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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.

- ⁵ 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
- 20 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

²⁵ 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

on biodiversity (Danovaro and Pusceddu, 2007; Coll et al., 2010). One major disturbance, coastal hypoxia and anoxia, has been exacerbated by eutrophication (Nixon, 1995; Zhang et al., 2010). No other environmental variable than dissolved oxygen has changed in shallow coastal seas and estuaries so drastically in such a short time (Diaz

and Rosenberg, 2008; Diaz, 2001). Hypoxia adversely affects the community structure and trophodynamics of marine ecosystems (Gray et al., 2002), for example by eliminating sensitive species and promoting more tolerant species (Dauer, 1993; Wu, 2002). The northern Adriatic is one of currently more than 400 eutrophication-associated

dead zones worldwide, with a global area of more than $245\,000$ km² (Diaz and Rosen-

- berg, 2008). As a shallow, semi-enclosed waterbody (mean depth 30 m) with water column stratification (Justić, 1991; Malej et al., 1995), soft bottoms, high riverine input mainly from the Po River, high productivity and long water residence time, it combines many of the features known to promote late summer hypoxia and anoxia (Stachowitsch and Avcin, 1988; Stachowitsch, 1991; Ott, 1992). These features, combined with
- anthropogenic eutrophication and massive marine snow events, qualify the northern Adriatic Sea as a sensitive marine ecosystem (Stachowitsch, 1986). It is at the same time one of the most heavily exploited and degraded seas worldwide (Lotze et al., 2010) and one of the most productive areas at several levels, from phytoplankton to fish, of the Mediterranean (Fonda Umani et al., 2005). Here, long-term decreases in
- the bottom-water oxygen content have been observed from the middle of the 20th century (Justić, 1991) until the early 1990s, which were connected with changes in and extensive mortalities of the epibenthic communities that characterize the soft bottoms (Stachowitsch, 1984; Justić et al., 1987; Ott, 1992).
- Fedra et al. (1976) named one such wide-ranging community, the community studied here, the Ophiothrix-Reniera-Microcosmus (ORM) community based on the dominant brittle stars Ophiothrix quinquemaculata (Delle Chiaje, 1828), sponges Reniera spp., and ascidians Microcosmus spp. This suspension-feeding community is aggregated into so-called multi-species clumps or bioherms, which show a wide and patchy distribution in the northern Adriatic Sea (Zuschin and Stachowitsch, 2009; McKinney, 2007).

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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 con-
- firmed and analysed in great detail experimentally using an underwater chamber on a small scale (0.25 m²) 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 mortal-
- ities 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.
- ²⁰ 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 ben-thopelagic Two-banded bream *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817) and the Common pandora *Pagellus erythrinus* (Linnaeus, 1758).

2.1 Study site

¹⁰ 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, ¹⁵ 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

 $_{\mbox{\tiny 25}}$ (PA3000UD, Unisense, Denmark) and four sensors for measuring oxygen, temperature

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 representa-

tive 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.

10 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

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 over-5 estimates 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.

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10 2.4 Longer-term recovery

These experiments were conducted on the same two 0.25 m² plots used for the shortterm 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 20 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. 25
 - 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

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 Chi² 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 20 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 25

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 and 31 individuals (after 62.5 h).
- ²⁵ 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

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 be-

- tween 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
- ¹⁰ (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

- 20 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 be-

⁵ come 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.

- ¹⁰ 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.

20 3.7 Longer-term recovery

The surface area of each experimental plot (inside the chamber) was 2500 cm^2 . At the start of the August experiment, 1939 cm^2 (77.5%) were covered by sessile organisms and 540 cm^2 (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-

strates were counted separately). After the increase in vagile forms during the shortterm observations (gastropods and hermit crabs, see above), this fauna decreased

markedly by day 6 of the long-term experiment. The value dropped from 540 cm² to 155 cm² coverage (6%) (Fig. 5a). The sessile fauna dropped from originally 1939 cm² to 12 cm² (0.5%). In September, the initial coverage of sessile fauna accounted for 631 cm² (25%) and of vagile fauna 663 cm² (26.5%). As in August, both fauna groups

