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**Post-anoxia
scavenging,
predation and
recovery**

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Short-term post-mortality predation and scavenging and longer-term recovery after anoxia in the northern Adriatic Sea

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Abstract

In the Mediterranean, the northern Adriatic Sea shows most features known to promote late-summer hypoxia and anoxia. These features, along with anthropogenic eutrophication and marine snow events, have led to repeated benthic mortalities here. The present study was designed to document the post-anoxia macrofauna dynamics. We deployed an underwater instrument to induce small-scale anoxia in situ (total area 0.5 m²). Two time-lapse camera deployments examined short-term scavenging of the moribund and dead organisms (multi-species clumps consisting of sponges and ascidians) over a 3-day period (August 2008: 71.5 h, September 2008: 67.5 h). Longer-term recovery (2 yr) in the same two plots was examined with an independent photo-series. Predators and scavengers arrived in a distinct sequence. The first to arrive were demersal (*Gobius niger*, *Serranus hepatus*) and benthopelagic fishes (*Diplodus vulgaris*, *Pagellus erythrinus*), followed by hermit crabs (*Paguristes eremita*, showing a clear day/night rhythm in presence) and gastropods (*Hexaplex trunculus*). This sequence of arrival is attributed to the relative speeds of the organisms and their densities. The scavengers remained in dense aggregations (e.g. up to 33 *P. eremita* individuals at one time) as long as the dead organisms were available. The whole sessile fauna was largely removed or consumed within 7 (August plot) and 13 (September plot) days after anoxia. No macroepibenthic recovery took place in the experimental plots one and two years after anoxia. This study underlines the sensitivity of this soft-bottom community and supports calls for reducing additional anthropogenic disturbances such as damaging commercial fishing practices that impede recolonization and threaten benthic community structure and function over the long-term.

1 Introduction

Dayton et al. (1995) established that coastal marine ecosystems are the world's most endangered habitats, and the Mediterranean is no exception, with documented effects

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They consist of a shelly base (bivalve or gastropod shell) overgrown by sessile organisms (sponges, ascidians) which, in turn, serve as elevated substrates for vagile and hemi-sessile species such as brittle stars, holothurians, hermit crabs and gastropods (Fedra et al., 1976; Zuschin and Pervesler, 1996). Such aggregations are also a food source for epibenthic crustaceans and fishes in the northern Adriatic and North Sea (Hampel et al., 2004). Filter- and suspension-feeder communities are an important stabilizing compartment in the overall marine ecosystem by removing enormous amounts of suspended material from the waterbody (Ott and Fedra, 1977). Such benthic communities have been termed a natural eutrophication control (Officer et al., 1982) and thus provide crucial ecological goods and services.

The damage to or loss of such communities therefore has ecosystem-wide implications. During hypoxia and anoxia, the benthic organisms in the ORM community show a distinct sequence of behaviours and mortalities. This has been documented in situ during larger-scale anoxias (Stachowitsch, 1984) and has been confirmed and analysed in great detail experimentally using an underwater chamber on a small scale (0.25 m^2) on the seafloor in 24 m depth. These behaviours include emergence of infauna species (Riedel et al., 2008b), unusual interactions including predation (Riedel et al., 2008a; Haselmair et al., 2010), altered locomotion and activity patterns (Pretterebner et al., 2012), and a clear sequence of mortalities (Riedel et al., 2012). For an overview of these responses see Riedel et al. (2013). The immediate behavioural responses during the course of hypoxia and anoxia until mortality of the macrobenthos are therefore now well documented (sample 4 d film available at: <http://phaidra.univie.ac.at/o:87923>). The longer-term implications are less well known. The collapse of benthic communities and recurring disturbances – in this case mortalities and repeated hypoxia/anoxia along with marine snow events – raise fundamental issues of ecosystem stability and resilience. One approach to addressing these issues is to examine post-disturbance events, typically successions. Various stages of succession (opportunists, an ecotone point, a transition zone) have been described early on (Pearson and Rosenberg, 1978). Overall, events proceed in the direction of more

stable “normal” communities with an increase in the number of species, abundance and biomass (Rosenberg et al., 2002).

Two basic recolonization strategies have been described: motile species can immigrate into denuded areas, in particular if the damage is rather small-scale or, when the affected areas are large, colonization depends mostly on post-larval settlement by pelagic recruits (Pearson and Rosenberg, 1978; Whitlatch et al., 1998; Norkko et al., 2010). The reestablishment of community structure on the soft bottoms of the northern Adriatic requires biogenic structures such as bivalve and gastropod shells or sea urchin tests as a substrate on which larvae of sessile and motile epifauna species can settle. Although such structures are abundant in the immediate post-mortality situation, sedimentation can cover them quickly and hamper new epigrowth. Compared to the mortality events, recovery is a much longer-term process (Stachowitsch, 1991; Stachowitsch and Fuchs, 1995). After bottom enrichment from a sulphite pulp mill in the Saltkallefjord, Sweden, the fauna in the central part of that fjord was examined in relation to oxygen deficiency and the presence of hydrogen sulphide. It took about 3 years for the top sediment to recover to a state suitable for macrofauna recolonization (Rosenberg, 1971). Intertidal communities from muddy sand habitats, for example, also have very slow biological and physical recovery rates (Dernie et al., 2003). Recovery of benthic communities after experimental trawling disturbances took more than 18 months (Tuck et al., 1998).

