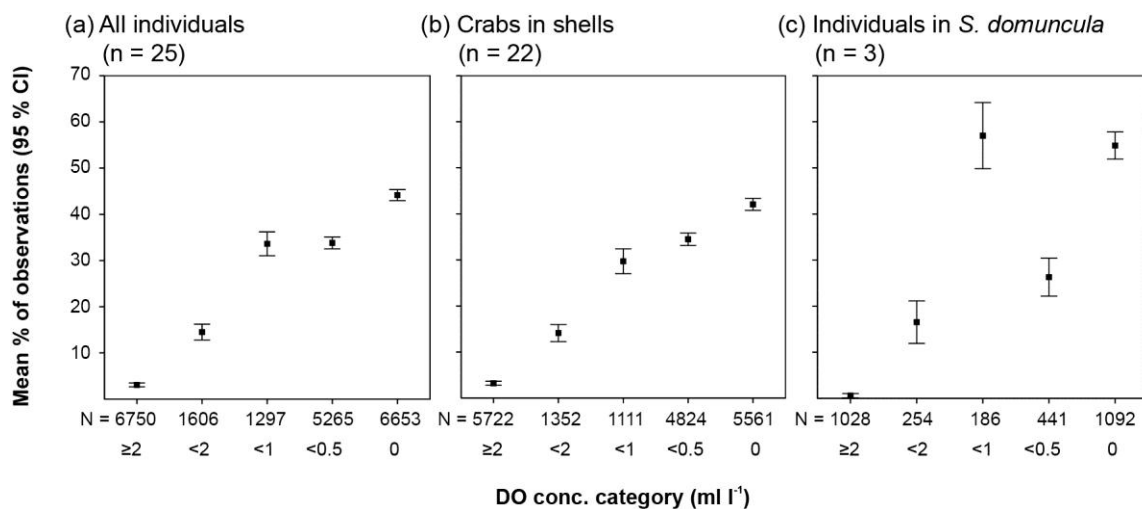
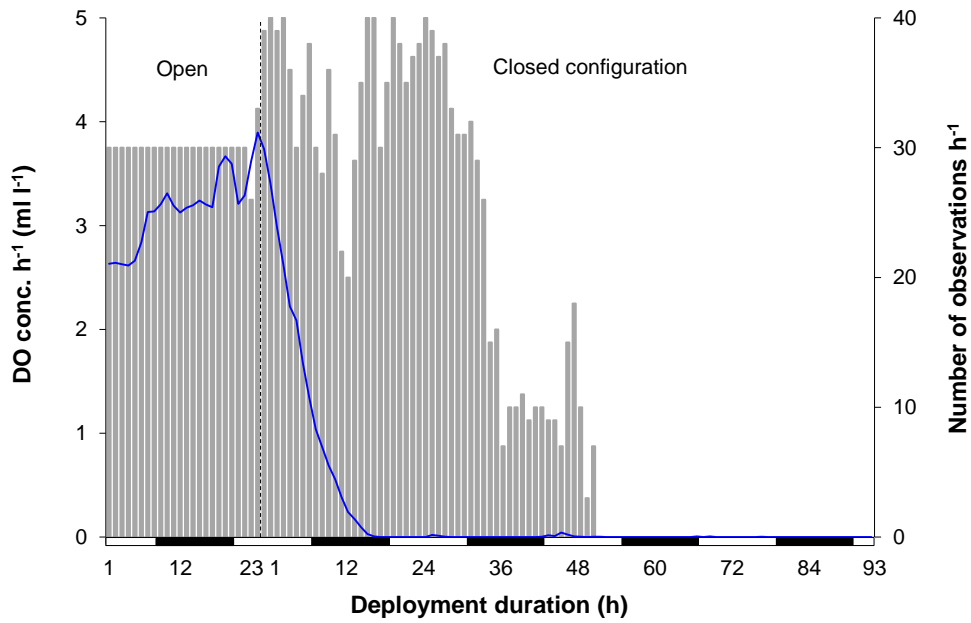


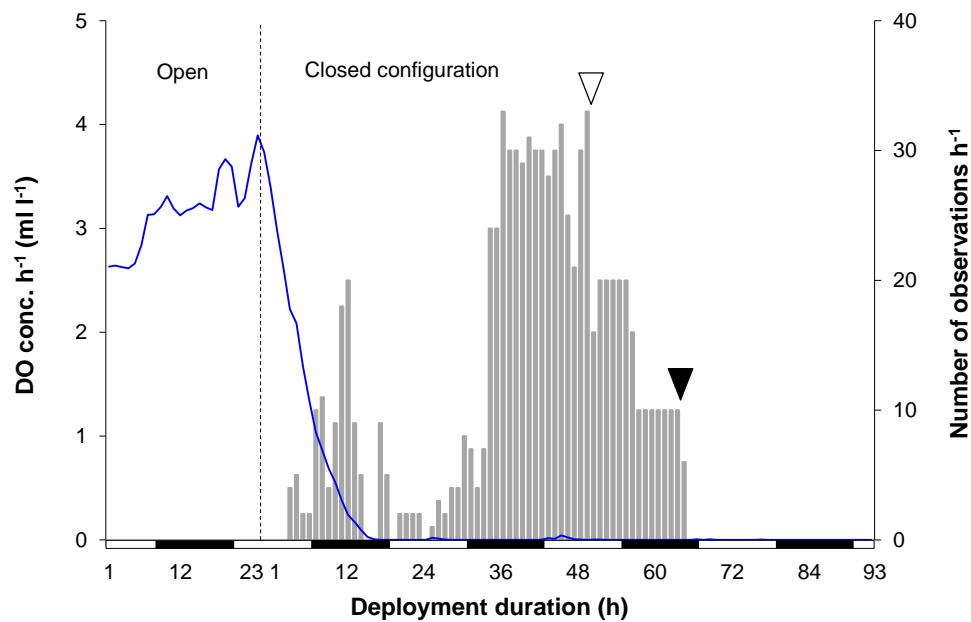
Fig. 10. Extended body posture (mean percentage) related to five oxygen thresholds: (a) all individuals, (b/d) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

Extension occurred in two peaks mostly (Fig. 11b). The second peak is higher and longer than the first. In the intervening period, body posture returned to normal (Fig. 11a). The decrease after the second peak reflects increased total emergence from the shell rather than return to normal posture (Fig. 11c).

(a) Normal body posture



(b) Extended body posture



(c) Outside of shell

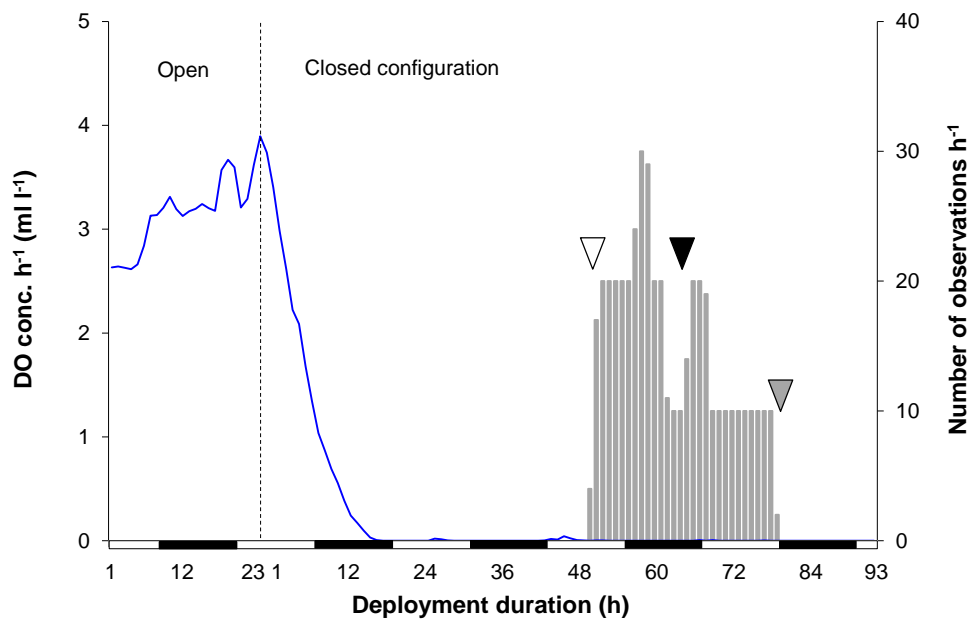


Fig. 11. Body postures (average number of the selected behaviour per hour) during deployment 11. $n = 3$ crabs in open, $n = 4$ in closed configuration. White and black bars represent day and night, respectively. White and black arrowheads show emergence from shell and death, respectively (50 % of individuals); grey arrowhead indicates death of all individuals.

3.4.6. Atypical shell position: overturned

Initially, most occupied housings (97, 98 and 98 % of observations during normoxia, mild hypoxia and moderate hypoxia, respectively) were normally positioned, with the aperture facing down (Fig. 12a). As DO values dropped further, an increasing number of shells was overturned (Fig. 13), with a highly significant increase at severe hypoxia (17 %) and another highly significant increase at anoxia (24 %; Fig. 12a).

The initiation and the number of overturned shells differed according to housing. Small crabs (17 %) and crabs in *S. domuncula* (38 %) showed an increase at anoxia (Fig. 12b/d), most evident in *S. domuncula* (Fig. 12d). Large shells (Fig. 12c) were overturned earlier, often at severe hypoxia (26 %).

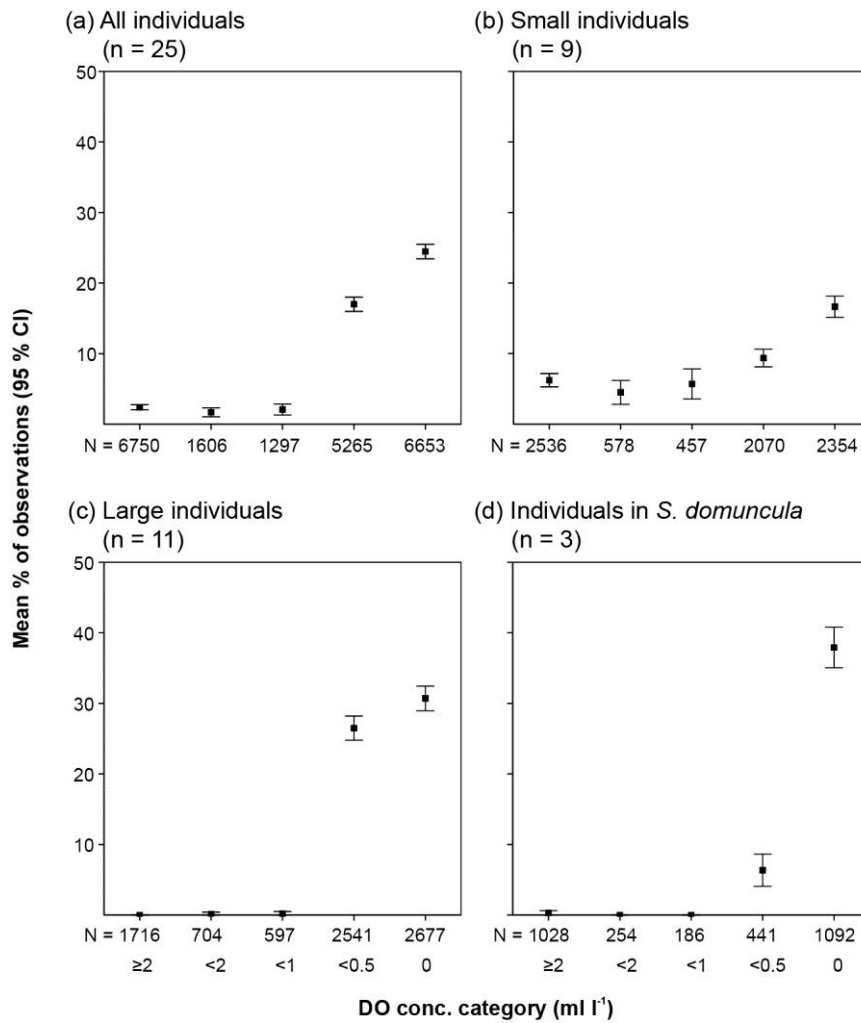


Fig. 12. Overturned hermit crab shells (mean percentage) related to five oxygen thresholds: (a) all individuals, (b – d) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

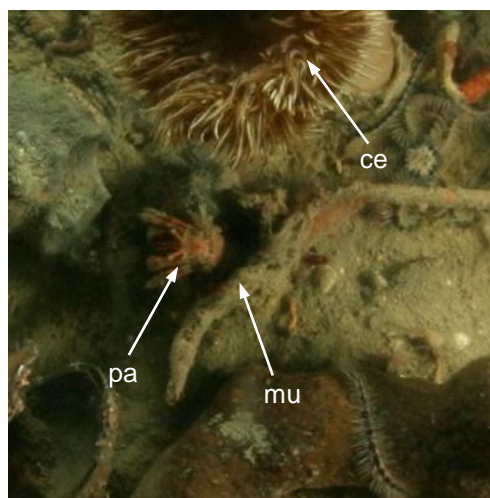


Fig. 13. *Paguristes eremita* (pa) extending from an overturned *Murex brandaris* shell (mu) at 16.1 h after anoxia ($36.7 \mu\text{mol l}^{-1} \text{H}_2\text{S}$) in deployment 11. Note extended anemone (*Cereus pedunculatus*, ce) at top.