- ⁵ decreased drastically and the trends in coverage by vagile fauna paralleled those of the sessile fauna. After 6 days, the sessile fauna fell to 286 cm² (11.5%), the vagile fauna to 154 cm² (6%) (Fig. 5b). In the "10-day" category (see Sect. 2), nearly the whole fauna was consumed (sessile) or had crawled away (vagile). Both 1 and 2 years after the start of the experiment, no macroscopic sessile epifauna was observed on either plat. The curve transformation of the set o
- plot. The exception was one sea anemone, *Cereus pedunculatus*, in the September experiment; it survived anoxia and was still present in both following years.
 Shells (> 1 cm) and smaller shelly material ("coquina") were visible in both plots (Fig. 6a, b). Overall, in both experiments shell coverage (Fig. 6a) fluctuated but re-
- mained relatively stable with similar shell values in the beginning and the end of the two experiments ("2 years"). More precisely, in August, shell cover increased from an initial 126 cm² to 185 cm² after 1 yr, with a drop after 2 yr to 62 cm². In September, coverage decreased 1 and 2 yr after the anoxia, with a minimum of 46 cm² after "2 years". In between, there was an increase to 139 cm² (at the 1-year-plus-10-day sampling).
- Coquina coverage (Fig. 6b), in contrast, fluctuated more widely and clearly increased over the course of the experiments. Here, the two experiments were less similar, with values of the September experiment always exceeding those of August.
- In the August experiment, no coquina was initially observed, but after 3–4 days the coverage increased. After "10-days" it fell again to 57 cm², followed by a peak of 842 cm² after 1-yr-plus-10 days. Note, however, that 10 days earlier, the value was
- ²⁵ zero, showing the potential for major fluctuations even over short time periods. In the September experiment, values initially decreased, but then steadily increased, dropping after 1 year but peaking again at 1499 cm² after an additional 10 days (i.e. 1year-plus-10-day sampling). Thus, values changed considerably within even a 10-day

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 remewed in the first days. The impered results are requested and the description 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 md^{-1} , with an average speed of 2.1 mh^{-1} (Stachowitsch, 1979); this is equiva-

- Ient to 3.5 cmmin⁻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*, 2.88–4.47 cmmin⁻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,
- ¹⁰ 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 individuals m⁻² (transect method: Pretterebner et al., 2012), which is slightly higher than in an earlier quadrat sampling (1.9 individuals m⁻² Stachowitsch, 1977). *H. trunculus*, in
- ¹⁵ turn, has a density of 0.2 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 softbodied 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

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 are some by trunculus on the single of Marcocomus and but other individuals was also as the single of the single of the second but other individuals are set.
- ¹⁵ 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 con-
- ²⁵ suming an ascidian (*Phallusia mammillata*). *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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(1979) observed the activity behaviour of *P. eremita* in the Gulf of Trieste and recognized two types of movement interruptions: (1) short stops related to feeding and investigating structures on the sediment and (2) longer pauses during the night hours reflecting a resting period. This was evident in our study by a semidiurnal and diur-

- ⁵ nal periodicity of presences. Moreover, an explanation for why only few individuals remained in the plot near their prey items at night might be that, in their dormant night phase, crabs do not aggregate or remain near larger prey items because it would increase the risk that they themselves would be consumed, along with the prey, by other, larger (fish) predators/scavengers. The same may hold true for *H. trunculus* based on
- the 9- and 12-h periodicity indicated by the time series analysis. Tolerance to hypoxia not only improves survival but may – depending on the behaviour and tolerance of both predator and prey – enable also more successful predation during and after low-oxygen events (Pihl et al., 1992). Molluscs, for example, are generally considered to be more tolerant to hypoxia than many other invertebrate
- ¹⁵ groups (Vaquer-Sunyer and Duarte, 2008). *H. trunculus* is among the more tolerant species in this soft-bottom community (Riedel et al., 2012) and also in the present study, 7 individuals survived the oxygen depletion during the September experiment. Although none of the *P. eremita* survived the experimental anoxia, hermit crabs were identified as more tolerant crustaceans (Riedel et al., 2012), improving their opportu-
- nities for predation during and after hypoxia. Depending on the severity of hypoxia, both species may be able to take advantage of more vulnerable prey. Such altered predator-prey relationships can affect community structure.