In the Gulf of Trieste northern Adriatic, Stachowitsch and Fuchs (1995) were unable to detect full recovery even after more than ten years, because recolonization was repeatedly interrupted by another source of disturbance, namely commercial fishing: the use of bottom trawls overturned or broke apart newly established multi-species clumps. Kollmann and Stachowitsch (2001) reported a negative influence in that elevated biogenic structures were either sheared off and uprooted (e.g. *Pinna* sp. shells) or overturned and crushed. Such effects are echoed elsewhere, with Rapido trawling significantly changing community structure and mean abundance of common taxa (Pranovi et al., 2000), or beam trawling altering the physical characteristics of the sea

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bottom (Kaiser and Spencer, 1996). The use of bottom gears reportedly increases oxygen consumption and nutrient concentrations, promotes phytoplankton primary production affects sessile epibenthic species and changes overall community structures (Riemann and Hoffmann, 1991). This includes potential long-term effects of fishing on bottom fauna (Jennings and Kaiser, 1998; Thrush and Dayton, 2002).

The reduction of long-lived suspension-feeding organisms is typically followed by a shift to a habitat dominated by detritus feeders, which can hinder the recovery of the suspension feeders by consuming them (Dayton et al., 1995). Such altered communities are often dominated by juvenile stages, mobile species and rapid colonizers (Pearson and Rosenberg, 1978; Dayton et al., 1995). In the Northern Adriatic Sea, for example, hermit crabs increased, while the designating community organisms such as brittle stars, sponges and ascidians decreased (Kollmann and Stachowitsch, 2001).

Such anthropogenic disturbance can lead to the loss of functional groups (top-down effect), compromising resilience and making ecosystems more vulnerable to additional threats such as pollution, and the capacity for self-repair is reduced (Folke et al., 2004). All these circumstances make benthic communities a long-term “memory” of disturbances (Stachowitsch, 1992). The present work was designed to assess both the immediate, short-term predation and scavenging processes after disturbance (artificially induced anoxia) and the longer-term recovery processes in the northern Adriatic Sea. We evaluated the experimentally affected areas by examining time-lapse films and by analysing photographic series. In the former, predators and scavengers were counted image by image, in the latter, the area occupied by recolonizers was calculated as a measure of recovery.

2 Material and methods

The activities of seven mobile species were examined. These encompass all the predators and scavengers that entered the experimental quadrats after the induced anoxia. They included two invertebrates and 4 vertebrates: one gastropod, the Banded dye

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murex *Hexaplex trunculus* (Linnaeus, 1758), the hermit crab *Paguristes eremita* (Linnaeus, 1767), and four fish species: the demersal Black goby *Gobius niger* (Linnaeus, 1758) and Brown comber *Serranus hepatus* (Linnaeus, 1758) as well as the benthopelagic Two-banded bream *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817) and the Common pandora *Pagellus erythrinus* (Linnaeus, 1758).

2.1 Study site

The study site is located in the Gulf of Trieste, in the northern Adriatic Sea (45° 32' 55.68" N 13° 33' 1.89" E) off Cape Madona, Slovenia (Fig. 1). The experimental site is about 2 km offshore at a depth of 24 m, near the oceanographic buoy of the Marine Biology Station in Piran (Slovenia). This position was chosen to minimize disturbance and damage by commercial fisheries. The soft bottom here is dominated by the ORM-community described above.

2.2 Experimental set-up

Two different chamber configurations are available. One is the closed configuration, which creates anoxia by sealing a 50 × 50 × 50 cm volume off from the surrounding water with plexiglass walls. Another is the open configuration, in which the plexiglass chamber is replaced by an open frame of the same size to observe behaviour under normoxic conditions. Four removable tapered metal tips stabilize both configurations in the sediment. Centrally, on a lid on top of the chamber or frame, a digital time-lapse camera (Canon EOS 30D) with a zoom lens (Canon EFS 10–22 mm) is positioned, flanked by two exchangeable battery packs (9Ah Panasonic, Werner light power, Unterwassertechnik, Germany) and two flashes (“midi analog” series 11897; Subtronic, Germany). The battery packs, combined with a specially designed electronic control circuit, enable the equipment to be operated for about 72 h. Finally, a datalogger unit (PA3000UD, Unisense, Denmark) and four sensors for measuring oxygen, temperature

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and hydrogen sulphide are placed on the lid (for a full description see Stachowitsch et al., 2007).

The present recovery experiments involved the following deployment protocol. The underwater device was initially positioned in its closed configuration over a representative multi-species clump (i.e. with both sponges and ascidians) on the sediment. After 72 h the plexiglass chamber was replaced by the open frame, i.e. the lid was briefly lifted and the chamber replaced by the open frame and the post-anoxia recovery experiment began. Within the next three days, post-mortality predation and scavenging were documented; the camera took images in 3-min intervals.