3.4.7. Emergence from shell

Paguristes eremita remained inside its shell from normoxia to severe hypoxia. Anoxia, however, triggered the emergence of 13 of 25 individuals (52 %) (Fig. 14). Hermit crabs emerged between 38.9 and 71.3 h of combined hypoxia and anoxia (mean = 52.8 h; SD = 8.5), whereby anoxia duration ranged from 10.3 to 48.6 h (mean = 24.4 h; SD = 11.8). During emergence, 77 % of the crabs were positioned on the sediment and 62 % of shells were still upright (Fig. 15). Once they abandoned their shell, the crabs moved around. An exception was one individual (in *M. brandaris*, deployment 11) that returned to its shell after 34.0 h of anoxia. Two images (12 min) before emerging, nearly the whole abdomen was visible. The crab remained emerged for 4 images (24 min) and moved around on top of its upright shell. It then turned around and partially inserted its abdomen back into the aperture. This crab remained inside for 2 images (12 min) before finally emerging again and climbing on an exposed infaunal sea urchin *Schizaster canaliferus* (Lamarck, 1816).

Emergence was clearly a precursor to mortality: eight of 13 crabs (62 %) that emerged from their shell died. Three of the remaining emerged crabs survived due to relatively brief durations of anoxia in the respective deployments. The final two individuals disappeared and could not be further evaluated.



Fig. 14. Dead *Paguristes eremita* (pa) (curved abdomen visible on bottom) next to its abandoned shell (overturned *Aporrhais pespelecani* (ap) at top left). Note typical serpulid-encrusted aperture.

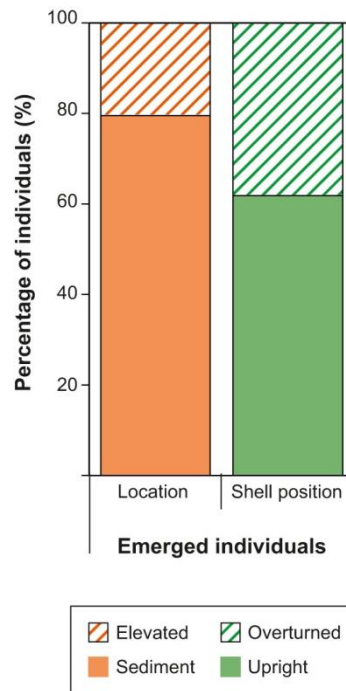


Fig. 15. Location and shell position during emergence of the crabs (n = 13); percentage of individuals indicated.

3.4.8. Inter- and intraspecific interactions

Short interactions and reactions were difficult to observe because photographs were taken in 6-min intervals. Inter- and intraspecific interactions were observed in 50 % of photographs at normoxia (Fig. 16a). During mild hypoxia this behaviour highly significantly increased (57 % of observations) and remained at a stable level during moderate and severe hypoxia (57 and 56 %, respectively) until anoxia caused a major drop (25 %). Intraspecific interactions occurred in all oxygen categories.

The pattern of interactions differed according to housing category. In crabs in small shells the increase occurred at mild hypoxia (from 53 to 67 %) followed by a subsequent decrease until anoxia (19 %; Fig. 16b). In large crabs the normoxic value was retained (43, 45 and 47 % during normoxia, mild and moderate hypoxia, respectively) until severe hypoxia triggered an increase (63 %; Fig. 16c) and anoxia initiated a drop (29 %). In contrast, the initial interactions were higher in sponge-inhabiting crabs (61 and 63 % during normoxia and mild hypoxia, respectively; Fig. 16d). A clear increase occurred at moderate hypoxia (92 %), with the value at anoxia dropping to the same value (29 %) as in large crabs.

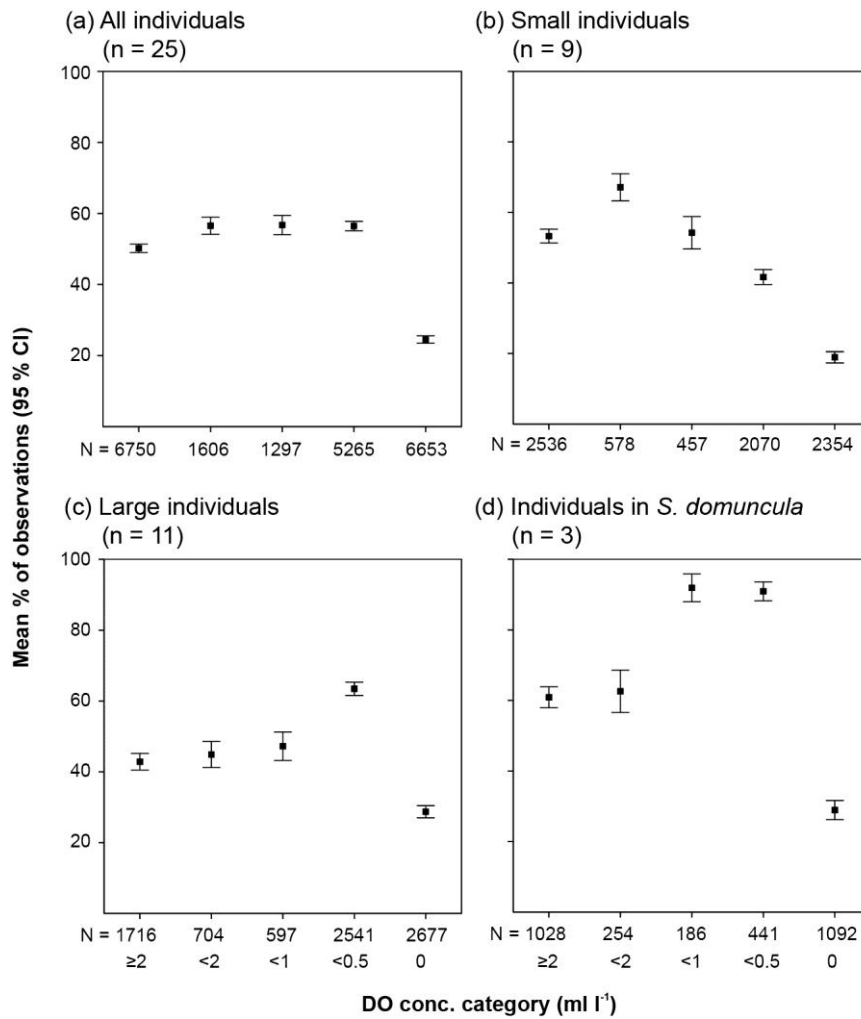


Fig. 16. Hermit crab interactions (mean percentage) related to five oxygen thresholds: (a) all individuals, (b – d) specific responses. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

During normoxia and mild hypoxia, more interactions occurred during the night than day (Fig. 17a/b). This behaviour changed at moderate hypoxia, with more interactions occurring during the day. More interactions during severe hypoxia were recorded during the night, and this pattern changed again during anoxia, with more interactions during the daytime phases. The day/night differences were highly significant during normoxia, moderate hypoxia and anoxia, and significant during mild and severe hypoxia (Appendix 1: Tab. 7).

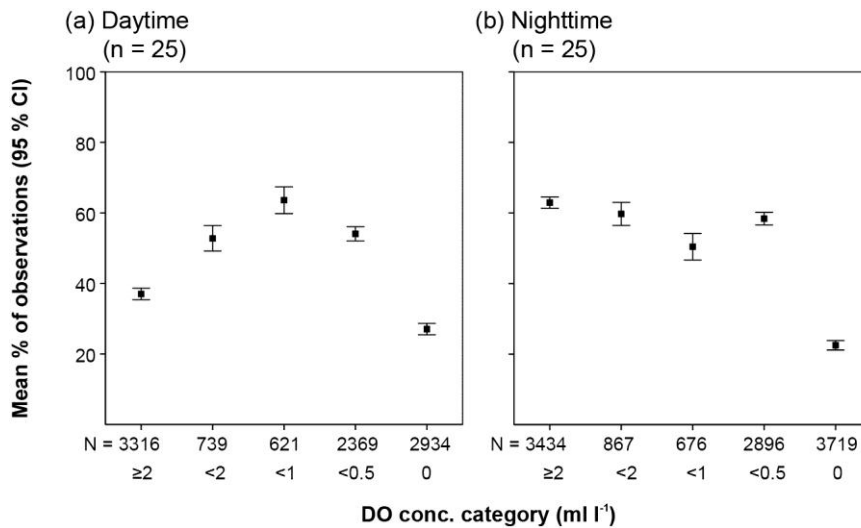


Fig. 17. Hermit crab interactions (mean percentage) related to five oxygen thresholds: (a) during the day, (b) during the night. (n): number of evaluated crabs in closed configuration. N: number of photographs evaluated in each oxygen category.

These day/night differences were also visible over the course of the individual deployments. In deployment 11, for example, the two major peaks (one during normoxia, one during anoxia) describe interactions that occurred at nighttime (Fig. 18). The final, small peak represents an interaction with the infaunal sea urchin *S. canaliferus* (see below).

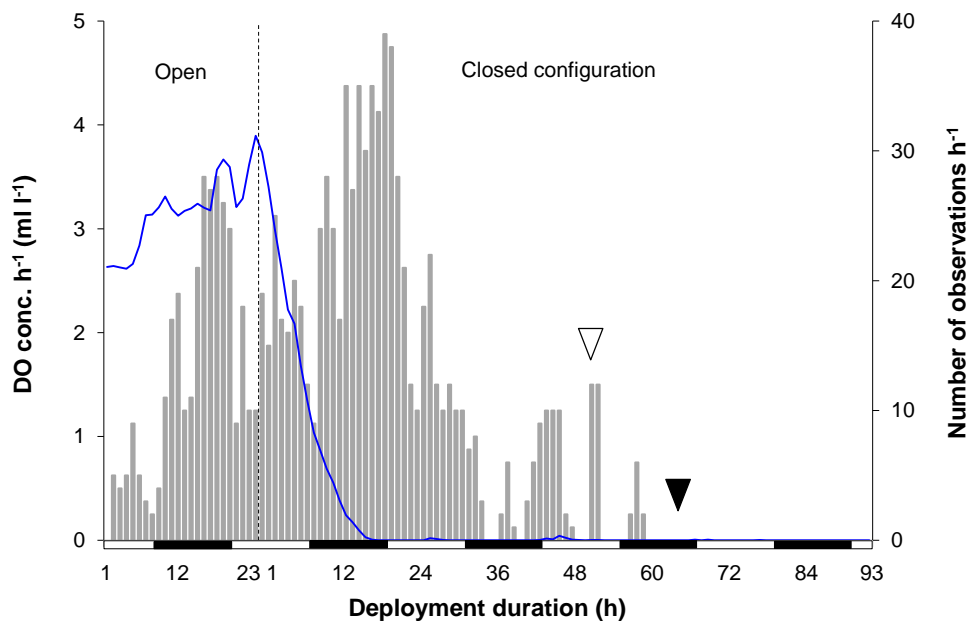


Fig. 18. Average number of interactions per hour during deployment 11. n = 3 crabs in open, n = 4 in closed configuration. White and black bars represent day and night, respectively. White and black arrowheads show emergence from shell and death, respectively (50 % of individuals).