The sea anemone *Cereus pedunculatus* (August plot) crept away from its original position 66 h and 15 min after the chamber was opened. Anemones, although normally firmly attached to a substrate, are known to be able to detach and move, providing a mechanism to leave unfavourable conditions (Rittschof et al., 1999). The hermit crab symbiont *Calliactis parasitica* (Couch, 1842) allows *Dardanus arrosor* (Herbst, 1796) to detach it mechanically by using specific behaviours, whereby the anemone then reattaches itself to the new shell (Ross, 1979). In the present experiment, the movement

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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 un-

favourable conditions. Accordingly, the disturbance experienced after the return of nor-moxic 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,

- ¹⁵ 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,
- ²⁰ 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 (larval calculation 2020). Additionally, also the birth acdimentation and a fishing.
- ²⁵ (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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was recorded despite immediately adjoining multi-species clumps and vagile organisms. Importantly, settlement and growth of sessile organisms depend on the presence of adequate substrates. In the northern Adriatic, these are typically gastropod and bivalve shells or echinoderm tests (Zuschin and Stachowitsch, 2009, and refer-

- ences herein). Although we recorded shells in our plots, they were apparently not large enough, sufficiently exposed, or available at larval settlement times. This is supported in the percent coverage by shells: it fluctuated and ultimately declined after two years. Small-scale factors that affect availability include manipulation by vagile species or use as camouflage by the sea urchins (Riedel et al., 2008b); large-scale factors include
- sedimentation and resuspension, which bury small or flat shells. Fishery gear such as dredges and bottom trawls resuspend enormous amounts of sediment, creating major turbidity and sedimentation events (M. Stachowitsch, personal observation). Such gear also overturned shells, crushed multi-species clumps and sheared off structures projecting from the bottom (e.g. pen shells), impacting newly settled invertebrates growing
- on them (Stachowitsch and Fuchs, 1995). Finally, the passage of large ships near the study site can also resuspend sediment. All these factors help explain the great variation in the visible coverage by shells, impacting larval-based recolonization. Such unstable conditions in the top sediment layer are also indicated by the increasing amount of coquina.
- Finally, one short-cut to the establishment of multi-species clumps in this community
 the deposition of heavily encrusted gastropod shells by hermit crabs (Stachowitsch, 1980) did not take place within our two plots in the two years examined.

Anoxia-related disturbance and recovery in the northern Adriatic has been described as "rapid death – slow recovery" (Stachowitsch, 1991): most organisms die shortly after anoxia is attained, but recovery takes years. The ORM-community showed little recovery 10 years after the collapse in 1983; although certain vagile fauna such as hermit crabs increased, larger multi-species clumps did not develop. This was attributed to

repeated anoxia and other disturbances such as dredging and trawling damage (Stachowitsch and Fuchs, 1995; Kollmann and Stachowitsch, 2001). Recovery is therefore 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 sur-

- vived 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 guinguemaculata. Kollmann and Stachowitsch (2001) consider that lebensspuren are helpful parameters to
- quantify community status and activity of mobile forms. Our lebensspuren observa-15 tions 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. 20

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 ex-25 pected 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

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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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References

5

- Blasnig, M.: LinkShort-term post-mortality predation and scavenging and longer-term recovery 10 after anoxia in the Northern Adriatic Sea, Master's thesis, University of Vienna, Vienna, 2012. 4376
 - Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil,
- B. S., Gasol, J. M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C. M., Lotze, H. K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., and Voultsiadou, E.: The biodiversity of the Mediterranean Sea: estimates, patterns, and threats, PLoS ONE, 5, e11842, doi:10.1371/journal.pone.0011842, 2010. 4369 20
- Danovaro, R. and Pusceddu, A.: Ecomanagement of biodiversity and ecosystem functioning in the Mediterranean Sea: concerns and strategies, Chem. Ecol., 23, 347–360, 2007. 4369 Dauer, D. M.: Biological criteria, environmental health and estuarine macrobenthic community structure, Mar. Pollut. Bull., 26, 249-257, 1993. 4369
- Dayton, P. K., Thrush, S. F., Agardy, M. T., and Hofman, R. J.: Viewpoint environmental effects 25 of marine fishing, Aq. Conserv. Mar. Freshw. Ecosys., 5, 205-232, 1995. 4368, 4372 Dernie, K. M., Kaiser, M. J., and Warwick, R. M.: Recovery rates of benthic communities following physical disturbance, J. Animal Ecol., 72, 1043-1056, 2003. 4371