2.3 Short-term predation and scavenging

Two experiments were performed. In the “August” experiment, post-disturbance images (open configuration) were evaluated beginning on 15 August 2009 (10:35 a.m.) until 18 August 2009 (10:05 a.m.). The “September” experiment extended from 14 September 2009 (03:25 p.m.) until 17 September 2009 (10:49 a.m.). The August experiment yielded a total of 1430 images, the September experiment 1384 images. This corresponds to an overall documentation time of 71.5 h in August and 67.5 h in September. The images were also processed into time-lapse movies using the Adobe Premiere 6.5 program (August recovery time-lapse film available at: https://phaidra.univie.ac.at/detail_object/0:262380). The fishes were analysed image by image: the data are summarized in 6-h steps. Because of the relatively slow movements of the hermit crabs and gastropods and the more gradual changes in their numbers, only every tenth image was evaluated for these groups. For every analysed image the present predator and scavenger species were recorded. For hermit crabs and gastropods, the different substrates (sponges, ascidians, sediment) they were on were recorded. Normally, the gastropods and hermit crabs are found only on the sediment surface. We therefore equate the dead and/or moribund organisms (sponges and ascidians) chosen by the organisms with their preferred prey item. The time and sequence of arrival/departure and the maximum number of individuals were recorded. Day/night

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activity (based on the time of sunrise and sunset, www.sun.exnatura.org) of the hermit crabs and the gastropods was analysed. Individual specimens of the same species could rarely be differentiated because colouration and sizes were typically very similar. Accordingly, the number of fish, gastropod and hermit crab individuals refers to the number of individuals visible over the respective time period. This number clearly overestimates the actual number of different individuals present because many individuals remained in the plot for extended periods. It does, however, capture the role that an individual or individuals played because they were present and exerted a scavenging or predatory influence.

2.4 Longer-term recovery

These experiments were conducted on the same two 0.25 m² plots used for the short-term time-lapse camera study. Here, the pre-disturbance surface area occupied by living sponges and ascidians, as well as by other hard structures and lebensspuren, was calculated using CorelDraw9 and Excel 2010 based on the photos taken from the closed configuration. The corresponding surface areas were then measured again days to years after anoxia. For this purpose, photos were taken with a hand-held camera. The images of the August plot were taken on 18 (day 1 of long-term experiment), 22, 24 and 25 August 2009, those of the September plot on 19 (day 1 of long-term experiment), 20, 23, and 30 September 2009. Both plots were also photographed twice in each following year, namely on 7 and 17 August 2010, and 6 and 7 August 2011. The objects were classified into seven categories: (1) sessile fauna (living), (2) sessile fauna (dead), (3) anemones (category 1 to 3 summarized as sessile fauna (living/dead)), (4) bivalve shells, (5) gastropod shells (category 4 and 5 summarized as shells), (6) small pieces of shells and areas covered with many tightly packed shell fragments (“coquina”) and (7) lebensspuren. We also documented new colonizers.

To better compare the two experiments, the times when the images were taken were categorized, e.g., 7–13 days is termed “10-days” in the following text. The data in the

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two sets of photographs taken after 1 yr and after 2 yr at each plot are averaged, and referred to as “1 year” and “2 years”, respectively, unless stated otherwise.

Time series analyses and cross-correlations were calculated to define the residence time of gastropods and hermit crabs in the plots. Graphs of time series analysis can be found in Blasnig (2012). A Chi^2 test was performed to determine the difference in the substrates chosen by gastropods and hermit crabs and between the experiments. For statistical analyses the program Past was used (Hammer et al., 2001).

3 Results

3.1 Short-term scavenging after anoxia

Moribund and dead sponges and ascidians attracted fishes, hermit crabs and gastropods in a rapid and distinct sequence. Numerous fishes arrived in the first hours. They were followed by hermit crabs (*Paguristes eremita*), which showed a rapid initial increase in the number of individuals. Finally, the gastropods (only *Hexaplex trunculus*) appeared (Fig. 2), with a slow increase of individuals.

3.2 The fishes

In the August 2009 experiment (71.5 h) we observed three different species, *Diplodus vulgaris*, *Serranus hepatus* and *Gobius niger*, and in the September 2009 experiment (67.5 h) additionally *Pagellus erythrinus*. In both experiments, the maximum number of individuals per species was present in the first six hours. *G. niger* was most abundant and showed a slowly decreasing trend, while the other species decreased rapidly to very low numbers. A maximum of three species were visible at the same time in a single image. In the first 6 h of the August experiment, all three species were present: *G. niger* with 83, *D. vulgaris* 35 and *S. hepatus* 26 individuals. The two latter species then decreased to very low numbers or zero in the successive 6-h periods. *G. niger* also decreased with time, but never fell below 22 observed individuals per 6 h (i.e. total

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number visible over this time period, not necessarily different individuals, see Sect. 2). In the September experiment, all four species were initially present and showed the highest abundance (individual per species) in the first 6-h time step: *G. niger* peaked with 80, *D. vulgaris* 18 and *S. hepatus* 13 individuals. Until the end of the experiment, the number of individuals decreased markedly.

3.3 The first 12 h: hermit crabs and gastropods

The first 12 h were evaluated separately to determine in more detail the order in which the individuals arrived and which organisms arrived first. In August, the first three *Paguristes eremita* were observed after 30 min and the number rapidly increased up to 19 individuals after 9 h. After 3 h the first *Hexaplex trunculus* arrived and the number of individuals slowly increased to 3 individuals after 8 h (Fig. 2a). In September, the first *P. eremita* appeared after 1 h, and numbers then increased up to 12 individuals after 6 h, before decreasing again to 9. Seven *H. trunculus* individuals survived the pre-anoxia deployment (Fig. 2b) and were present and visible from the start. After 30 min the first new gastropod entered the frame. Two hours later, 3 individuals again left the area (5 present), but thereafter the number increased steadily (maximum 17).