3.4.9. The spectrum of interspecific interactions

Interspecific interactions with the following organisms were recorded: the brittle stars *O. quinque maculata* and *Ophiura* spp., the crabs *P. longimana*, *P. spinifer*, *Nepinnotheres pinnotheres* (Linnaeus, 1758), *Macropodia* sp., the anemone *Cereus pedunculatus* (Pennant, 1777), the holothurian *O. planci*, the sea urchin *P. microtuberculatus*, the infaunal sea urchin *S. canaliferus*, the ascidian *Microcosmus sulcatus* (Coquebert, 1797), the gastropods *H. trunculus* and *M. brandaris*, the bivalve *Corbula gibba* (Olivi, 1792), the zoanthid *Epizoanthus arenaceus* (Delle Chiaje, 1823), infaunal worms, shrimps, a limpet and serpulid tubeworms.

Oxygen depletion triggered atypical interactions with the infaunal sea urchin *S. canaliferus*, which emerged from the sediment at severe hypoxia and interactions occurring during anoxia: one with a hermit crab and one with a sea anemone *Calliactis parasitica* (Couch, 1842), which was attached to a hermit crab shell. In one case, *S. canaliferus* was used by the crab as an elevated substratum. The crab was in contact with a *S. canaliferus* for 5.3 h. The crab then emerged from its shell and climbed on top of the sea urchin (Fig. 19a), where it remained for 1.8 h. A moribund, immobile state on the sediment with partly body movements followed and the crab died 15.9 h after the interaction. The interactions mainly involved crabs still inside of their shells, except for the above case.

In response to decreasing DO concentrations, the crabs *P. longimana* often positioned themselves on occupied shells. During mild and moderate hypoxia, 11 and 15 interactions, respectively, occurred with individuals or aggregations of *P. longimana* on shells. During severe hypoxia and anoxia, 43 such interactions took place: *P. longimana* remained on the shell for extended periods (maximum 23.2 h). Aggregations of up to 9 of *P. longimana* individuals were recorded. *Ophiura* spp. – a species normally partially buried in the sediment – is another example in which shells served as elevated sites. During severe hypoxia and anoxia, *Ophiura* spp. was commonly observed on hermit crabs.

Most interspecific interactions (241) occurred with the brittle star *O. quinque maculata*. Initially, some brittle stars showed escape reactions when approached by a hermit crab: the brittle stars interrupted their filter-feeding posture and changed location. Other brittle star individuals did not react, and slight contact of

the arm tips and the crabs was recorded several times. This contact lasted between 6 min to 17.3 h, whereby the larger value reflects moribund individuals of *O. quinquemaculata*. A common brittle star response to hypoxia was that such escape reactions ceased entirely. At mild hypoxia, the number and duration of interactions increased. During severe hypoxia, moribund brittle stars commonly clung to hermit crab-occupied shells: some were positioned on top of the shells and completely covered them with their arms (Fig. 19b/c). The longest coverage of a hermit-crab-occupied shell by a brittle star lasted for 21.7 h. Interactions with *O. quinquemaculata* ceased during anoxia because the brittle stars had died.

Interactions with *H. trunculus* took place during normoxia, ceased during mild hypoxia, re-occurred at severe hypoxia and were the highest during anoxia. Interactions with *S. canaliferus* were also recorded late in the deployments.

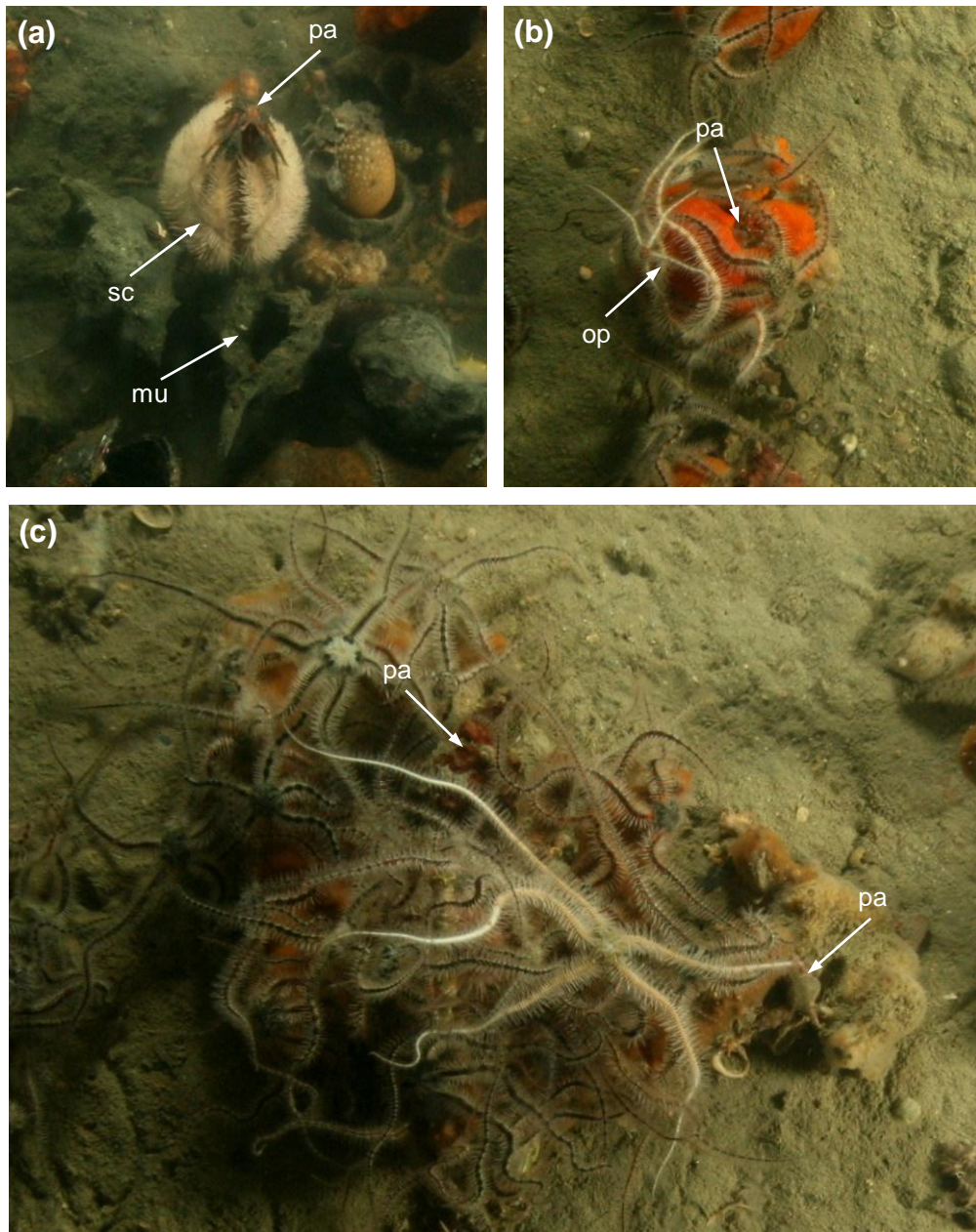


Fig. 19. Atypical interactions: (a) shell-less hermit crab *Paguristes eremita* (pa) on top of emerged infaunal sea urchin *Schizaster canaliferus* (sc) at 35 h after anoxia ($243.2 \mu\text{mol l}^{-1} \text{H}_2\text{S}$) in deployment 11. Note abandoned, overturned *Murex brandaris* (mu) shell on the sediment. Bent-over *Cereus pedunculatus* partially extended from tube on right. (b) brittle star *Ophiothrix quinquemaculata* (op) individuals cling to *Suberites domuncula*-covered shell inhabited by *P. eremita* (pa) during severe hypoxia ($0.38 \text{ ml l}^{-1} \text{DO}$, no H_2S) in deployment 9. (c) aggregation of *O. quinquemaculata* individuals and hermit crabs (pa) on a multi-species clump during mild hypoxia ($1.26 \text{ ml l}^{-1} \text{DO}$, no H_2S) in deployment 10.

3.5. Mortality

Overall, 36 % of the hermit crabs ($n = 9$) died, all of them during anoxia. These 9 individuals were observed in 3 different deployments (2, 7, 11). These deployments were among those in which anoxia occurred faster and lasted longer (exception: deployment 2 with an intermediate oxygen peak). Hermit crabs died between 52.2 and 73.5 h after combined hypoxia and anoxia (mean = 60.9 h; SD = 7.8), whereby anoxia durations ranged from 18.4 to 62.1 h (mean = 37.7 h; SD = 16.6). At anoxia, H_2S began to develop. Mortality occurred at H_2S values ranging from 116.5 to 248 $\mu\text{mol l}^{-1}$ (mean = 128.1 $\mu\text{mol l}^{-1}$; SD = 9.8). Mortality was highly significantly affected by the development and values of H_2S and significantly affected by the duration of anoxia (Appendix 1: Tab. 8). 89 % of crabs were positioned on the sediment and 56 % of shells were overturned when the crabs died (Fig. 14/20). Eight of 9 crabs (89 %) were outside their shell at death. The first shell-less individuals died 2.3 h and the last 18.4 h after emergence (mean = 8.4 h; SD = 5.1).

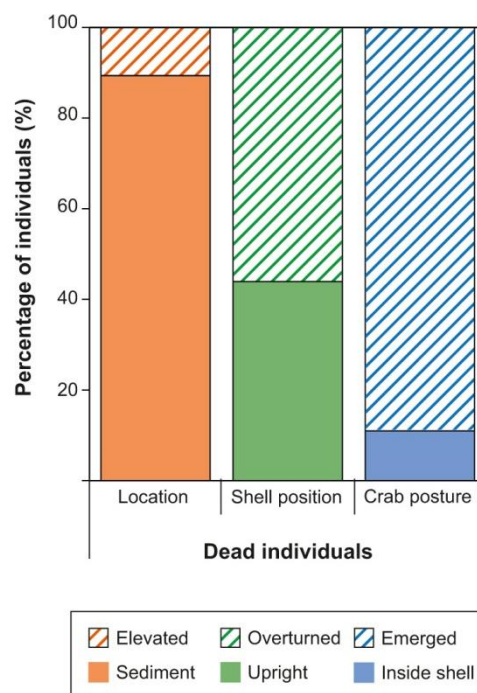


Fig. 20. Dead individuals ($n = 9$); percentage of individuals with respect to location, shell position, and crab posture.

Three of 25 individuals could not be evaluated fully (deployment 2: duration 81.1 h after anoxia), i.e. only until 20.1, 34.1 and 45.8 h of anoxia. Two were already outside their shells and disappeared behind multi-species clumps. Poor visibility prevented evaluating the third crab, which was still inside its shell toward the end of the deployment.

3.6. Survival

52 % of observed individuals ($n = 13$) survived the experiment (5 different deployments: 8, 9, 10, 12, 13). Hermit crabs survived 30.2 to 78.0 h of hypoxia and anoxia (mean = 58.8 h; SD = 14.15), whereby anoxia durations ranged from 8.5 to 25.1 h (mean = 20.8 h; SD = 4.9). The corresponding H_2S concentrations were between 0 to 126.1 $\mu\text{mol l}^{-1}$ (mean = 42.2 $\mu\text{mol l}^{-1}$; SD = 48.2) at the end of deployments. Most of the survivors were on the sediment (69 %), with upright shells (69 %) and inside their shell (77 %). The duration of hypoxia and anoxia and development of H_2S varied in different deployments, whereby survivors were typically present only in those that stopped after briefer anoxia and lower H_2S concentrations. Three of 13 individuals survived relatively high H_2S concentration of 121.1 $\mu\text{mol l}^{-1}$ and 25.1 h of anoxia. These values were below the mean H_2S concentrations of 128.1 $\mu\text{mol l}^{-1}$ and mortality time of 37.7 h after anoxia. The remaining 10 crabs survived the end of the deployment with a maximum 24.2 h of anoxia and relatively low H_2S concentrations (maximum 21.0 $\mu\text{mol l}^{-1}$). Deployments with surviving individuals were too short to induce death.