Diaz, R. J.: Overview of hypoxia around the world, J. Environ. Qual., 30, 275-281, 2001. 4369

Paper

Discussion Paper

Discussion Paper

Discussion Paper

- Diaz, R. J. and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science, 321, 926–929, 2008. 4369
- Erlandsson, J. and Kostylev, V.: Trail following, speed and fractal dimension of movement in a marine prosobranch, *Littorina littorea*, during a mating and a non-mating season, Mar. Biol., 122, 87–94, 1995. 4382
- Fanelli, E., Badalamenti, F., D'Anna, G., Pipitone, C., Riginella, E., and Azzurro, E.: Food partitioning and diet temporal variation in two coexisting sparids, *Pagellus erythrinus* and *Pagellus acarne*, J. Fish Biol., 78, 869–900, 2011. 4382
- Fedra, K., Ölscher, E. M., Scherübel, C., Stachowitsch, M., and Wurzian, R. S.: On the ecology
 of a north Adriatic benthic community: distribution, standing crop and composition of the macrobenthos, Mar. Biol., 38, 129–145, 1976. 4369, 4370
 - Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S.: Regime shifts, resilience, and biodiversity in ecosystem management, Annu. Rev. Ecol. Evol. Syst., 35, 557–581, 2004. 4372
- Fonda Umani, S., Milani, L., Borme, D., de Olazabal, A., Parlato, S., Precali, R., Kraus, R., Lučić, D., Njire, J., Totti, C., Romagnoli, T, Pompei, M., and Cangini, M.: Inter-annual variations of planktonic food webs in the northern Adriatic Sea, Sci. Total Environ., 365, 218–231, 2005. 4369
 - Gray, J., Wu, R., and Or, Y.: Effects of hypoxia and organic enrichment on the coastal marine environment, Mar. Ecol. Prog. Ser., 238, 249–279, 2002. 4369

20

20

- Günther, C.: Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales?, Netherlands J. Sea Res., 30, 45–56, 1992. 4385
 - Hammer, O., Harper, D. A. T., and Ryan, P. D.: PAST: Paleontological statistics software package for education and data analysis, Palaeontol. Electron., 4, 9, 2001. 4376
- Hampel, H., Cattrijsse, A., and Mees, J.: Changes in marsh nekton communities along the salinity gradient of the Schelde river, Belgium and the Netherlands, Hydrobiologia, 515, 137– 146, 2004. 4370
 - Haselmair, A., Stachowitsch, M., Zuschin, M., and Riedel, B.: Behaviour and mortality of benthic crustaceans in response to experimentally induced hypoxia and anoxia in situ, Mar. Ecol. Prog. Ser., 414, 195–208, 2010. 4370, 4381
- Jenkins, S. R., Mullen, C., and Brand, A. R.: Predator and scavenger aggregation to discarded by-catch from dredge fisheries: importance of damage level, J. Sea Res., 51, 69–76, 2004. 4381

4389

- Jennings, S. and Kaiser, M. J.: The effects of fishing on marine ecosystems, Adv. Mar. Biol., 34, 201–352, 1998. 4372
- Jones, H. P. and Schmitz, O. J.: Rapid recovery of damaged ecosystems, PLoS ONE, 4, e5653, doi:10.1371/journal.pone.0005653, 2009. 4381, 4385
- Justić, D.: Hypoxic conditions in the Northern Adriatic Sea: historical development and ecological significance, Geol. Soc. Lond. Spec. Publ., 58, 95–105, 1991. 4369
 - Justić, D., Legović, T., and Rottini-Sandrini, L.: Trends in oxygen content 1911–1984 and occurence of benthic mortality in the Northern Adriatic Sea, Est. Coast. Shelf. Sci., 25, 435– 445, 1987. 4369
- Kaiser, M. J. and Spencer, B. E.: The effects of beam-trawl disturbance on infaunal communities in different habitats, J. Animal Ecol., 65, 348–358, 1996. 4372
 - Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J., and Karakassis, I.: Global analysis of response and recovery of benthic biota to fishing, Mar. Ecol. Prog. Ser., 311, 1–14, 2006. 4387
- Kollmann, H. and Stachowitsch, M.: Long-term changes in the benthos of the Northern Adriatic Sea: a phototransect approach, PSZNI: Mar. Ecol., 22, 135–154, 2001. 4371, 4372, 4386, 4387
 - Koplovitz, G. and McClintock, J. B.: An evaluation of chemical and physical defenses against fish predation in a suite of seagrass-associated ascidians, J. Exp. Mar. Biol. Ecol., 407, 48– 53, 2011. 4383
- Labropoulou, M. and Eleftheriou, A.: The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection, J. Fish Biol., 50, 324–340, 1997. 4382
- Lotze, H., Coll, M., and Dunne, J.: Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean, Ecosystems, 14, 198–222,
 - doi:10.1007/s10021-010-9404-8, 2010. 4369
 Malej, A., Mozetic, P., Malačič, V., Terzic, S., and Ahel, M.: Phytoplankton responses to freshwater inputs in a small semi-enclosed gulf (Gulf of Trieste, Adriatic Sea), Mar. Ecol. Prog. Ser., 120, 111–121, 1995. 4369
- McKinney, E.: The Northern Adriatic Ecosystem: Deep Time in a Shallow Sea, Columbia University Press, New York, 2007. 4369
 - Nixon, S. W.: Coastal marine eutrophication: a definition, social causes, and future concerns, Ophelia, 41, 199–219, 1995. 4369