3.4 Day/night activity

In both experiments the number of *Paguristes eremita* varied considerably over time. The values decreased in all three nights examined and increased conspicuously during daylight hours (Fig. 3). During the day the number of individuals in August increased to 24 (45.5 h after anoxia) and 33 (after 71 h), while at night, values fell to 6 and to 3 (after 38 h and 58 h, respectively). In September, the number of individuals during daylight hours peaked at 28 (17.5 h after the anoxia) and dropped to only 2 (after 37 h) and 3 individuals (after 62.5 h). The time series analysis for *P. eremita* showed highly significant peaks at 21.2 h (August), 28.4 h and 54 h (September), a significant peak at 12.4 h (August), and distinct but not significant peaks at 15.5 h and 57.2 h (August) and

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at 10.8 h (September) (data not shown). These peaks demonstrate a semidiurnal and diurnal periodicity.

Hexaplex trunculus showed a relatively slow but constant increase, levelling off somewhat over the last day. The peak number was 8 individuals at three periods between 46.5 and 65.5 h in August, and 17 individuals after 38.5 h in September. At the end of both experiments, 4 (August: 71.5 h) and 13 (September: 67.5 h) *H. trunculus* were still present in the plots. The time series analysis showed highly significant peaks at 18.5 and 38.1 (August) as well as 13.5 h, 27.0 h and 60.0 h (September). Visible but not significant peaks are present at 8.2 h, 9.7 h and 11.2 h (August) as well as at 18 h (September). These peaks point to a periodicity of 9 h and 12 h as well as multiples thereof.

The fishes show highly significant peaks at 9.9 h (August) as well as 12.3 h and 21.6 h (September) and visible but not significant peaks at 30.1 h (August) 6.4 h and 7.8 h (September). This points to a semidiurnal and a roughly diurnal periodicity.

3.5 Preferred substrates/prey items

The substrates that *Paguristes eremita* and *Hexaplex trunculus* chose were different and consistent in both experiments. Hermit crabs were observed on the sediment, on sponges and on ascidians, whereas *H. trunculus* occurred mainly on ascidians and to a lesser extent on the sediment (Fig. 4). All categories (i.e. compared species-experimental month pairs) are significantly different from each other. Importantly, there are bigger interspecific than intraspecific differences, i.e. the differences between the species (*P. eremita* in August and September versus *H. trunculus* in August and September) are bigger than between the months (*P. eremita* in August versus September and *H. trunculus* in August versus September) (Table 1).

The duration of the stay of 9 *Paguristes eremita* and 9 *Hexaplex trunculus* individuals was calculated. The individuals were chosen based on their recognizability (e.g. epigrowth on shell). This duration averaged 5 h and 19 min for *P. eremita* and 12 h and 9 min for *H. trunculus*. Thus, on average, the gastropods stayed nearly 7 h longer than

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the hermit crabs. In the August experiment, several *P. eremita* dragged off the ascidian *Phallusia mammillata*. Within 53 h, they dragged it (along with an attached anemone *Cereus pedunculatus* and the ascidian *Microcosmus* sp.) 8 cm in one direction, then 21 cm in the opposite direction, just outside the frame. The ascidian, which had become discoloured, was then partially consumed by the end of the film, with pieces being visibly torn off.

3.6 Sea anemones

The August experiment contained three sea anemones *Cereus pedunculatus*: two attached to ascidians (a *Microcosmus* sp. and *P. mammillata*), one next to a large sponge. All three survived the anoxia but showed extreme elongation and rotations. One was carried outside the frame by hermit crabs (attached to *P. mammillata*, see above), the second was also flipped out of the frame (attached to *Microcosmus*), probably by hermit crabs.

The third individual, immediately adjoining the sponge, fully emerged from the substrate and began to crawl away 66 h and 15 min after the end of the artificial anoxia (opening of plexiglass chamber). At the end of the short-term evaluation (film: 71.5 h, 18 August) the specimen was still positioned inside the frame. During the subsequent longer-term evaluation the same anemone was still alive and visible at that position on the image of 22 August. Two days later the anemone disappeared from the images.

3.7 Longer-term recovery

The surface area of each experimental plot (inside the chamber) was 2500 cm². At the start of the August experiment, 1939 cm² (77.5 %) were covered by sessile organisms and 540 cm² (21.5 %) by vagile fauna (most of the latter represented by hermit crabs and gastropods; total values can exceed 100 % because animals on living substrates were counted separately). After the increase in vagile forms during the short-term observations (gastropods and hermit crabs, see above), this fauna decreased

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period. With few exceptions (early period in August), coquina always covered a larger surface than larger shells.

The coverage by lebensspuren (vagile fauna, endofauna burrow openings etc.) in the September experiment was high and varied considerably, ranging between 418 and 1360 cm² (data not shown). Insufficient visibility prevented evaluating lebensspuren on one date (6 days after removing the chamber) in September (in August, poor visibility prevented evaluation during the first 7 days after chamber removal).

4 Discussion

In the northern Adriatic, decreases in dissolved oxygen cause rapid mortalities of macroepibenthic communities (Stachowitsch, 1984), which are an important stabilizing compartment in this and other shallow marine ecosystems (Ott and Fedra, 1977). Here, the recolonization of the benthic compartment is very slow (Stachowitsch, 1991), additionally hampered by harmful fishing activities. The recovery of marine ecosystems with slow successions could take 40 years or even longer (Jones and Schmitz, 2009).

The present study extends prior investigations on the behavioural responses (Stachowitsch et al., 2007; Haselmair et al., 2010; Pretterebner et al., 2012; Riedel et al., 2008a,b, 2013) and mortality sequences (Riedel et al., 2012) to artificial anoxia using a specially designed underwater device. It helps fill in the gap between ecosystem collapse and community recovery by examining short-term scavenging and longer-term recovery processes.

