

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 Rosenberg, 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 confirmed 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 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

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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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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 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 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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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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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 references 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

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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

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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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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

4395

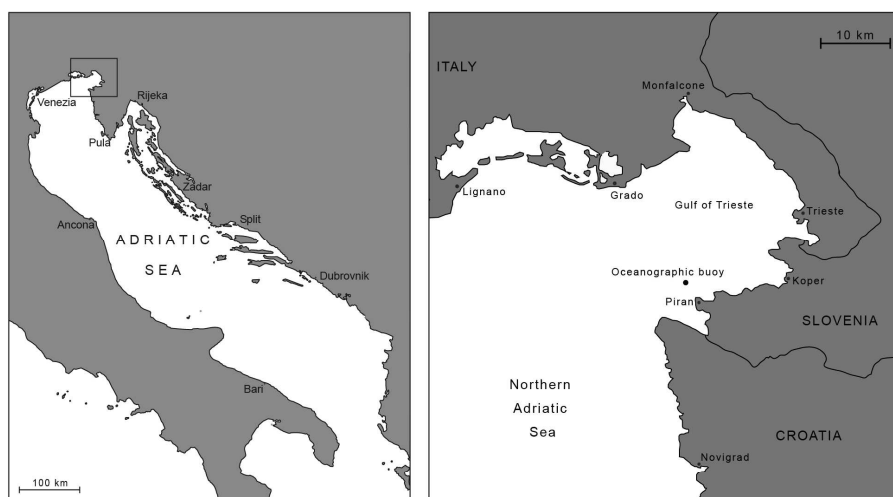


Fig. 1. Study site; (1) the northern Adriatic Sea (left), (2) Piran in the Gulf of Trieste (right) (map after Haselmair, 2008).

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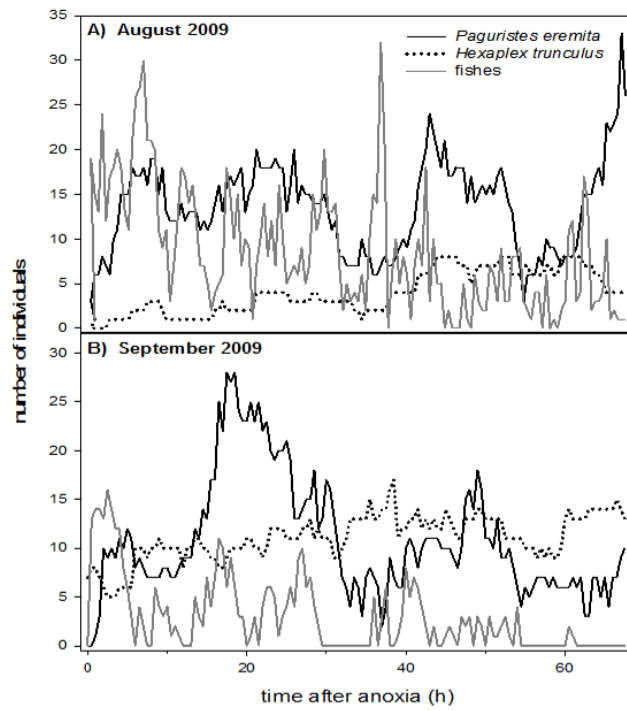


Fig. 2. (A) Arrival and presence of fishes, hermit crabs and gastropods after anoxia at the August 2009 plot and **(B)** September 2009 plot.

4397

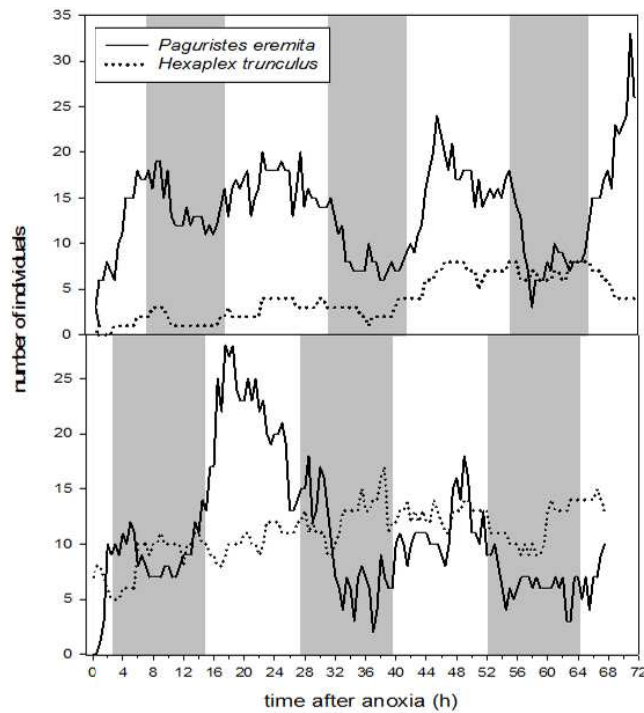


Fig. 3. Day/night activity of *Paguristes eremita* and *Hexaplex trunculus* after anoxia. White bars mark daylight hours, grey bars night. Above: August 2009 plot, below: September 2009 plot. Night is about 1 h 30 min longer in September.