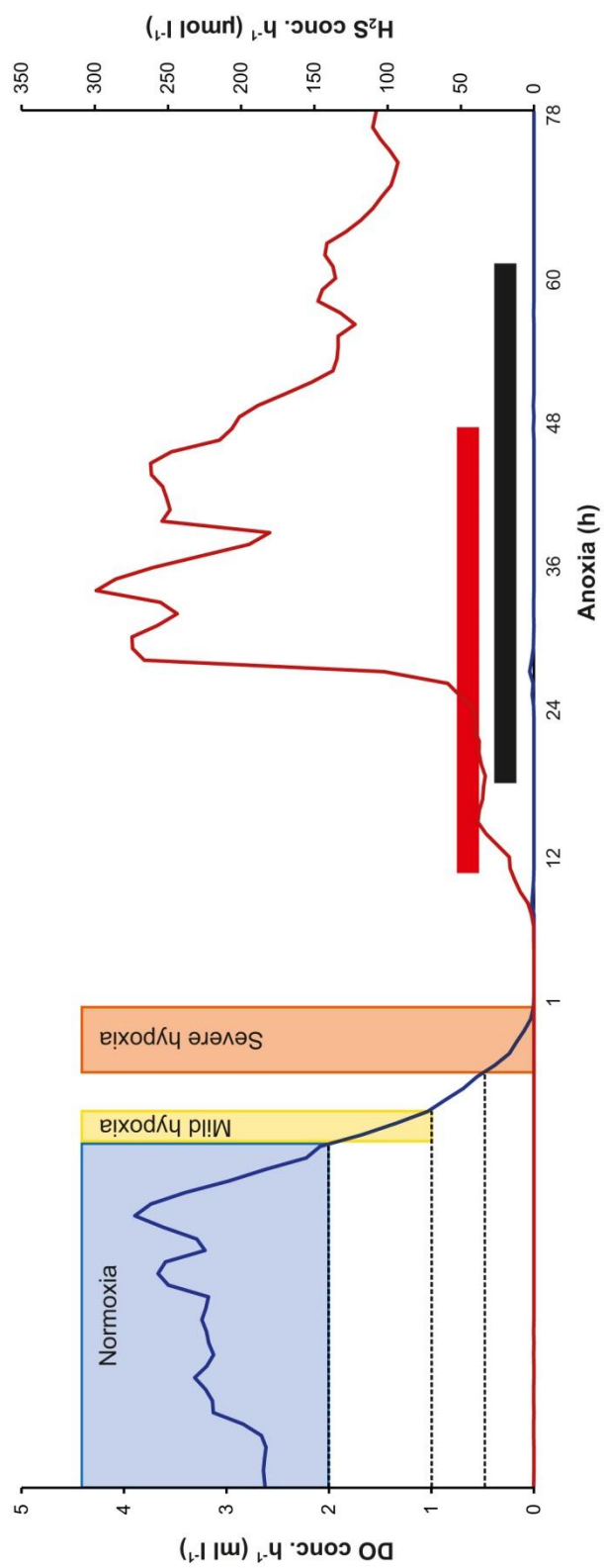


Fig. 21. Sequence of atypical behavioural responses to oxygen thresholds, anoxia duration and H₂S development: normal body posture – crab extended from upright shell – crab extended from overturned shell – crab outside shell – mortality. Hours in pictograms are mean values from begin of anoxia.

4. Discussion

4.1. Responses to decreasing dissolved oxygen concentrations

This study provides a new and detailed account of the full range of hermit crab behaviours during declining DO- and rising H₂S concentrations and correlates the specific responses with oxygen thresholds. The reactions to decreasing DO demonstrate a succession of atypical behaviours, ultimately leading to mortality (Fig. 21).

In situ observations and time-lapse films confirm that *P. eremita* typically remains on the sediment surface between multi-species clumps (Stachowitsch, 1979). As oxygen levels decreased, however, the hermit crabs tended to migrate from the sediment onto multi-species clumps. Ultimately, most returned to the sediment before death. Avoidance of hypoxic areas is a common strategy of crustaceans (Diaz and Rosenberg, 1995; Pihl et al., 1991; Renaud, 1986). In the Neuse River Estuary (North Carolina, USA), trawl collections showed that the blue crab *Callinectes sapidus* migrated horizontally from deeper to shallower, better oxygenated sites (Bell and Eggleston, 2005). Large numbers of the West Coast rock lobster *Jasus lalandii* migrate shoreward during hypoxic conditions at high tides in the greater Elands Bay region (West coast, South Africa; Cockcroft, 2001). They, however, cannot return fast enough during ebb tides, leading to mass strandings. Hypoxic bottom water affects the vertical distribution of fish and crustaceans (mantis shrimp *Squilla empusa* and blue crab *C. sapidus*): migrations in the water column have been documented to avoid unfavourable conditions (Hazen et al., 2009; Pihl et al., 1991).

Hermit crabs responded similarly to a wide range of bioherm-associated crustaceans from the Northern Adriatic Sea, which first emerge from their hiding places and then escape either horizontally or vertically onto elevated substrates (Haselmair et al., 2010). In the Northern Adriatic Sea, sublittoral sediment bottoms are flat and extensive. Accordingly, hypoxia can affect several hundred to thousands of km² (Stachowitsch, 1984) making it unlikely that benthic invertebrates can reach more oxygenated sites by escaping horizontally. Multi-species clumps represent the only elevated structures on the sediment surface, and oxygen concentrations in the deployments were generally higher 20 cm above bottom than on the bottom. This reflects the normal declining oxygen gradients within the benthic boundary layer and

increasing concentrations into the water column (Diaz and Rosenberg, 1995; Jørgensen, 1980). Migration onto multi-species clumps, therefore, may provide a refuge for hermit crabs from short-term hypoxia.

Mild hypoxia induced such initial avoidance behaviour in hermit crabs. The same threshold for this behaviour was reported in most bioherm-associated crustaceans apart from the more tolerant pea crab *N. pinnotheres* (a symbiont in bivalves and sea squirts; Schmitt et al., 1973 in: McDermott, 2009;) and the nut crab *Ebalia tuberosa* (Haselmair et al., 2010). The blue crab *Callinectes similis* actively detects and avoids DO below 2.3 ppm (Das and Stickle, 1994). The penaeid shrimp *Metapenaeus ensis* moves away from oxygen-depleted water (0.5 mg l⁻¹ DO), seeking normoxic conditions (3.0 mg l⁻¹ DO; Wu et al., 2002). The white shrimp *Penaeus setiferus* and the brown shrimp *Penaeus aztecus* avoid hypoxic conditions below 1.5 and 2.0 ppm DO, respectively (Renaud, 1986). Physiological mechanisms to actively detect dropping oxygen concentrations (and thus impending hypoxia) (Breitburg, 1992) and to orientate towards more favourable conditions (Bell et al., 2003) are essential to successfully avoid hypoxia. For example, the deep-water hermit crab *Parapagurus pilosimanus* adjusts its orientation and movement according to oxygen gradients and currents (Rowe and Menzies, 1968).

The density of *P. eremita* was high during the recent transect survey on this Northern Adriatic sediment bottom (2.4 individuals m⁻²), slightly higher than in an earlier sampling (1.9 m⁻²; Stachowitsch, 1977). *Paguristes eremita* is a highly mobile crustacean with an average speed of 1.8 m h⁻¹ (Stachowitsch, 1979). Based on earlier time-lapse films, these crabs were estimated to move 21.6 m per day but remained within a defined radius (based on the high tagging relocation rate). Locomotion is non-directed, apparently determined by multi-species clumps on the sediment and by intraspecific encounters. Shorter interruptions of locomotion involved examining or feeding on structures on and under the sediment; longer breaks during the night indicated a resting phase. Hermit crabs responded to 2.0 ml l⁻¹ DO with reduced locomotion, and at 0.5 ml l⁻¹ DO locomotion ceased (Fig. 7a). This pattern was only briefly interrupted by “escape movement” after emergence from the shell. Juvenile Norway lobster *Nephrops norvegicus* also alter their behaviour pattern (Eriksson and Baden, 1997). The first response to 30 % oxygen saturation is generally prolonged inactivity, decreased walking and digging,

with escape bursts of swimming; this may correspond with the initial less-active behaviour of hermit crabs.

Most crustaceans try to escape by first increasing their locomotion, later becoming immobile at species-specific thresholds. Reducing locomotory activities is a typical mechanism to save energy that is needed for respiration (Johansson, 1997; Mistri, 2004). Bioherm-associated crustaceans in the Northern Adriatic Sea increase their locomotion threefold with declining oxygen, followed by decreased activity between 1.0 and 0.5 ml l⁻¹ DO (Haselmair et al., 2010). In the brackish-water shrimps *Palaemonetes varians* (Hagerman and Uglow, 1984) and *Crangon crangon* (Hagerman and Szaniawska, 1986), ~50 % oxygen saturation caused restless swimming followed by immobility at <10 mmHg DO and 30 % oxygen saturation, respectively. The position of crabs on multi-species clumps and their decreased locomotion were concurrent events at this threshold. The clumps are relatively small (decimetre range), restricting locomotion if the crabs want to stay on them. We therefore interpret decreased locomotion and immobility as a combination of saving energy and the restriction to relatively small elevated sites.

The overall activity pattern of hermit crabs changed with decreasing oxygen concentrations. *Paguristes eremita* follows a diurnal activity pattern. It is mostly active during the day and moves less during the night: lengthy stops during the night suggested a resting phase (Stachowitsch, 1979). Thus, during a 12-h daytime phase, the number of individuals moving within the time-lapse camera's field of vision in that study was fivefold compared to nighttime. During normoxia, the activity pattern we observed here corresponds with that reported by Stachowitsch (1979). At the beginning and end of oxygen decline – during mild hypoxia and anoxia – no such day/night rhythm was exhibited. During moderate and severe hypoxia, the diurnal activity pattern was detected again. When DO dropped below 2 ml l⁻¹, crabs tried to avoid the unfavourable conditions, causing them to be active both day and night. During anoxia, hermit crabs were moribund, which resulted in no difference in locomotion between day- and nighttime. This irregular activity pattern is hypoxia-induced and interpreted as a response to environmental stress. Altered activity patterns have been reported in bioherm-associated crustaceans, for example *P. longimana*. That crab has a cryptic lifestyle and its visible presence is restricted to nighttime (Haselmair et al., 2010). From moderate hypoxia on, however, *P. longimana* was exposed and visible both day and night.

As opposed to locomotion, hermit crab body movements steadily increased as DO values fell from 2.0 to 0.5 ml l⁻¹. Thereafter, during severe hypoxia and anoxia, body movements decreased. General body movements combined with movements of the pleopods (Lancester, 1988) or abdomen (Gerlach et al., 1976) create water currents to deliver sufficient gill respiratory current in the hermit crab *Pagurus bernhardus*; pleopod movements also remove faeces from inside the shell. Hypoxia triggers increased pleopod beating in the Norway lobster *N. norvegicus* to create a sufficient water flow through the burrow (Gerhardt and Baden, 1998). Brief injection of hypoxic water (2 ppm DO), however, did not change the pleopod beating rate in the hermit crab *Dardanus arrosor* (Innocenti et al., 2004). In addition to pleopod movements, increased frequency of scaphognathite beating under declining oxygen concentrations has been described in certain crustacean species (McMahon, 2001). Accordingly, body movements in *P. eremita* are interpreted as a response to hypoxic stress but may also create an additional water movement inside the shell.