4.1 Short-term scavenging after anoxia

After the artificial anoxia, the moribund and dead organisms attracted predators and scavengers. This process resembles that described after damage done by benthic fisheries in the north Irish Sea (Jenkins et al., 2004), where most of the dead material was removed in the first days. The images revealed a clear sequence of

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predators/scavengers. The quick arrival of fishes is attributed to their swimming speed (Planes et al., 1997, e.g. *Diplodus vulgaris*: 12.3 cm s^{-1}), which is clearly several hundred times faster than the next arriver, *Paguristes eremita*. These hermit crabs travel up to 21.6 m d^{-1} , with an average speed of 2.1 m h^{-1} (Stachowitsch, 1979); this is equivalent to 3.5 cm min^{-1} . Based on arrival time, *Hexaplex trunculus* may be the slowest of these three species. The speeds of *H. trunculus* were not measured, but considering the speeds of other, smaller gastropods (e.g. *Littorina littorea*, $2.88\text{--}4.47 \text{ cm min}^{-1}$ Erlandsson and Kostylev, 1995) and the similar size of large *P. eremita* and adult *H. trunculus*, the speeds of the hermit crabs and gastropods may be similar. In such cases, arrival times would also depend on a species' density, with more abundant species having a greater probability of having individuals closer to the experiment plots. In the ORM-community in the northern Adriatic Sea, *P. eremita* has a density of $2.4 \text{ individuals m}^{-2}$ (transect method: Pretterebner et al., 2012), which is slightly higher than in an earlier quadrat sampling ($1.9 \text{ individuals m}^{-2}$ Stachowitsch, 1977). *H. trunculus*, in turn, has a density of $0.2 \text{ individuals m}^{-2}$ in the northern Adriatic Sea (Wurzian, 1982). Note, however, that our site is close to an oceanographic buoy, whose anchor chains are heavily overgrown with mussels, and detached mussels are found directly under the buoy. Accordingly, the density of *H. trunculus*, which feeds on such mussels, is very high in this area. Without this bias, we would expect the gastropods to arrive in greater numbers at a much later date.

Fishes were conspicuously abundant in the first six hours after opening the chamber. This is the time when the most food items were available, including smaller soft-bodied organisms freshly emerged from the sediment and cryptic fauna from sponges and other multi-species clumps. The fishes were dominated by *Gobius niger*, which feeds on polychaetes, amphipods, mysids and decapods (Richards and Lindeman, 1987). *Pagellus erythrinus* mainly preys on benthic organisms such as polychaetes, brachyuran crabs and benthic crustaceans (Fanelli et al., 2011), *Serranus hepatus* on invertebrates, mainly decapods (Labropoulou and Eleftheriou, 1997), and *Diplodus vulgaris* on benthic echinoids such as *Echinocyamus pusillus* (Möller, 1776) and

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Psammechinus microtuberculatus (Blainville, 1825), but also decapods and bivalves (Pallaoro et al., 2006). *P. eremita* and *H. trunculus* apparently mainly fed on material that remained after the fishes had already been present for several hours. Based on their positions, this was mainly ascidians (*Phallusia mammilata*, *Microcosmus* sp.) and sponges. The time-lapse camera approach was unable to provide direct evidence that the fishes also fed on sponges or ascidians, i.e. the act of feeding was never captured in an image, although the fish were often positioned in an oblique angle with the mouth facing down. Ascidians rely on chemical (Lindquist et al., 1992) and physical defences (e.g. tunic toughness: Koplovitz and McClintock, 2011) against predation, although the efficiency and strategies vary greatly between species (Tarjuelo et al., 2002). These mechanisms may still be partly effective in freshly dead individuals, making them unattractive/unsuitable for fishes as the quickest post-anoxia arrivals. (Young, 1989), for example, observed ascidians being eaten by gastropods, which insert their proboscis into a siphon of the ascidians and consume them. Our evaluation showed some *H. trunculus* on the siphon of *Microcosmus* sp., but other individuals were also positioned on other parts of the ascidians.

To better determine which food sources the crabs and the gastropods prefer, we evaluated the substrates on which they positioned themselves, equating the chosen dead or moribund species with the preferred prey. In some cases, these substrates were clearly eaten and reduced in size, although we cannot exclude that smaller species associated with the sponges or ascidians may have been preyed upon. While both species feed on sponges and ascidians, *H. trunculus* was much more frequently positioned on *Microcosmus*. Thus, the interspecific differences were greater than intraspecific differences. The August images also showed *P. eremita* dragging off and consuming an ascidian (*Phallusia mammilata*). *H. trunculus*, in contrast, crawled up the ascidians and typically remained there for several hours: on average, the gastropods stayed within the frame more than twice as long as the crabs. This is in line with Sawyer et al. (2009), who documented 10.5 h, 5.2 h and 2.9 h for feeding and manipulating the mussel prey in three selected *H. trunculus* individuals in this community. Stachowitsch

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of *C. pedunculatus* is intriguing because it occurred in the re-oxygenated environment rather than during anoxia. One explanation is that the high density of feeding hermit crabs may have disturbed the anemone and caused it to release the attachment and move. An alternate explanation would be that the adjoining dead sponge caused unfavourable conditions. Accordingly, the disturbance experienced after the return of normoxic conditions was apparently more severe than the effects of anoxia: in none of the many other experiments that evaluated behaviour did anemones ever move away during severe hypoxia or anoxia (with or without H₂S conditions), although they showed a series of severe stress reactions including body contractions, rotation and extension (Riedel et al., 2008b, 2013).