Paper

Discussion Paper

Discussion Paper

Discussion Paper

- Norkko, J., Norkko, A., Thrush, S. F., Valanko, S., and Suurkuukka, H.: Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in softsediment communities, Mar. Ecol. Prog. Ser., 413, 253–266, 2010. 4371
- Officer, C. B., Smayda, T. J., and Mann, R.: Benthic filter feeding: a natural eutrophication control, Mar. Ecol. Prog. Ser., 9, 203–210, 1982. 4370
- Ott, J. A.: Adriatic benthos: problems and perspectives, in: Marine Eutrophication and Population Dynamics, edited by: Colombo, D., Ferrari, I., Ceccherelli, V., and Rossi, R., 25th European Marine Biology Symposium, Olsen and Olsen, Fredensborg, Denmark, 367–378, 1992. 4369, 4385
- Ott, J. A. and Fedra, K.: Stabilizing properties of a high-biomass benthic community in a fluctuating ecosystem, Helgoland Wiss. Meer., 30, 485–495, 1977. 4370, 4381

 Pallaoro, A., Santić, M., and Jardas, I.: Feeding habits of common two-banded sea bream, *Diplodus vulgaris* (Sparidae), in the eastern Adriatic Sea, Cybium, 30, 19–25, 2006. 4383
 Pearson, T. H. and Rosenberg, R.: Macrobenthic succession in relation to organic enrichment

- and pollution of the marine environment, Oceanogr. Mar. Biol. Annu. Rev., 16, 229–231, 1978. 4370, 4371, 4372, 4385
 - Pihl, L., Baden, S., Diaz, R., and Schaffner, L.: Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea, Mar. Biol., 112, 349–361, 1992. 4384
- Planes, S., Hertel, O., and Jouvenel, J.: Analysis of condition and swimming performance in juveniles of white sea bream, *Diplodus vulgaris*, J. Mar. Biol. Assoc. UK, 77, 913–916, 1997. 4382
 - Pranovi, F., Raicevich, S., Franceschini, G., Farrace, M. G., and Giovanardi, O.: Rapido trawling in the Northern Adriatic Sea: effects on benthic communities in an experimental area, J. Mar. Sci., 57, 517–524, 2000. 4371
- Pretterebner, K., Riedel, B., Zuschin, M., and Stachowitsch, M.: Hermit crabs and their symbionts: reactions to artificially induced anoxia on a sublittoral sediment bottom, J. Exp. Mar. Biol. Ecol., 411, 23–33, 2012. 4370, 4381, 4382
 - Richards, W. J. and Lindeman, K. C.: Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis, Bull. Mar. Sci., 41, 392– 410, 1987. 4382
- Riedel, B., Stachowitsch, M., and Zuschin, M.: Sea anemones and brittle stars: unexpected predatory interactions during induced in situ oxygen crises, Mar. Biol., 153, 1075–1085, 2008a. 4370, 4381