Decreasing oxygen concentrations initiated a sequence of atypical crab postures along with an altered shell position: extension from the shell during mild hypoxia, overturned shells during severe hypoxia and emergence beginning approximately 24 h after anoxia. Extension from the shell increased (percentage of observations) up until anoxia, and nearly 50 % of all crabs were extended at anoxia. The number of overturned shells increased throughout anoxia. Both phases exposed the crab more to potential predators. Before emergence, crabs showed only body movements, but no locomotion. Emergence from the shell was associated with an escape reaction in all except 1 of 13 emerged individuals and occurred after a mean of 26.9 h after anoxia. This involved a spurt of locomotion lasting on average 3.7 h. Hermit crabs are confronted with additional costs involved with carrying their shells (Herreid and Full, 1986). In the land hermit crab *Coenobita compressus*, for example, the oxygen consumption rate is the same in motionless crabs outside or in shells. During slow locomotion, however, the crabs in shells require twice as much oxygen as shell-less individuals. Emergence along with increased locomotion is therefore interpreted as a last attempt to escape in an energy-saving mode. During the prolonged duration of anoxia at which this behaviour occurs, the risk of predation is probably low: most predators, with the exception of muricid gastropods and anemones such as *C. pedunculatus* are moribund, dead or have left the area (fishes).

Hermit crabs have been reported to emerge from their shells after exposure to various environmental stresses: hypoxia (Riedel et al., 2008b; Stachowitsch, 1984), extreme thermal stress (Bertness, 1982), high temperature and desiccation (Taylor, 1981), when pursued (Greenaway, 2003) and during dredging (Young, 1979). Intertidal organisms such as the hermit crab *Pagurus samuelis* are commonly subjected to disturbances in the form of flooding and sedimentation, which lead to oxygen deficiency in the surrounding areas (Shives and Dunbar, 2010). In a laboratory study the hermit crab reacted to burial by sediment with emergence from the shell. An upwards-facing aperture was the precursor for emergence after burial-induced hypoxia. Not all shells occupied by *P. eremita* were overturned: nearly two-thirds the crabs emerged from normally positioned shells. Hypoxic conditions can impact other shell-related behaviours. Such conditions change the benefits associated with different shells, altering shell selection: investigation of new shells is shortened and crabs inhabit significantly lighter and smaller shells (Côté et al., 1998). This change reduces the internal spaciousness of the shell, increases predation and impacts reproduction. Nonetheless, these drawbacks are apparently outweighed by the reduced energy costs.

4.2. Housing-specific responses

The size and weight of the different shells probably caused certain housing-specific responses of hermit crabs. Avoidance behaviour onto multi-species clumps and the amount of interactions differed according to housing category: crabs in *S. domuncula* spent the most time on such clumps and also had the most interactions, followed by small and then large individuals. Large shells were overturned already during severe hypoxia, while small shells and *S. domuncula*-covered shells were first overturned during anoxia. Tolerance and responses of crustaceans generally vary between adults and juveniles, e.g. the juvenile Norway lobster *N. norvegicus* is more sensitive to hypoxia (Eriksson and Baden, 1997). Additionally, oxygen consumption is dependent on weight (Bridges and Brand, 1980), thus probably contributing to different size-related responses. Larger individuals climb less onto elevated substrate during decreasing DO and may save energy by remaining on the sediment due to their higher shell weight. The pronounced upward movement of crabs in *S. domuncula* shells may be interpreted as an attempt to keep the sponges alive,

although only few such individuals were evaluated. The escape of sponge-inhabiting crabs onto multi-species clumps, which are common refuges from hypoxia in this community, may explain the increased interactions (see below). The sea anemone *C. parasitica*, frequently attached to large shells, provides protection from predation (Williams and McDermott, 2004) and thus decreases interactions in large crabs.

Behavioural reactions of crabs in *S. domuncula* differed the most, including additional intensified body movements, extension from shell and decreased locomotion. The oxygen content in the tissue of the symbiotic sponge is only 50 to 60 % that of the surrounding water (Gatti et al., 2002). The aperture of the occupied shell is typically closely surrounded by the sponge, reducing the opening of the shell. The tightly enclosed crab may be sealed off more from the ambient conditions. Such reduced water exchange may prompt the crab to extend more often during moderate hypoxia and anoxia and increase body movements during mild, moderate and severe hypoxia.

4.3. Atypical interactions

Interactions with other species increased during exposure to $<2 \text{ ml l}^{-1}$ DO, but then decreased during anoxia. Hypoxia led to a series of atypical events. These included dampened reactions upon an encounter (no avoidance, shorter flight distances of other organisms), interactions with normally hidden or buried organisms, interactions with other organisms aggregating on elevated substrates, and even organisms climbing onto crab-occupied shells.

Interestingly, peaks of interactions do not correspond with the activity rhythm of crabs, e.g. locomotion peaks. During normoxia, most of the interactions occurred at night, whereas hermit crabs are day-active. At mild hypoxia, interactions increased and remained at a stable level throughout severe hypoxia. Crab locomotion, however, first decreased during mild hypoxia and then again during severe hypoxia. During anoxia, interactions were halved and hermit crabs were mainly immobile (exception: “escape movement” after emergence). Most interactions may be explained by initiation by nocturnal organisms, by increased activity of other organisms during the day and by the artefact of long-lasting contact with and between moribund organisms.

To avoid low DO, for example, one hermit crab climbed onto the sea urchin *S. canaliferus*, an atypical substrate. Such emerging infauna species broadened the range of potential interactions (Pados, 2010).

Conversely, the occupied shells themselves became an atypical substratum for other species such as the crab *P. longimana* and the brittle stars *Ophiura* sp. and *O. quinquemaculata*. Individuals of *P. longimana* emerge from their hiding places during mild and moderate hypoxia, use any available elevated structures, leading to aggregations on ascidians, for example (Haselmair et al., 2010). Normally, *Ophiura lacterosa* and *O. quinquemaculata* escape when hermit crabs approach, pointing to predator-prey relationships (Stachowitsch, 1979; Wurzian, 1982). This reaction upon an approach, however, disappeared, and during severe hypoxia and anoxia *Ophiura* spp. individuals even positioned themselves on the shells. During decreased DO concentrations, hermit crabs and other organisms were located on multi-species clumps, and such unusual aggregations on restricted areas increase the chances of interactions. For example, *O. quinquemaculata* typically aggregates on multi-species clumps (Stachowitsch, 1979). These brittle stars ceased to react to the crabs during mild hypoxia, and moribund individuals commonly clung to shells during severe hypoxia.

Elsewhere, hypoxia-induced migrations of organisms can lead to concentrations in oxygenated refuge habitat, increasing the number of biological interactions (Lenihan et al., 2001). The ultimate effect of a spatial overlap with competitors or predators under such conditions, however, is affected by the relative tolerance of predator and prey to anoxia (Breitburg et al., 1994; Kolar and Rahel, 1993; Riedel et al., 2008a). In the Northern Adriatic, for example, an atypical interspecific interaction event was documented involving the symbiotic sea anemone *C. parasitica* attached to a hermit crab shell and the brittle star *O. quinquemaculata*: the highly tolerant sea anemone consumed the moribund brittle star during low DO (Riedel et al., 2008a). Crustaceans are known to be less tolerant than anemones, and *P. eremita*, for example, when suffering from hypoxia, was never observed to consume moribund prey.

During anoxia, the number of interactions decreased and involved for example the more tolerant gastropod *H. trunculus* and the emerged sea urchin *S. canaliferus*.

4.4. Mortality and tolerance

Among the hypoxia-sensitive crustaceans (Gray et al., 2002; Theede et al., 1969), *P. eremita* is relatively tolerant to oxygen deficiencies and H₂S. Hermit crabs first died during prolonged anoxia (mean = 37.7 h). During a mass mortality event in 1983 in the Gulf of Trieste, few crabs were alive on the 5th day after the onset of hypoxia/anoxia, and on the 7th day no living individuals were observed (Stachowitsch, 1984). Previous studies with hermit crabs have mainly involved laboratory experiments and dealt with short-term exposure to low DO, mainly focusing on survival. *Pagurus* spp. survived 0.6 mg l⁻¹ DO for one hour and was then returned to normal oxygen conditions (Marshall and Leverone, 1994). Other hermit crabs survived burial (and the related, induced hypoxia) for 12 h (Shives, 2010). The intertidal hermit crab *Clibanarius vittatus* typically survived 5.5 h in oxygen-free seawater: only 1 of 5 tested individuals died (Wernick and Penteado, 1983).

A general critical DO concentration for the onset of benthic mortality is 1 ml l⁻¹, with wide-ranging mortality at about 0.5 ml l⁻¹ (Diaz and Rosenberg, 1995). These thresholds, however, might be underestimated for crustaceans: recent approaches suggest a median lethal concentration (LC₅₀) of 2.45 mg l⁻¹ DO (SD = 0.14), with a median lethal time (LT₅₀) of 55.5 h (SD = 12.4; Vaquer-Sunyer and Duarte, 2008). Generally, susceptibility to hypoxia varies among taxonomic groups, with crustaceans and fishes being among the sensitive organisms while molluscs, cnidarians and priapulids are relatively tolerant. Beyond this broad pattern, tolerance differs among species within a particular taxonomic group. Bioherm-associated crabs such as *P. longimana* and *Galathea* spp. are sensitive, while *E. tuberosa* and *N. pinnotheres* are more tolerant, the latter two dying last (after 34.2 and 78 h of anoxia, respectively; Haselmair et al., 2010).

Mortality in hermit crabs was attributable significantly to the duration of anoxia but highly significantly to the development and level of H₂S. The tolerance of organisms to oxygen depletion alone is difficult to study because anoxia is generally accompanied by the presence of H₂S (Vismann, 1991). The occurrence of H₂S is an additional impact that reduces survival time by an average of 30 % (Vaquer-Sunyer and Duarte, 2010b). H₂S blocks the activity of cytochrome c oxidase, which explains its toxic character at nanomolar to low micromolar concentrations for most aerobic organisms (Bagarinao, 1992). Hermit crabs died at a mean of 128.1 µmol l⁻¹ H₂S. In

the examined benthic community, however, mortalities could often be attributed to oxygen depletion alone: many organisms, including the crab *P. longimana*, died before H₂S developed. *N. pinnotheres* tolerates low H₂S concentrations (maximum 19.2 μmol l⁻¹; Haselmair et al., 2010). Mud-shrimps (Thalassinidea), for example, burrow in the sediment and are physiologically adapted to an environment that is hypoxic and exhibits extremely high sulphide concentrations (Johns et al., 1997).

Tolerance to oxygen depletion depends on the physiological and behavioural adaptations to hypoxia (Wu, 2002). Hermit crabs showed visible responses to low DO: avoidance by seeking better-oxygenated multi-species clumps and altered behaviour to reduce energy consumption, including immobility and emergence from shells. Hermit crabs, when exposed to hypoxia, attempt to maintain oxygen delivery. *Clibanarius vittatus*, for example, is an “oxygen conformer” with decreased oxygen uptake during declining concentrations. Below 5 % oxygen saturation, respiration rates remain at a steady level, indicating an elevated ventilation (Wernick and Penteadó, 1983). The hermit crab *P. samuelis* responds to hypoxia by meeting the demands for aerobic respiration with anaerobic fermentation, which is indicated by increasing lactate levels in the hemolymph, such as during hypoxia caused by burial (Shives, 2010). Increased duration of burial increases the chance of mortality, but large stored energy reserves in the form of glycogen likely prolong survival.

One hypothesis might be that hermit crabs, being enclosed in relatively tight fitting, impermeable calcareous shells, have evolved – in analogy to sediment-burrowing crustaceans – to be somewhat more tolerant to low DO concentrations than other, free-living crustaceans.

4.5. Symbionts

The sea anemone *C. parasitica* is a well-known hermit crab symbiont (Williams and McDermott, 2004). Behavioural reactions of *C. parasitica* have been documented in detail in earlier EAGU deployments (Riedel et al., 2008a; 2008b). During normal oxygen conditions, the tentacle crown is open and directed downwards, towards the sediment: it sweeps across the bottom when the crabs move (Fig. 6; Stachowitsch 1980). The sea anemone responds to hypoxia by directing the open tentacle crown upwards (Riedel et al., 2008a; 2008b). As oxygen decreases, individuals start rotating their crown. During anoxia, the tentacle crown is contracted and again faces

down. Ultimately, some of these sea anemones detach from the shell substrate (Jørgensen, 1980; Riedel et al., 2008a; Sagasti et al., 2001). In the Northern Adriatic, *C. parasitica* individuals survived between 28 and 35 h of anoxia. Other studies demonstrated that anemones are especially resistant, surviving prolonged exposure to anoxia (Jørgensen, 1980; Wahl, 1984). This tolerance is attributed to a combination of switching from aerobic to anaerobic pathways, metabolic depression and elongation to increase the surface area for gas exchange (Sassaman and Mangum, 1972; Shick, 1991).