4.2 Longer-term recovery

Even 2 years after anoxia, no macroepibenthic recovery was observed in either of our experimental plots. Benthic recolonization is scale-dependent and can involve larval settlement (extensively damaged areas) and immigration by vagile organisms, which may be more important for small-scale recovery (Pearson and Rosenberg, 1978; Günther, 1992; Whitlatch et al., 1998). Past mortalities in the northern Adriatic Sea ranged from restricted sites (several km²; Stachowitsch, 1992) to thousands of square kilometres (Ott, 1992). The worldwide second largest anthropogenic dead zone is in the Gulf of Mexico, covering a mean area of 17 000 km² (Turner et al., 2008). Accordingly, larval settlement would be expected to define recolonization – a long-term process. However, the extensive loss of the characteristic aggregations of sessile sponges and ascidians (multi-species clumps as larval producers) during mortalities in the northern Adriatic points to the difficulty in restoring community structure and function. Moreover, recovery from human disturbances can take longer than from natural disturbances (Jones and Schmitz, 2009). Additionally, also the high sedimentation rate and fishing activities may hinder successful epigrowth.

In our small-scale experiment, both recolonization strategies are conceivable. Although the experimental area was tiny compared with past hypoxia events, no recovery

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also determined by the frequency of disturbance. After benthic trawling the recovery time for slowly growing sponges could take 8 yr (Kaiser et al., 2006); sponge recolonization in Alaska, without further disturbances, could take decades (Rooper et al., 2011). It is therefore unsurprising that we did not observe any recovery of sessile organisms during our experiment.

Vagile fauna is an important part of this macrobenthic community. The rapid decrease of sessile organisms (moribund or dead sponges and ascidians) within the first 6 days (August) and 13 days (September) after anoxia is attributed to their removal or consumption by the mobile animals that entered the experimental plots (or that survived inside the plots (*H. trunculus* in September experiment)). The subsequent decline in food items was correlated with a corresponding drop in these organisms. The coverage of the plots by vagile fauna after 1 and 2 years consisted mainly of *P. eremita*, *H. trunculus*, *Psammechinus microtuberculatus* and *Ophiothrix quinquemaculata*. Kollmann and Stachowitsch (2001) consider that lebensspuren are helpful parameters to quantify community status and activity of mobile forms. Our lebensspuren observations in the September plot revealed a coverage of between 418 and 1360 cm². This is equivalent to 17 and 54 % of the whole plot and points to abundant vagile fauna in our study area. Such high densities may also keep larval recruits low: grazing on and manipulation of the shells that the multi-species clumps initially require to grow on (Zuschin et al., 1999) could also help explain the lack of recovery.

As opposed to recolonization and succession, where using small-scale experiments to predict larger-scale responses may not be possible (Zajac et al., 1998), we consider our results on scavenging and predation in the small plots to be valid for larger spatial scales. The distinct sequence of arrivals (fish, followed by hermit crabs and finally gastropods) – related to the relative speeds of the organisms – could be expected on the large scale as well. In wide-ranging anoxia in the northern Adriatic Sea and elsewhere, the process would be delayed: immediate immigration would be slower due to the greater distances involved (Stachowitsch et al., 2012), but the sequence would presumably be the same as observed in the present experiments. Scaling up

our small-scale experiments therefore points to alarming long-term effects and calls for intense management measures to reduce further pollution and physical destruction of shallow marine environments.

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Table 1. Chi² test for differences between categories of chosen substrates/prey by *Paguristes eremita* and *Hexaplex trunculus* in the two experiments (2009).

	Chi ²	<i>p</i>
<i>P. eremita</i> Aug vs. <i>P. eremita</i> Sep	156.75	≪ 0.001
<i>H. trunculus</i> Aug vs. <i>H. trunculus</i> Sep	24.779	≪ 0.001
<i>H. trunculus</i> Aug vs. <i>P. eremita</i> Aug	660.55	≪ 0.001
<i>H. trunculus</i> Sep vs. <i>P. eremita</i> Sep	1010.2	≪ 0.001
<i>P. eremita</i> Aug vs. <i>H. trunculus</i> Sep	1084.1	≪ 0.001
<i>P. eremita</i> Sep vs. <i>H. trunculus</i> Aug	687.74	≪ 0.001

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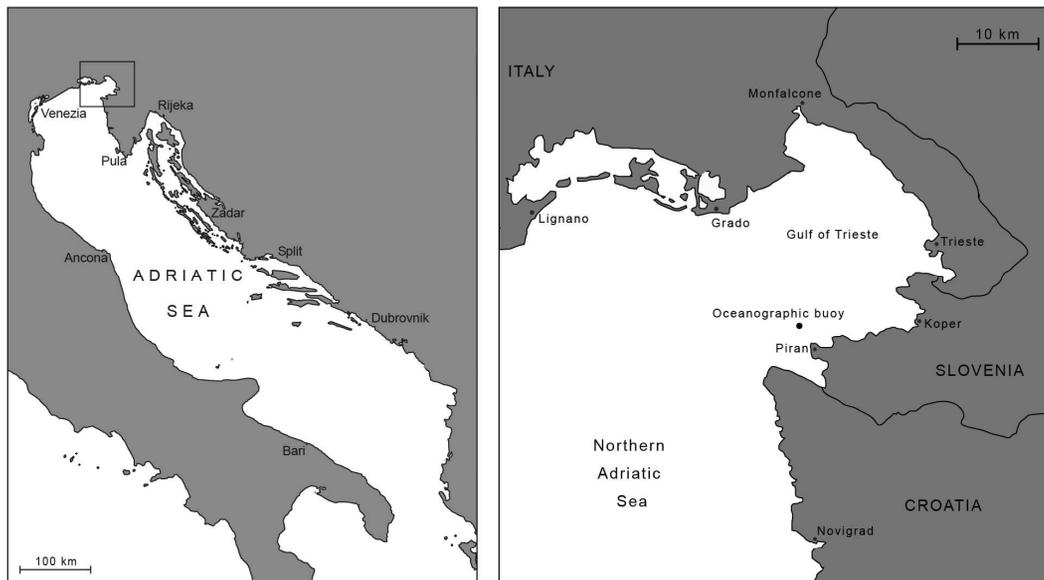