- Riedel, B., Zuschin, M., Haselmair, A., and Stachowitsch, M.: Oxygen depletion under glass: behavioural responses of benthic macrofauna to induced anoxia in the Northern Adriatic, J. Exp. Mar. Biol. Ecol., 367, 17–27, 2008b. 4370, 4381, 4385, 4386
- Riedel, B., Zuschin, M., and Stachowitsch, M.: Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario, Mar. Ecol. Prog. Ser., 458, 39–52, 2012. 4370, 4381, 4384
 - Riedel, B., Pados, T., Pretterebner, K., Schiemer, L., Steckbauer, A., Haselmair, A., Zuschin, M., and Stachowitsch, M.: Effect of hypoxia and anoxia on invertebrate behaviour: ecological perspectives from the species to community level, Biogeosciences, in preparation, 2013.
- Riemann, B. and Hoffmann, E.: Ecological consequences of dredging and bottom trawling in the limfjord, Denmark, Mar. Ecol. Prog. Ser., 69, 171–178, 1991. 4372
 - Rittschof, D., McFarland, S., Stocker, E., and Randall Brooks, W.: Movement of anemones symbiotic with hermit crabs: effects of light, gravity, flow and conspecifics, Mar. Freshw. Behav. Physiol., 32, 193–205, 1999. 4384
- Rooper, C. N., Wilkins, M. E., Rose, C. S., and Coon, C.: Modelling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska, Cont. Shelf Res., 31, 1827–1834, 2011. 4387
 - Rosenberg, R.: Recovery of the littoral fauna in Saltkallefjorden subsequent to discontinued operations of a sulphite pulp mill, Thalass. Jugosl., 7, 341–351, 1971. 4371
- Ross, D. M.: Stealing of the symbiotic anemone, *Calliactis parasitica*, in intraspecific and interspecific encounters of three species of Mediterranean pagurids, Can. J. Zool., 57, 1181– 1189, 1979. 4384
 - Sawyer, J. A., Zuschin, M., Riedel, B., and Stachowitsch, M.: Predator-prey interactions from in situ time-lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic), J. Exp. Mar. Biol. Ecol., 371, 10–19, 2009. 4383
- Stachowitsch, M.: The hermit crab microbiocoenosis: the role of mobile secondary hard bottom elements in a North Adriatic benthic community, in: Biology of Benthic Organisms, edited by: Keegan, B., O'Ceidigh, P., and Boaden, P., Proc. 11th Europ. Mar. Biol. Symp, Pergamon Press, London, 549–558, 1977. 4382

25

Stachowitsch, M.: Movement, activity pattern, and role of hermit crab population in sublittoral epifaunal community, J. Exp. Mar. Biol. Ecol., 39, 135–150, 1979. 4382, 4383

- Stachowitsch, M.: The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Paguristes cuanensis*, PSZNI Mar. Ecol., 1, 73–101, 1980. 4386
- Stachowitsch, M.: Mass mortality in the Gulf of Trieste: the course of community destruction, PSZNI Mar. Ecol., 5, 243–264, 1984. 4369, 4370, 4381
- Stachowitsch, M.: The Gulf of Trieste: a sensitive ecosystem, Nova Thalassia, 8, 221–235, 1986. 4369
- Stachowitsch, M.: Anoxia in the northern Adriatic Sea: rapid death, slow recovery, in: Modern and Ancient Continental Shelf Anoxia, edited by: Tyson, R. V. and Pearson, T., vol. 58, Ge-
- ological Society Special Publication Edn., The Geological Society, London, 119–129, 1991.
 4369, 4371, 4381, 4386
 Steebowiteeb Mit Boothia communities: autrenhisation's "memory mode", merine constal automatical sectors.
 - Stachowitsch, M.: Benthic communities: eutrophication's "memory mode", marine coastal eutrophication, Sci. Total Environ., 126, 1017–1028, 1992. 4372, 4385
- Stachowitsch, M. and Avcin, A.: Eutrophication-induced modifications of benthic communities,
 in: Eutrophication of the Mediterranean Sea: Receiving Capacity and Monitoring of Long-Term Effects, vol. 5, UNESCO Technical Reports in Marine Science, 67–80, 1988. 4369
 - Stachowitsch, M. and Fuchs, A.: Long-term changes in the benthos of the Northern Adriatic Sea, Annales, 7, 7–16, 1995. 4371, 4386
- Stachowitsch, M., Riedel, B., Zuschin, M., and Machan, R.: Oxygen depletion and benthic mortalities: the first in situ experimental approach to documenting an elusive phenomenon, Limnol. Oceanogr. Methods, 5, 344–352, 2007. 4381
 - Stachowitsch, M., Riedel, B., and Zuschin, M.: Anoxia: evidence for eukaryote survival and paleontological strategies, vol. 21, Cellular origin, life in extreme habitats and astrobiology, in: The Return of Shallow Shelf Seas as Extreme Environments: Anoxia and Macrofauna Reaction in the Northern Adriatic Sea, Springer, Dordrecht, 2012. 4387
- Reaction in the Northern Adriatic Sea, Springer, Dordrecht, 2012. 4387 Tarjuelo, I., López-Legentil, S., Codina, M., and Turon, X.: Defence mechanisms of adults and larvae of colonial ascidians: patterns of palatability and toxicity, Mar. Ecol. Prog. Ser., 235, 103–115, 2002. 4383
 - Thrush, S. F. and Dayton, P. K.: Disturbance to marine benthic habitats by trawling and dredging: implication for marine biodiversity, Annu. Rev. Ecol. Syst., 33, 449–473, 2002. 4372
- Tuck, I. D., Hall, S. J., Robertson, M. R., Armstrong, E., and Basford, D. J.: Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch, Mar. Ecol. Prog. Ser., 162, 227–242, 1998. 4371