Reactions of other symbionts were documented during the mass mortality in 1983 (Stachowitsch, 1984). During normal oxygen conditions, colonial ascidians (Didemnidae) form rigid colonies around the whole shell. During that event, these ascidians drooped to the sediment. Most symbionts were apparently dead on the 2nd day after the onset of that event, apart from *C. parasitica* and the zoanthid *E. arenaceus*. One day later, the dead symbiotic sponge *S. domuncula* changed its colour and spherical shape, also drooping. *Epizoanthus arenaceus*, another common symbiont (Ates, 2003; Stachowitsch, 1980), was among the survivors one week after the event.

A laboratory study revealed that another known hermit crab symbiont, the barnacle *Balanus improvisus* (Williams and McDermott, 2004), reacts to hypoxia by vertically extending its feeding appendages without the normal movement of feeding (Sagasti et al., 2001). These authors also demonstrated that bryozoans, a common shell-inhabiting group, are tolerant to hypoxia by forming a resting state.

4.6. Conclusions

Hypoxia and anoxia have changed the community structure in the Northern Adriatic Sea. After mass mortalities, the typical, designating genera have become less abundant whereas the number of hermit crabs increased (Kollmann and Stachowitsch, 2001). The present study sheds light on the reactions of hermit crabs to such low dissolved oxygen events and helps explain their success in this benthic community.

Hermit crabs respond with a succession of atypical behaviours including:

- avoidance of low DO by seeking higher multi-species clumps
- decreased locomotory activity to save energy
- altered activity patterns
- changed level of body movements
- atypical body posture: extension from shell
- moribund phase: immobile crabs in overturned shells
- emergence from shell along with an “escape movement”
- atypical interspecific interactions
- mortality

The relative tolerance of hermit crabs to anoxia, coupled with their high mobility and their great range of symbionts, indicates that they play an important role in recovery after oxygen depletion (Stachowitsch, 1979). Hermit crabs, as scavengers and predators, are attracted by discards and moribund benthos after disturbance by trawl fishery (Groenewold and Fonds, 2000; Rumohr and Kujawski, 2000). A similar process can be expected after anoxia-induced community disturbance. This highlights the significance of hermit crabs as potential survivors of short-term hypoxia and as recolonizers of affected areas. Hermit crab shells also represent important structures for larval attachment after low oxygen events, especially since most non-motile structures become covered by sediment (Stachowitsch, 1984). The magnitude of restructuring will depend in part on the susceptibility of symbionts. Tolerant symbionts such as sea anemones may survive deposition of the shell and result in the establishment of new multi-species clumps (Stachowitsch, 1979), thereby accelerating recovery. After small-scale or patchy anoxias, crabs with complete undamaged symbiont communities may move in from the unaffected surroundings and colonize the denuded areas. Such processes may be crucial in the world’s increasing number of anoxia-related “dead zones”.

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6. Abstract

Hermit crabs play an important role in the Northern Adriatic Sea due to their abundance, wide range of symbionts, and function in structuring the benthic community. Among the crustaceans, which are a sensitive group to oxygen depletion, the hermit crab *Paguristes eremita* is relatively tolerant. A specially designed underwater device (EAGU – experimental anoxia generating unit) was deployed to artificially create and document small-scale hypoxia and anoxia (0.25 m²) on a sublittoral soft bottom in 24 m depth in the Gulf of Trieste. This approach successfully simulated typical seasonal low dissolved oxygen (DO) events in the Northern Adriatic Sea, and enabled studying the behaviour and mortality of *P. eremita*.

The crabs exhibited a sequence of atypical responses and ultimately mortality, which was correlated with five oxygen thresholds. Initially, at mild hypoxia (2.0 to 1.0 ml l⁻¹ DO), hermit crabs showed an avoidance response by moving onto better oxygenated, elevated substrata. This was accompanied by a series of responses including decreased locomotory activity, increased body movements and extension from the shell. During a moribund phase at severe hypoxia (0.5 to 0.01 ml l⁻¹ DO), crabs were mostly immobile in overturned shells and body movements decreased. Anoxia triggered emergence from the shell, with a last brief “escape movement” of shell-less crabs. The activity pattern of normally day active crabs was altered during mild hypoxia and anoxia. Atypical interspecific interactions were initiated: the crab *Pisidia longimana* increasingly aggregated on hermit crab shells from mild hypoxia to anoxia, and a hermit crab used the emerged infaunal sea urchin *Schizaster canaliferus* as an elevated substrate during anoxia. Response patterns partially varied according to the housing of crabs; small and large shells, and the sponge *Suberites domuncula*. Mortality occurred after extended anoxia (~1.5 d) and increased hydrogen sulphide levels (H₂S ~128 µmol). Hermit crab shells are heavily overgrown by symbionts, forming mobile aggregations of benthic organisms which structure the overall community. The tolerance of certain symbionts (e.g. the sea anemone *C. parasitica*) may influence and accelerate community recovery after oxygen crisis.

This study emphasizes the important role of relatively tolerant hermit crabs in this benthic community as potential survivors and recolonizers of affected areas.

7. Zusammenfassung

Einsiedlerkrebse bewohnen eine Vielzahl an Lebensräumen, von polaren bis zu tropischen Meeren, vom Supralitoral bis zu Tiefseeegräben. Sie spielen sowohl als Räuber, Filtrierer, Aas- und Detritusfresser eine wichtige Rolle (Schembri, 1982). Die vielfältigen Symbiosen der Einsiedlerkrebse erhöhen die Biodiversität ihrer Lebensräume (Reiss et al., 2003). Die Weichbodengemeinschaft der Nordadria ist durch Aggregationen von Makroepifauna, sogenannten Biohermen, gekennzeichnet. Diese Bioherme besitzen meist sekundäre Hartbodenelemente als Basis, hauptsächlich Schalen und Schalenstücke (Stachowitsch, 1977) und weisen eine sehr hohe Biomasse auf (Fedra et al., 1976). Einsiedlerkrebse haben in dieser epibenthischen Lebensgemeinschaft eine hohe Dichte (1.88 Individuen m⁻²). *Paguristes eremita* (Linnaeus, 1767) ist die dominierende Einsiedlerkrebsart, gefolgt von *Pagurus cuanensis* (Bell, 1845) (Stachowitsch, 1977). Ihrer Größe entsprechend bewohnen kleine Individuen Gastropodenschalen von *Aporrhais pespelecani* (Linnaeus, 1758), während größere Individuen Schalen von *Murex brandaris* (Linnaeus, 1758) und *Hexaplex trunculus* (Linnaeus, 1758) bevorzugen (Stachowitsch, 1980).

Gastropodengehäuse der Einsiedlerkrebse stellen wichtige sedimentfreie und harte Strukturen für die Anhaftung von Epifauna in benthischen Weichböden-gemeinschaften dar. Leere Schalen werden meist rasch zusedimentiert, sofern sie nicht Einsiedlerkrebse als Gehäuse und Schutz dienen (Creed, 2000; Stachowitsch, 1977). Einsiedlerkrebse können aufgrund dessen als Ökosystem-Ingenieure bezeichnet werden: Durch die Benutzung der Gastropodenschalen beeinflussen sie die Abundanz und Verbreitung von Invertebraten (Gutiérrez et al., 2003; Jones et al., 1994; 1997; Williams and McDermott, 2004). Der Aufwuchs von *P. eremita* besteht aus mehr als 110 epizoischen und endolithischen Arten (Stachowitsch, 1980). Die hohe Anzahl, Größe und vielfältige Artenzusammensetzung des Aufwuchses (Stachowitsch, 1980; Williams and McDermott, 2004) stellen eine stabile und dennoch mobile Mikrobiozönose dar (Stachowitsch, 1977). Die Zusammensetzung der Symbionten beeinflusst die Funktionsfähigkeit des Gehäuses und somit die mögliche Dauer der Bewohnbarkeit des Krebs'. Ein konstruktiver Prozess umfasst Gehäuse verstärkende Arten, welche die Lebensdauer der Schale verlängern, z.B. Seescheiden oder der Schwamm *Suberites domuncula* (Olivi, 1792). Ein destruktiver

Prozess, ausgelöst durch Gehäuse zerstörende Arten, schwächt die Schale und verringert die Dauer ihrer Bewohnbarkeit, z.B. der Schwamm *Cliona* sp. oder die Bivalve *Gastrochaena dubia* (Pennant, 1777). Dies führte zu einer neuen Einteilung der Einsiedlerkrebssymbionten, welche auf deren Einfluss auf die Tragedauer und Funktionstüchtigkeit des Gehäuses basiert (Verlängerung oder Verkürzung). Einsiedlerkrebse verlassen beschädigte Gehäuse. Nach der Deponierung des Gehäuses sind Überleben und eine weitere Entwicklung einiger Symbionten möglich: Ehemals von Einsiedlerkrebsen bewohnte Gehäuse bilden die Basis vieler bestehender Bioherme. Aufgrund dessen spielen Einsiedlerkrebse eine wichtige Rolle in der Strukturierung dieser gesamten Lebensgemeinschaft.

Innerhalb der marinen Ökosysteme sind seichte Küstengewässer am meisten von anthropogenen Einflüssen gefährdet. Eutrophierung sowie Stratifikation der Wassersäule können zu einem verminderten Gehalt an gelöstem Sauerstoff (DO) am Meeresboden führen und wurden als Umweltproblem erkannt (Diaz, 2001). Hypoxie ($DO < 2 \text{ ml l}^{-1}$) und Anoxie (kein Sauerstoff) haben seit den 1960er Jahren weltweit exponentiell zugenommen und sind heute bedeutende Stressfaktoren in seichten marinen Ökosystemen (Diaz and Rosenberg, 2008). Die Empfindlichkeit der benthischen Organismen in Bezug auf Hypoxie ist unterschiedlich, generell reagieren anfangs alle mit atypischen Verhaltensweisen sowie physiologischen Anpassungen (Diaz and Rosenberg, 1995; Gray et al., 2002; Wu, 2002). Lang andauernde Sauerstoffkrisen betreffen großflächige Gebiete auf dem Meeresboden und führen zu Massensterben der benthischen Fauna (in der Adria; Stachowitsch, 1984), sogenannte „Todeszonen“ (Diaz and Rosenberg, 2008). Hypoxie verändert nicht nur die Struktur und Funktion von benthischen Lebensgemeinschaften, sondern führt zu Beeinträchtigungen auf allen Ebenen: von der Veränderung biogeochemischer Prozesse (Conley et al., 2009) bis zur Verringerung der Bereitstellung von Ökosystemdienstleistungen (Sala and Knowlton, 2006). Durch die Erwärmung der Ozeane werden zusätzlich verringerte Überlebenszeiten der Organismen und eine erhöhte Empfindlichkeit gegen niedrige Sauerstoffkonzentrationen vorhersagbar (Vaquer-Sunyer and Duarte, 2010a).

Aufgrund der besonderen Gegebenheiten, die wesentlich zur Entstehung von Sauerstoffkrisen beitragen, zählt die Nordadria zu den weltweit nahezu 400 anerkannten „Todeszonen“ (Diaz and Rosenberg, 2008). Folgende Faktoren spielen dabei eine wesentliche Rolle:

- ein seichtes Binnenmeer mit vermehrtem Nährstoffeintrag und
- Stratifikation der Wassersäule im Sommer (Justić et al., 1993).