Fig. 1. Study site; (1) the northern Adriatic Sea (left), (2) Piran in the Gulf of Trieste (right) (map after Haselmair, 2008).

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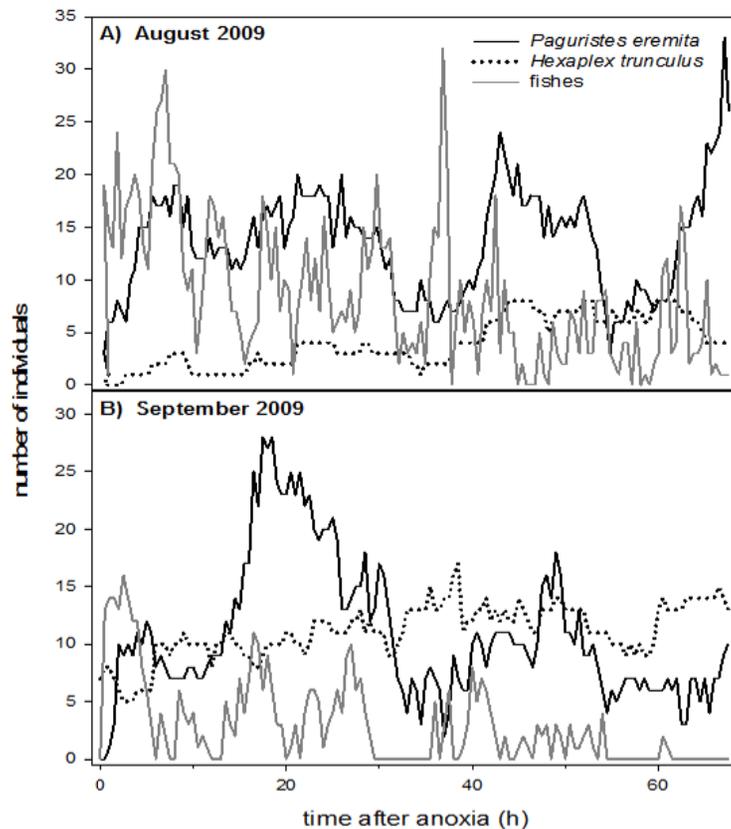


Fig. 2. (A) Arrival and presence of fishes, hermit crabs and gastropods after anoxia at the August 2009 plot and (B) September 2009 plot.

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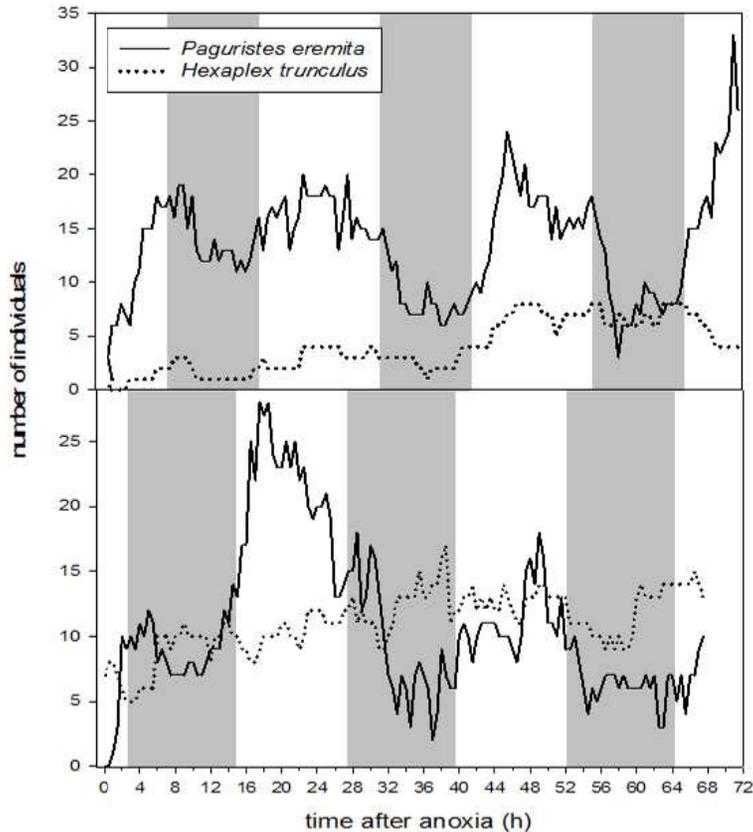


Fig. 3. Day/night activity of *Paguristes eremita* and *Hexaplex trunculus* after anoxia. White bars mark daylight hours, grey bars night. Above: August 2009 plot, below: September 2009 plot. Night is about 1 h 30 min longer in September.