4393

- Turner, R. E., Rabalais, N. N., and Justić, D.: Gulf of Mexico hypoxia: alternate states and a legacy, Environ. Sci. Technol., 42, 2323–2327, 2008. 4385
- Vaquer-Sunyer, R. and Duarte, C.: Thresholds of hypoxia for marine biodiversity, P. Natl. Acad. Sci., 105, 15452–15457, 2008. 4384
- Whitlatch, R. B., Lohrer, A. M., Thrush, S. F., Pridmore, R. D., Hewitt, J. E., Cummings, V. J., and Zajac, R. N.: Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences, Hydrobiologia, 375–376, 217–226, 1998. 4371, 4385
- Wu, R. S.: Hypoxia: from molecular responses to ecosystem responses, Mar. Pollut. Bull., 45, 35–45, 2002. 4369
- Wurzian, R. S.: Die Funktion der Räuber der Makro-Epifauna in einer sublitoralen Benthos Gemeinschaft im Golf von Triest, Ph.D. thesis, University of Vienna, Vienna, 1982. 4382
 Young, C. M.: Distribution and dynamics of an intertidal ascidian pseudopopulation, Bull. Mar. Sci., 45, 288–303, 1989. 4383
- Zajac, R., Whitlatch, R., and Thrush, S.: Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors, Hydrobiologia, 375–376, 227–240, 1998. 4387
 - Zhang, J., Gilbert, D., Gooday, A. J., Levin, L., Naqvi, S. W. A., Middelburg, J. J., Scranton, M., Ekau, W., Peña, A., Dewitte, B., Oguz, T., Monteiro, P. M. S., Urban, E., Rabalais, N. N., Ittekkot, V., Kemp, W. M., Ulloa, O., Elmgren, R., Escobar-Briones, E., and Van der Plas, A. K.:
- Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development, Biogeosciences, 7, 1443–1467, doi:10.5194/bg-7-1443-2010, 2010. 4369 Zuschin, M. and Pervesler, P.: Secondary hardground-communities in the Northern Gulf of Trieste, Adriatic Sea, Senckenbergiana Mar., 28, 53–63, 1996. 4370
 - Zuschin, M. and Stachowitsch, M.: Epifauna-dominated benthic shelf assemblages: lessons from the modern Adriatic Sea, Palaios, 24, 211–221, 2009. 4369, 4386
- Zuschin, M., Stachowitsch, M., Pervesler, P., and Kollmann, H.: Structural features and taphonomic pathways of a high-biomass epifauna in the Northern Gulf of Trieste, Adriatic Sea, Lethaia, 32, 299–317, 1999. 4387

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	Chi ²	p
P. eremita Aug vs. P. eremita Sep	156.75	≪ 0.001
H. trunculus Aug vs. H. trunculus 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
P. eremita Aug vs. H. trunculus Sep	1084.1	≪ 0.001
P. eremita Sep vs. H. trunculus Aug	687.74	≪ 0.001

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



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



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





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).

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