Die Nordadria dient daher als Vorzeigemodell für ein empfindliches Ökosystem, das jahreszeitlich von Sauerstoffkrisen betroffen ist (Crema et al., 1991). Das Auftreten letzterer ist jedoch schwer voraussagbar. Um die Auswirkungen der Sauerstoffkrisen auf die benthischen Lebensgemeinschaften zu untersuchen wurde ein spezielles Unterwasserinstrument, der EAGU („experimental anoxia generating unit“), entwickelt (Stachowitsch et al., 2007), welches kleinflächig Hypoxie und Anoxie erzeugt. Der EAGU ist mit einer Unterwasserkamera und mehreren Sensoren (Sauerstoff, Schwefelwasserstoff, pH-Wert, Temperatur) ausgestattet, um den Ablauf bei einer Sauerstoffkrise umfassend aufzeichnen zu können. Zuerst wird ein Metallrahmen über die zu untersuchenden Bioherme und Organismen gestellt, um das Verhalten während normoxischer Verhältnisse aufzuzeichnen. Danach wird der Rahmen durch eine Plexiglas-kammer ausgetauscht. Aufgrund der Respiration der eingeschlossenen Organismen sinkt allmählich der Sauerstoffgehalt. Mithilfe des EAGUs ist es möglich eine Sauerstoffkrise zu simulieren und Verhaltensreaktionen, intra- und interspezifische Interaktionen und Mortalitäten der Organismen zu untersuchen.

Diese Studie beschäftigt sich mit den Auswirkungen von abnehmendem Sauerstoffgehalt auf das Verhalten des Einsiedlerkrebse *P. eremita*. Die Verhaltensänderungen wurden mit fünf Sauerstoffgrenzwerten in Bezug gesetzt und stellten eine Abfolge von atypischen Reaktionen und letztlich Mortalität dar.

- **Normoxie ($\geq 2,0 \text{ ml l}^{-1} \text{ DO}$):** Bei Normoxie wurde ein für Einsiedlerkrebse typisches Verhalten festgestellt.
- **Milde Hypoxie (2,0 bis $1,0 \text{ ml l}^{-1} \text{ DO}$):** Während dieser versuchte *P. eremita* geringe Sauerstoffkonzentrationen zu vermeiden und flüchtete auf höher gelegene, sauerstoffreichere Bioherme. Dieses Verhalten wurde von einer Reihe von Reaktionen begleitet: verringerte lokomotorische Aktivität, erhöhte Körperbewegungen und ein Herausstrecken aus der Schale, sodass Teile des weichen Carapax' oder sogar des Abdomens sichtbar wurden.

- **Moderate Hypoxie (1,0 bis 0,5 ml l⁻¹ DO):** Zuvor initiierte Verhaltensänderungen waren auch während moderater Hypoxie sichtbar.
- **Fortgeschrittene Hypoxie (0,5 bis 0,01 ml l⁻¹ DO):** Diese war von einer subletalen Phase gekennzeichnet. Die meist unbeweglichen Krebse befanden sich in umgedrehten Gehäusen mit nach oben gerichteten Öffnungen und reduzierten ihre Körperbewegungen.
- **Anoxie (0 ml l⁻¹ DO):** Während Anoxie verließen Einsiedlerkrebse ihre Gehäuse und versuchten zu flüchten. Nach längerer Anoxie (~1,5 Tage) und einer erhöhten Schwefelwasserstoffkonzentration (~128 µmol) lösten diese beiden Faktoren den Tod der Krebse aus.

Der Tag-Nacht-Rhythmus der normalerweise tagaktiven Einsiedler war während milder Hypoxie und Anoxie verändert. Atypische interspezifische Interaktionen wurden beobachtet z.B. von milder Hypoxie bis Anoxie war die Krabbe *Pisidia longimana* (Risso, 1816) meist auf Einsiedlerkrebsegehäusen aggregiert, während Anoxie benutze ein Einsiedlerkrebse einen hervor getretenen infaunalen Seeigel *Schizaster canaliferus* (Lamarck, 1816) als Zufluchtsort.

Einsiedlerkrebse sind im Vergleich zu den meist wenig hypoxieresistenten Crustaceen relativ tolerant gegenüber Sauerstoffkrisen. Diese relativ hohe Toleranz der Einsiedlerkrebse sowie deren hohe Mobilität deuten darauf hin, dass diese eine wichtige Rolle in der Wiederbesiedelung nach einer Sauerstoffkrise spielen (Stachowitsch, 1979). Einsiedlerkrebse, welche Aasfresser und Räuber sind, werden nach Störungen durch Schleppnetzfisherei von sterbenden benthischen Organismen angezogen (Groenewold and Fonds, 2000; Rumohr and Kujawski, 2000). Ein ähnlicher Prozess könnte auch nach Störungen durch Anoxie induziert werden. Dies unterstreicht die Bedeutung der Einsiedlerkrebse als Überlebende kurz andauernder Hypoxie und Wiederbesiedler der beeinträchtigten Gebiete. Die Gehäuse der Einsiedlerkrebse könnten wichtige Strukturen für die Anhaftung von Organismen und Larven nach Sauerstoffkrisen darstellen (Stachowitsch, 1984). Das Ausmaß und der Erfolg dieser Wiederbesiedelung könnten von der Empfindlichkeit der Symbionten beeinflusst werden. Tolerante Symbionten wie z.B. die Seeanemone

Calliactis parasitica (Couch, 1842) könnten überleben, die Ablagerung des Gehäuses zum Aufbau neuer Bioherme beitragen (Stachowitsch, 1979) und damit die Wiederherstellung beschleunigen. Solche Prozesse könnten angesichts der weltweiten Zunahme an „Todeszonen“ entscheidend sein.

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9. Curriculum vitae

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07/2008 Marine biological field course on the Mediterranean fauna and flora, Centre for Marine Research, Rovinj, Croatia

11/2007 Reef ecology course, Dahab, Egypt

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North Sea course: biotope Wadden Sea, Sylt, Germany

Conferences

- | | |
|------------------|--|
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10. Appendix 1

Tab. 2. Results of the Mann-Whitney *U*-test for behavioural differences in the number of observations in the five oxygen categories: all *P. eremita* individuals. Category: selected behaviour. Comparison refers to oxygen categories: 1: normoxia; 2: mild hypoxia; 3: moderate hypoxia; 4: severe hypoxia; 5: anoxia. Bold: highly significant ($P < 0.001$); Underlined numbers: significant differences ($P < 0.05$).

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	Z	<i>P</i> -value
Elevated location	1 vs. 2	4172295.0	26963671.0	-18.435	<0.001
	1 vs. 3	3303076.0	26094452.0	-18.087	<0.001
	1 vs. 4	15036146.0	37827522.0	-18.179	<0.001
	1 vs. 5	19040138.0	41831514.0	-18.987	<0.001
	2 vs. 3	1025682.0	2316103.0	-0.814	0.416
	2 vs. 4	3904744.0	17767489.0	-5.450	<0.001
	2 vs. 5	4924616.0	27059147.0	-5.728	<0.001
	3 vs. 4	3101630.5	16964375.5	-6.007	<0.001
	3 vs. 5	3911612.5	26046143.5	-6.266	<0.001
	4 vs. 5	17482790.5	39617321.5	-0.198	0.843
Locomotion	1 vs. 2	4962632.0	6253053.0	-7.448	<0.001
	1 vs. 3	4055879.0	4897632.0	-5.889	<0.001
	1 vs. 4	14400455.0	28263200.0	-29.326	<0.001
	1 vs. 5	18359644.0	40494175.0	-30.688	<0.001
	2 vs. 3	1030046.0	2320467.0	-0.829	0.407
	2 vs. 4	3782920.0	17645665.0	-15.239	<0.001
	2 vs. 5	4818967.0	26953498.0	-14.366	<0.001
	3 vs. 4	3017552.5	16880297.5	-15.668	<0.001
	3 vs. 5	3844369.0	25978900.0	-14.772	<0.001
	4 vs. 5	17386940.0	31249685.0	-1.960	<u>0.050</u>
Body movement	1 vs. 2	4064110.0	26848735.0	-19.544	<0.001
	1 vs. 3	2512007.5	25296632.5	-29.956	<0.001
	1 vs. 4	14944837.5	37729462.5	-18.411	<0.001
	1 vs. 5	20523117.5	43307742.5	-10.849	<0.001
	2 vs. 3	858251.5	2148672.5	-9.571	<0.001
	2 vs. 4	3842036.5	17704781.5	-6.450	<0.001
	2 vs. 5	4465084.5	26599615.5	-12.190	<0.001
	3 vs. 4	2502095.5	16364840.5	-17.267	<0.001
	3 vs. 5	2846900.5	24981431.5	-22.874	<0.001
	4 vs. 5	16236065.5	38370596.5	-8.163	<0.001
Extended	1 vs. 2	4800899.0	27585524.0	-18.406	<0.001
	1 vs. 3	3040763.0	25825388.0	-37.116	<0.001
	1 vs. 4	12309435.0	35094060.0	-44.969	<0.001
	1 vs. 5	13230037.0	36014662.0	-56.102	<0.001
	2 vs. 3	842483.5	2132904.5	-12.152	<0.001
	2 vs. 4	3411827.5	4702248.5	-14.875	<0.001
	2 vs. 5	3758219.5	5048640.5	-21.928	<0.001
	3 vs. 4	3407792.5	4249545.5	-0.131	0.896
	3 vs. 5	3859531.5	4701284.5	-7.028	<0.001
	4 vs. 5	15700907.5	29563652.5	-11.476	<0.001
Shell overturned	1 vs. 2	5381289.0	6671710.0	-1.741	0.082
	1 vs. 3	4363443.0	5205196.0	-0.693	0.488
	1 vs. 4	15175215.0	37959840.0	-28.030	<0.001
	1 vs. 5	17498268.0	40282893.0	-37.554	<0.001
	2 vs. 3	1037319.5	2327740.5	-0.794	0.427
	2 vs. 4	3580187.5	4870608.5	-15.764	<0.001
	2 vs. 5	4124890.5	5415311.5	-20.476	<0.001
	3 vs. 4	2905022.5	3746775.5	-13.847	<0.001
	3 vs. 5	3348528.0	4190281.0	-18.166	<0.001
	4 vs. 5	16205530.0	30068275.0	-9.914	<0.001

Table 2 (continued)

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value
Interaction	1 vs. 2	5077117.0	27861742.0	-4.562	<0.001
	1 vs. 3	4091141.5	26875766.5	-4.315	<0.001
	1 vs. 4	16660417.5	39445042.5	-6.800	<0.001
	1 vs. 5	16684991.5	38819522.5	-30.725	<0.001
	2 vs. 3	1039321.0	2329742.0	-0.113	0.910
	2 vs. 4	4224001.0	18086746.0	-0.063	0.949
	2 vs. 5	3631590.0	25766121.0	-24.960	<0.001
	3 vs. 4	3404174.5	17266919.5	-0.194	0.846
	3 vs. 5	2923870.0	25058401.0	-23.221	<0.001
	4 vs. 5	11921272.0	34055803.0	-35.555	<0.001

Tab. 3. Results of the Mann-Whitney *U*-test for behavioural differences in the number of observations in the five oxygen categories: *P. eremita* in small shells. For explanation see Tab. 2.