4398

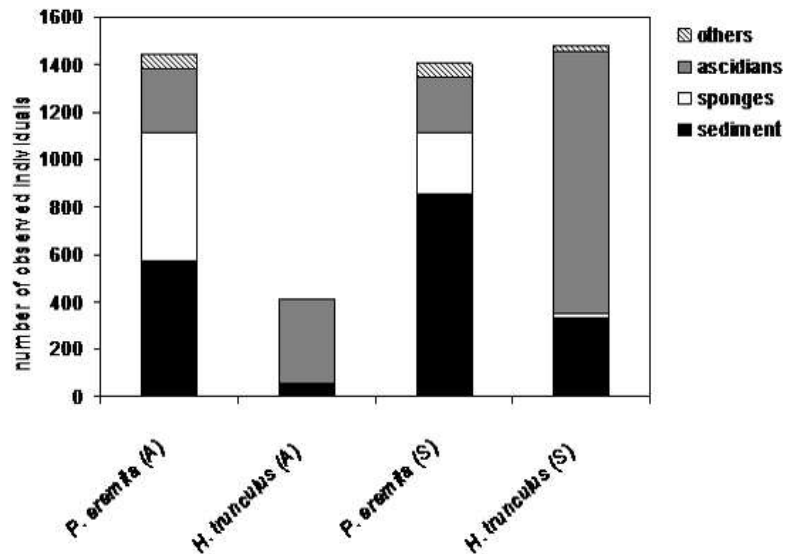


Fig. 4. Substrates/prey chosen after anoxia by *Paguristes eremita* and *Hexaplex trunculus* in the August 2009 (A) and September 2009 (S) experiments (others: frame or substrate other than sponges, ascidians or sediment).

4399

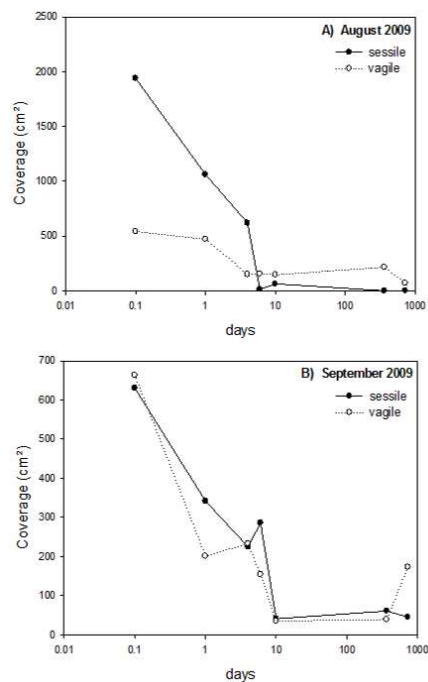


Fig. 5. Coverage of sessile (dead and living) and vagile fauna after anoxia in the August 2009 (above) and September 2009 (below) plot. Note different scales on y-axis. Start of experiment defined as 0.1; values measured inside closed chamber (original coverage).

4400

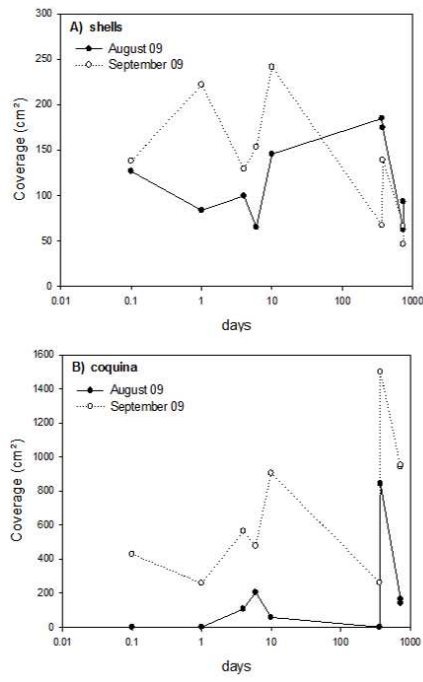


Fig. 6. Coverage of shells after anoxia of the August and September 2009 plot (above) and of coquina (below). Note different scales on y-axis. Start of experiment defined as 0.1 and initial values measured inside closed chamber (original coverage).