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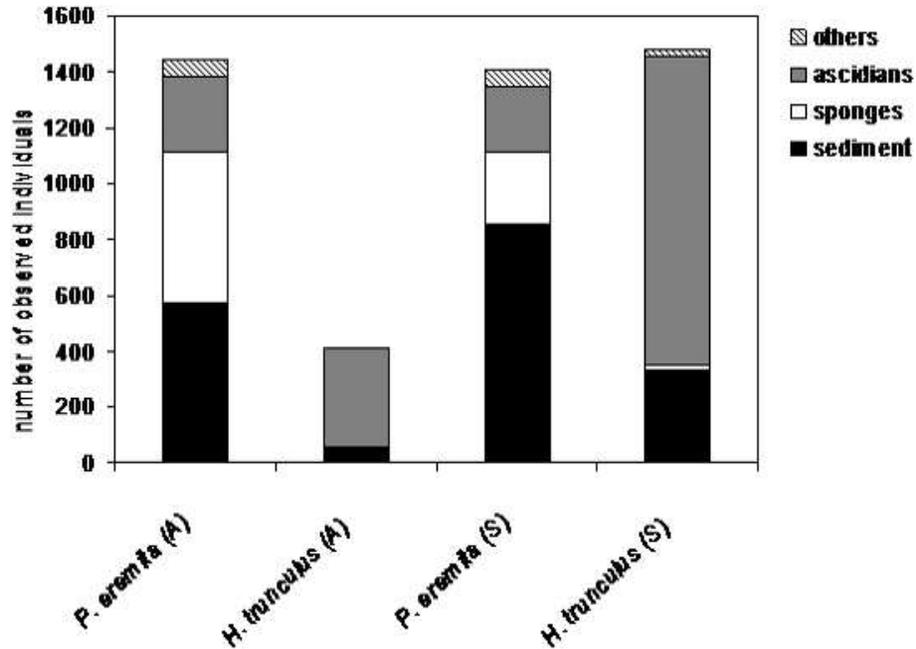


Fig. 4. Substrates/prey chosen after anoxia by *Paguristes eremita* and *Hexaplex trunculus* in the August 2009 (A) and September 2009 (S) experiments (others: frame or substrate other than sponges, ascidians or sediment).

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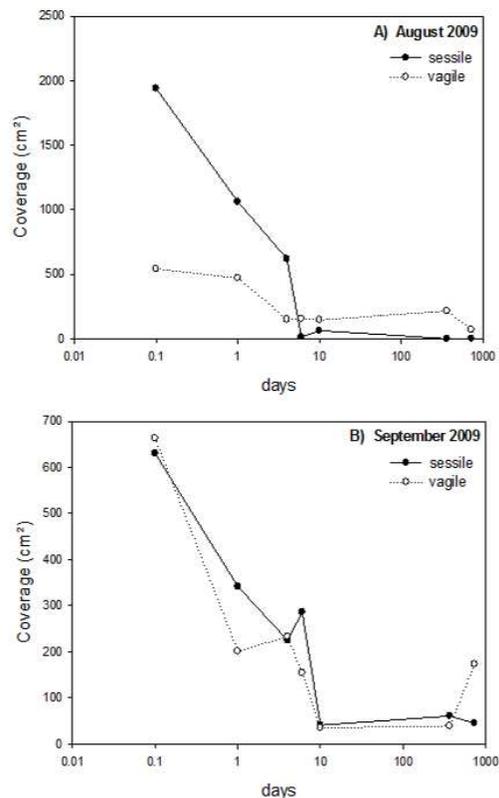


Fig. 5. Coverage of sessile (dead and living) and vagile fauna after anoxia in the August 2009 (above) and September 2009 (below) plot. Note different scales on y-axis. Start of experiment defined as 0.1; values measured inside closed chamber (original coverage).

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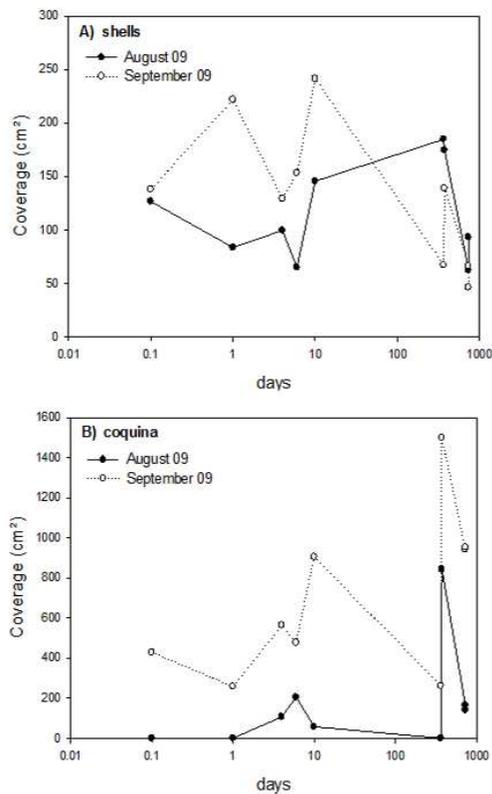


Fig. 6. Coverage of shells after anoxia of the August and September 2009 plot (above) and of coquina (below). Note different scales on y-axis. Start of experiment defined as 0.1 and initial values measured inside closed chamber (original coverage).