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value
Elevated Location	1 vs. 2	585239.0	3802155.0	-8.928	<0.001
	1 vs. 3	523541.5	3740457.5	-3.922	<0.001
	1 vs. 4	2207417.0	5424333.0	-10.834	<0.001
	1 vs. 5	2899071.0	6115987.0	-2.075	<u>0.038</u>
	2 vs. 3	118211.5	222864.5	-3.353	<u>0.001</u>
	2 vs. 4	572819.0	2716304.0	-1.809	0.071
	2 vs. 5	562794.0	3334629.0	-7.529	<0.001
	3 vs. 4	443444.0	548097.0	-2.417	<u>0.016</u>
	3 vs. 5	501430.5	3273265.5	-2.706	<u>0.007</u>
	4 vs. 5	2119033.0	4890868.0	-8.688	<0.001
Shell overturned	1 vs. 2	720210.0	887541.0	-1.593	0.111
	1 vs. 3	576341.0	680994.0	-0.443	0.658
	1 vs. 4	2542298.0	5759214.0	-3.992	<0.001
	1 vs. 5	2673782.0	5890698.0	-11.524	<0.001
	2 vs. 3	130500.0	297831.0	-0.871	0.384
	2 vs. 4	569074.0	736405.0	-3.753	<0.001
	2 vs. 5	597620.0	764951.0	-7.487	<0.001
	3 vs. 4	455576.0	560229.0	-2.527	<u>0.012</u>
	3 vs. 5	478919.0	583572.0	-6.027	<0.001
	4 vs. 5	2259008.0	4402493.0	-7.127	<0.001
Interaction	1 vs. 2	631648.0	3848564.0	-6.036	<0.001
	1 vs. 3	573944.0	3790860.0	-0.377	0.707
	1 vs. 4	2319724.0	4463209.0	-7.852	<0.001
	1 vs. 5	1959096.0	4730931.0	-24.900	<0.001
	2 vs. 3	115087.0	219740.0	-4.219	<0.001
	2 vs. 4	446057.0	2589542.0	-10.829	<0.001
	2 vs. 5	352524.0	3124359.0	-23.002	<0.001
	3 vs. 4	413510.5	2556995.5	-4.901	<0.001
	3 vs. 5	347904.0	3119739.0	-16.021	<0.001
	4 vs. 5	1882249.0	4654084.0	-16.536	<0.001

Tab. 4. Results of the Mann-Whitney *U*-test for behavioural differences in the number of observations in the five oxygen categories: *P. eremita* in large shells. For explanation see Tab. 2.

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value	
Elevated location	1 vs. 2	521290.0	1994476.0	-10.454	<0.001	
	1 vs. 3	385845.0	1859031.0	-16.065	<0.001	
	1 vs. 4	1964127.0	3437313.0	-9.981	<0.001	
	1 vs. 5	2208185.0	3681371.0	-4.647	<0.001	
	2 vs. 3	187081.5	435241.5	-4.603	<0.001	
	2 vs. 4	860546.5	4090157.5	-2.413	0.016	
	2 vs. 5	849606.5	4434109.5	-7.310	<0.001	
	3 vs. 4	646512.0	3876123.0	-8.412	<0.001	
	3 vs. 5	632779.5	4217282.5	-13.611	<0.001	
	4 vs. 5	3195400.0	6779903.0	-6.653	<0.001	
	Shell overturned	1 vs. 2	603174.0	2076360.0	-1.561	0.118
		1 vs. 3	511368.0	1984554.0	-1.695	0.090
1 vs. 4		1602744.0	3075930.0	-23.232	<0.001	
1 vs. 5		1591590.0	3064776.0	-25.457	<0.001	
2 vs. 3		210090.5	458250.5	-0.117	0.907	
2 vs. 4		658806.5	906966.5	-15.245	<0.001	
2 vs. 5		654298.5	902458.5	-16.812	<0.001	
3 vs. 4		558868.5	737371.5	-14.088	<0.001	
3 vs. 5		555056.0	733559.0	-15.551	<0.001	
4 vs. 5		3257588.0	6487199.0	-3.370	0.001	
Interaction		1 vs. 2	591624.0	2064810.0	-0.926	0.355
		1 vs. 3	489667.5	1962853.5	-1.867	0.062
	1 vs. 4	1730899.5	3204085.5	-13.259	<0.001	
	1 vs. 5	1972870.5	5557373.5	-9.612	<0.001	
	2 vs. 3	205206.0	453366.0	-0.847	0.397	
	2 vs. 4	728486.0	976646.0	-8.870	<0.001	
	2 vs. 5	790026.0	4374529.0	-8.172	<0.001	
	3 vs. 4	635587.5	814090.5	-7.282	<0.001	
	3 vs. 5	651174.0	4235677.0	-8.758	<0.001	
	4 vs. 5	2220481.0	5804984.0	-25.161	<0.001	

Tab. 5. Results of the Mann-Whitney *U*-test for behavioural differences in the number of observations in the five oxygen categories: *P. eremita* in *S. domuncula*. For explanation see Tab. 2.

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value
Elevated location	1 vs. 2	42720.0	571626.0	-19.392	<0.001
	1 vs. 3	30842.0	559748.0	-17.350	<0.001
	1 vs. 4	81938.0	610844.0	-22.434	<0.001
	1 vs. 5	250280.0	779186.0	-25.837	<0.001
	2 vs. 3	23513.0	55898.0	-0.282	0.778
	2 vs. 4	54088.0	151549.0	-1.936	0.053
	2 vs. 5	122224.0	719002.0	-5.101	<0.001
	3 vs. 4	39418.5	136879.5	-1.962	<u>0.050</u>
	3 vs. 5	89034.0	685812.0	-4.587	<0.001
	4 vs. 5	220458.0	817236.0	-4.509	<0.001
Locomotion	1 vs. 2	123104.0	155489.0	-2.244	<u>0.025</u>
	1 vs. 3	84748.0	102139.0	-3.990	<0.001
	1 vs. 4	190804.0	288265.0	-8.558	<0.001
	1 vs. 5	475600.0	1072378.0	-12.354	<0.001
	2 vs. 3	22288.0	39679.0	-2.081	<u>0.037</u>
	2 vs. 4	50341.0	147802.0	-6.124	<0.001
	2 vs. 5	125428.0	722206.0	-7.713	<0.001
	3 vs. 4	39180.0	136641.0	-3.457	<u>0.001</u>
	3 vs. 5	97584.0	694362.0	-3.491	<0.001
	4 vs. 5	239442.0	336903.0	-0.872	0.383
Body movement	1 vs. 2	73233.0	602139.0	-13.179	<0.001
	1 vs. 3	33383.0	562289.0	-17.035	<0.001
	1 vs. 4	125252.5	654158.5	-16.094	<0.001
	1 vs. 5	554348.0	1083254.0	-0.645	0.519
	2 vs. 3	18620.0	51005.0	-5.347	<0.001
	2 vs. 4	55538.5	87923.5	-0.232	0.816
	2 vs. 5	79507.0	676285.0	-12.832	<0.001
	3 vs. 4	32671.5	130132.5	-5.487	<0.001
	3 vs. 5	36717.0	633495.0	-16.731	<0.001
	4 vs. 5	136027.5	732805.5	-15.767	<0.001
Extended	1 vs. 2	109730.0	638636.0	-11.987	<0.001
	1 vs. 3	41678.0	570584.0	-24.452	<0.001
	1 vs. 4	168373.0	697279.0	-16.368	<0.001
	1 vs. 5	256678.0	785584.0	-27.647	<0.001
	2 vs. 3	14066.0	46451.0	-8.862	<0.001
	2 vs. 4	50536.0	82921.0	-2.957	<u>0.003</u>
	2 vs. 5	85543.0	117928.0	-11.010	<0.001
	3 vs. 4	28428.0	125889.0	-7.333	<0.001
	3 vs. 5	99387.0	696165.0	-0.541	0.588
	4 vs. 5	172042.5	269503.5	-10.140	<0.001
Shell overturned	1 vs. 2	130175.0	162560.0	-0.862	0.389
	1 vs. 3	95325.0	112716.0	-0.737	0.461
	1 vs. 4	212943.5	741849.5	-7.401	<0.001
	1 vs. 5	350130.0	879036.0	-21.773	<0.001
	2 vs. 3	23622.0	41013.0	0.000	1.000
	2 vs. 4	52451.0	84836.0	-4.096	<0.001
	2 vs. 5	86106.0	118491.0	-11.789	<0.001
	3 vs. 4	38409.0	55800.0	-3.513	<0.001
	3 vs. 5	63054.0	80445.0	-10.209	<0.001
	4 vs. 5	164787.0	262248.0	-12.346	<0.001

Table 5 (continued)

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value
Interaction	1 vs. 2	128332.0	657238.0	-0.499	0.618
	1 vs. 3	65928.0	594834.0	-8.200	<0.001
	1 vs. 4	158593.0	687499.0	-11.500	<0.001
	1 vs. 5	381916.0	978694.0	-14.796	<0.001
	2 vs. 3	16692.0	49077.0	-7.012	<0.001
	2 vs. 4	40139.5	72524.5	-9.085	<0.001
	2 vs. 5	92002.0	688780.0	-10.108	<0.001
	3 vs. 4	40600.5	138061.5	-0.406	0.684
	3 vs. 5	37578.0	634356.0	-16.347	<0.001
4 vs. 5	91518.0	688296.0	-22.014	<0.001	

Tab. 6. Results of the Mann-Whitney *U*-test for behavioural differences in the number of observations in the five oxygen categories: *P. eremita* in shells. For explanation see Tab. 2.

Category	Comparison	Mann-Whitney <i>U</i>	Wilcoxon <i>W</i>	<i>Z</i>	<i>P</i> -value	
Elevated location	1 vs. 2	3399254.0	19772757.0	-8.963	<0.001	
	1 vs. 3	2706929.0	19080432.0	-10.111	<0.001	
	1 vs. 4	12570529.0	28944032.0	-10.016	<0.001	
	1 vs. 5	15166898.0	31540401.0	-5.548	<0.001	
	2 vs. 3	730623.0	1645251.0	-1.378	0.168	
	2 vs. 4	3156628.0	14794528.0	-2.182	<u>0.029</u>	
	2 vs. 5	3479195.0	18944336.0	-5.291	<0.001	
	3 vs. 4	2521110.5	14159010.5	-3.721	<0.001	
	3 vs. 5	2775051.0	18240192.0	-6.650	<0.001	
	4 vs. 5	12843330.5	28308471.5	-4.630	<0.001	
	Body movement	1 vs. 2	3526634.0	4441262.0	-7.037	<0.001
		1 vs. 3	2966681.0	3584397.0	-4.855	<0.001
1 vs. 4		11081900.0	22719800.0	-28.424	<0.001	
1 vs. 5		12943926.0	28409067.0	-28.053	<0.001	
2 vs. 3		734807.0	1649435.0	-1.458	0.145	
2 vs. 4		2906296.0	14544196.0	-14.395	<0.001	
2 vs. 5		3390235.0	18855376.0	-12.649	<0.001	
3 vs. 4		2330330.0	13968230.0	-15.888	<0.001	
3 vs. 5		2719158.0	18184299.0	-14.172	<0.001	
4 vs. 5		13270690.0	24908590.0	-2.568	<u>0.010</u>	
Extended		1 vs. 2	3037512.0	19411015.0	-15.499	<0.001
		1 vs. 3	1943652.0	18317155.0	-25.364	<0.001
	1 vs. 4	11972517.0	28346020.0	-14.542	<0.001	
	1 vs. 5	14311744.0	30685247.0	-11.553	<0.001	
	2 vs. 3	620512.0	1535140.0	-8.628	<0.001	
	2 vs. 4	2992956.0	14630856.0	-5.433	<0.001	
	2 vs. 5	3329688.0	18794829.0	-7.757	<0.001	
	3 vs. 4	1993732.5	13631632.5	-15.500	<0.001	
	3 vs. 5	2199289.5	17664430.5	-17.841	<0.001	
	4 vs. 5	12983092.5	28448233.5	-3.368	<u>0.001</u>	

Tab. 7. Results of the Pearson χ^2 -test for differences between day- and night phases of the selected behaviour in the five oxygen categories: all *P. eremita* individuals. For explanation see Tab. 2.

Category	Oxygen category	χ^2	df	P-value
Locomotion	1	279.048	1	<0.001
	2	0.695	1	0.404
	3	4.485	1	<u>0.034</u>
	4	7.589	1	<u>0.006</u>
	5	0.465	1	0.495
Interaction	1	452.560	1	<0.001
	2	7.892	1	<u>0.005</u>
	3	22.849	1	<0.001
	4	9.880	1	<u>0.002</u>
	5	18.397	1	<0.001

Tab. 8. Results of linear regressions to identify factors affecting mortality and survival of *P. eremita*. Bold: highly significant ($P < 0.001$); Underlined numbers: significant differences ($P < 0.05$).

Factor	Unstandardized Coefficients		Standardized Coefficients	t	P-value
	B	Std. Error	Beta		
Closed configuration	-0.002	0.013	-0.061	-0.157	0.877
Hypoxia duration	0.029	0.018	0.710	1.569	0.135
Anoxia duration	-0.012	0.005	-0.339	-2.250	<u>0.038</u>
H₂S concentration	-0.337	0.074	-0.907	-4.541	<0.001